UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD

ECOLOGÍA

EFECTO DE LA ESTRUCTURA DE PAISAJES ANTRÓPICOS SOBRE LOS PRIMATES

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

CARMEN GALÁN ACEDO

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MORELIA, MICHOACÁN. **ENERO, 2019.**

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Ciencias Biológicas

COORDINACIÓN

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M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Por medio de la presente me permito informar a usted, que el Subcomité de Biología Experimental y Biomedicina del Posgrado en Ciencias Biológicas, en su sesión ordinaria del día **01 de octubre de 2018**, aprobó el siguiente jurado para la presentación del examen para obtener el grado de **DOCTORA EN CIENCIAS** a la alumna **GALÁN ACEDO CARMEN,** con número de cuenta **515046623,** con la tesis titulada, **"EFECTO DE LA ESTRUCTURA DE PAISAJES ANTRÓPICOS SOBRE LOS PRIMATES"** dirigida por el **DR. VICTOR ARROYO RODRÍGUEZ**.

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ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 20 de noviembre de 2018

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

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A mi padre†

ÍNDICE

Lista de figuras vi

Lista de cuadros y tablas xii

Resumen xiv

Abstract xvii

Capítulo 1 Introducción general 1

Capítulo 2 A global assessment of primate responses to landscape structure 21
En revisión Biological Reviews

Capítulo 3 Drivers of the spatial scale that best predict primate responses to landscape structure 53
Publicado en Ecography (2018)

Capítulo 4 Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests 70
Aceptado en Landscape Ecology

Capítulo 5 Impact of landscape structure on two endangered primates across rainforest regions with different land-use intensity 94

Capítulo 6 The conservation value of human-modified landscapes for the world's primates 120
Aceptado en Nature Communications

Capítulo 7 Ecological traits of the world's primates 138
En revisión en Scientific Data

Capítulo 8 Discusión general y conclusions 149

Literatura citada 157

Material Suplementario 170

LISTA DE FIGURAS

Capítulo 1

Figura 1. Ejemplo de un gradiente de heterogeneidad composicional y configuracional. Cada cuadrado representa un paisaje y los colores representan diferentes tipos de coberturas dentro del paisaje. Las flechas señalan un incremento en la heterogeneidad de la composición o la configuración del paisaje. La heterogeneidad en la composición aumenta con el incremento en el tipo de coberturas y la heterogeneidad en la configuración con el aumento de la complejidad espacial de dichas coberturas. Extraído de Fahrig et al. (2011).

Figura 2. Localización de las zonas de estudio en México (a). Las figuras a color son las regiones donde se hizo la colecta de datos (b): Marqués de Comillas (Chiapas), el valle de Uxpanapa (Veracruz), la región de Los Tuxtlas y la Región 8 Norte. En rojo se muestran los doce fragmentos seleccionados por región. Los polígonos verde oscuro simbolizan el bosque, los verde claro las áreas abiertas, los azules el agua y los blancos los poblados.

Capítulo 2

Figure 1. Patch and landscape approaches in ecological studies. In patch-scale studies, both ecological responses and predictor variables are measured in different (and independent) focal patches distributed across the study region. Studies with a landscape approach are those that assess the effect of landscape variables on ecological responses. The responses can be measured in three ways: within equal-sized sample sites at the centre of each landscape (i.e. site-landscape design), within focal patches at the centre of each landscape (i.e. patch-landscape studies) or within several sample sites or patches across the landscape (i.e. landscape scale design). In site- and patch-landscape designs, landscape variables are measured within a specified radius from the centre of the sites/patches. In all cases, multiple landscapes need to be sampled in order to ask questions about the influence of landscape structure on an ecological response. Note that in landscape-scale studies, the sites or patches located near the edge of the landscape can be affected by the landscape context beyond the bounds of the sample landscape. For simplicity of illustration, habitat patches (green polygons) are embedded in a homogeneous (white areas) anthropogenic matrix (modified from Arroyo-Rodríguez & Fahrig, 2014; Andresen *et al.*, 2018).

Figure 2. Global distribution of primate studies with a landscape approach (diamonds) (A). Pink vs. orange diamonds refer to studies that assess or not the scale of landscape effect on primates, respectively. Primate species richness is represented in blue colors (based on Pimm *et al.*, 2014). The proportion and absolute number (above each column) of individual effects tested per geographic region is also indicated (B).

Figure 3. Designs of published primate studies that use a landscape approach (n = 34 studies). The proportion (represented by the size of black vertical lines) of studies with different study designs is indicated, as is the type of buffer used to determine the extents of the replicate landscapes (site- and patch-landscape study designs only), the presence/absence of spatial overlap between landscapes, the number of scales within which landscape variables were measured, the cases in which the scale of effect (SE) was tested, and the range of scales tested. The latter was measured as the largest scale divided by the smallest scale. ‘Site and patch’ in the first column refers to a review that used both site-landscape and patch-landscape study designs. NI = no information available, which includes studies that do not specify the buffer type and one landscape-scale study where this information is not applicable.

Figure 4. Proportions (and numbers in bars) of positive, negative and neutralull responses (n = 121 responses from 33 studies) of primates to landscape composition variables (defined in Table 1), separately assessing studies that evaluated or did not evaluate the scale of landscape effect (SE) (A). The proportion of positive and negative significant responses is also indicated, separately showing the impact of forest cover (B), land cover richness (C), landscape quality index (D) and matrix quality (E).

Figure 5. Proportions (and number in boxes) of positive, negative and null responses (n = 39 responses from 9 studies) of primates to landscape configurational variables per se (i.e. controlling the effect of forest cover) (A) and to landscape configuration variables (n = 29 responses from 4 studies) without controlling the effect of forest cover (B), separately for studies that assessed or not the scale of effect (SE). The arrow points to those cases in which forest cover was controlled, indicating primate responses to habitat fragmentation (C), and corridor abundance (D) and mean inter-patch isolation (E).

Capítulo 3

Figure 1. Location of the study regions, focal forest patches (in red) and their respective surrounding local landscape in southeastern Mexico. The 13 different-sized landscapes (buffers, in black lines) around the geographic center of each focal patch are also

indicated. For simplicity, we do not add all classified land covers in each region, but only those with higher contrast (i.e. forest cover is indicated with dark green, cattle pastures and annual crops with light green, water bodies in blue, and white polygons represent human settlements).

Figure 2. Association between landscape size (x-axis) and the strength of the relationship (parameter estimate, y-axis) between each landscape attribute and each response variable (i.e. encounter rate and immature-to-female ratio) of spider monkeys in the Marques de Comillas (MCR) and Uxpanapa regions (UR). The scale of effect is indicated within each panel with vertical lines (a continuous line for the encounter rate, and a dashed line for IF ratio). Dotted lines indicate the cases in which the scale of effect was equal to the smallest or largest scale evaluated, thus suggesting that the scale of effect was outside the study range (Jackson & Fahrig 2015).

Figure 3. Association between landscape size (x-axis) and the strength of the relationship (parameter estimate, y-axis) between each landscape attribute and each response variable (i.e. encounter rate and immature-to-female ratio) of howler monkeys in four rainforest regions. The Uxpanapa (UR), Los Tuxtlas (LTR) and 8th North (8NR) regions are occupied by mantled howler monkeys (*Alouatta palliata mexicana*), and the Marqués de Comillas region (MCR) is occupied by black howler monkeys (*Alouatta pigra*). Vertical lines indicate the scale of effect for the encounter rate (continuous line) and IF ratio (dashed line). Dotted lines are scales of effect equal to the smallest or largest scale evaluated, which suggests that the scale of effect was outside the study range (Jackson & Fahrig 2015).

Figure 4. The scale of landscape effect in Mexican primates, separately assessing for differences among species (a), between response variables (b), among landscape predictors (c) and among rainforest regions (d). Center lines show the medians, box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots, crosses represent sample means, and bars indicate 95% confidence intervals of the means. Abreviations: FC = Forest Cover, MF = Matrix Functionality, PD = Patch Density, ED = Edge Density, CD = Connectors' Density, MCR = Marques de Comillas Region, UR = Uxpanapa Region, LTR = Los Tuxtlas Region, and 8NR = 8th North Region.

Capítulo 4

Figure 1. Location of the two study regions, focal forest patches (in red) and their respective surrounding local landscape in southeastern Mexico. An example of a focal patch and their respective landscape is also indicated. For simplicity, we do not add all classified land covers in each region, but only those with higher contrast (forest cover is indicated with dark green, cattle pastures and annual plantations with light green, water bodies in blue, and white polygons represent human settlements).

Figure 2. Predictor variables included in 95% set of models (bars) for the two study regions, Marqués de Comillas region and Uxpanapa region. The importance of each variable is shown by the sum of Akaike weights ($\sum w_i$, panels). We assessed the impact of forest cover (FC), matrix functionality (MF) and forest patch density (PD). The percentage of deviance explained by each complete model (goodness-of-fit of each complete model) is also indicated. Positive (+) or negative (-) effects of each landscape predictor on each response variable are indicated at the side of the parameter estimates.

Capítulo 5

Figure 1. (a) Location of the four study regions in southeastern Mexico. (b) Study regions are ordered from the least to the most disturbed: MC = Marqués de Comillas, (c) UR = Uxpanapa region, (d) LT = Los Tuxtlas and (e) 8N = 8th North region. Red marks represent the selected study forest patches. For simplicity, we do not add all classified land covers in each region, but only those with higher contrast (forest cover is indicated with dark green, open areas with light green, water bodies in blue, and white polygons represent human settlements).

Figure 2. Predictor variables included in 95% set of models (bars) for the two response variables, abundance and reproductive success of howler monkeys, and for the four study regions (MC = Marqués de Comillas, UR = Uxpanapa region, LT = Los Tuxtlas, 8N = 8th North region). Black howler monkeys (*Alouatta pigra*) inhabit MC, while mantled howler monkeys (*Alouatta palliata mexicana*) inhabit the other three regions. The importance of each variable is shown by the sum of Akaike weights ($\sum w_i$). We assessed the impact of three landscape predictors: forest cover (FC), matrix functionality (MF) and forest patch density (PD). The percentage of deviance explained by each complete model (i.e. goodness-of-fit of each complete model) is indicated in each panel. Positive (+) or negative (-) effects of each landscape predictor on each response variable are indicated. When the unconditional variance was higher than the

model-averaged parameter estimates we do not indicate the sign (+/-) of effect, because such patterns suggest caution with interpretation of parameter estimates (see Table 3).

Capítulo 6

Figure 1. Geographic distribution of studies reporting the use of different anthropic land covers (ALCs) by primates. Spatial location of each study (**a**). Proportion of species using ALCs (n = 147 species) compared to the total proportion of species (n = 504 species) in each biogeographic realm (**b**). African primates were classified in two groups, those from mainland Africa and those from Madagascar, because these two land masses span the distribution of two highly divergent taxa of primates (catarrhines and strepsirrhines, respectively). Number of primate species recorded using each of five ALCs (**c**). Proportion of primate species using each ALC type in each realm (**d**). ALCs are categorized as human settlements (HS), open areas (OA), tree plantations (TP), connectors (CO), and secondary forests (SF). Species richness data in (**a**) was extracted from Pimm *et al.* (2014).

Figure 2. Activities of primates in each anthropic land cover (ALC) type. The proportion (and total numbers above each column and within column sections) of records for travelling, resting, foraging or all activities in different ALC types is indicated. ALCs include human settlements (HS), open areas (OA), tree plantations (TP), connectors (CO), and secondary forests (SF). The total number of records varies because some studies report activities for more than one primate species whereas others do not report any primate activity.

Figure 3. Conservation status and population trends of primate species using anthropic land covers (ALCs) compared to all the world's primates. The proportion (and total number above bars) of primate species within each IUCN threat category (**a**), and population trend (**b**), are shown. We tested for differences in frequencies with Chi-square tests of goodness of fit (*$P \leq 0.05$, **$P \leq 0.01$) between primates using ALCs and all the world's primates, by separately assessing primate species that used different types of ALCs (HS = human settlements, OA = open areas, TP = tree plantations, CO = connectors, and SF = secondary forest). From higher to lower extinction risk, threat categories include: Critically endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT) and Least Concern (LC). We excluded species classified as Data Deficient and Not Evaluated in (**a**), and those whose population trends are unknown in (**b**).

Figure 4. Ecological traits of primate species that have been recorded using anthropic land covers (ALCs). The proportions (and total number above bars) of primate species exhibiting different diel activity patterns (**a**), modes of locomotion (**b**), body mass classes (**c**) and forest specialization or not (**d**). We tested for differences in frequencies with Chi-square tests of goodness of fit ($*P \leq 0.05$, $**P \leq 0.01$) between primates using ALCs and all the world's primates, by separately assessing primate species that used different ALC types (HS = human settlements, OA = open areas, TP = tree plantations, CO = connectors, and SF = secondary forest). Body mass (BM) was classified as small (< 2 kg), medium (2-10 kg) or large (>10 kg). We excluded from analyses those species for which we found no information.

Figure 5. Distribution of the use of anthropic land covers (ALCs) across the primate phylogeny. Use of ALCs (present/absent) is indicated for each of the 352 species with phylogenetic data, based on the molecular timetree of Dos Reis *et al.* (2018). All genera with ≥ 2 species are labeled, and branches are color-coded by realm.

Capítulo 7

Figure 1. Summary of the ecological traits of the word's primates included in the database. From left to right pictures represent: home range size gradient from small to large; locomotion types are terrestrial, both locomotion types, and arboreal; diel activity includes diurnal, nocturnal and cathemeral; trophic guild includes folivore, folivore-frugivore, frugivore, insectivore, omnivore, and gummivore (the latter not depicted); body mass gradient from small to large; habitat type includes seven categories (see text) but only two are depicted as examples (forest and savannah); IUCN conservation status includes seven categories, with five depicted here CR critically endangered, EN endangered, VU vulnerable, NT near threatened and LC least concern; population trend is represented by three graphs indicating increasing, stable and decreasing populations; geographic realm is represented by a global map. Images used with permission from Microsoft.

LISTA DE CUADROS Y TABLAS

Capítulo 1

Cuadro 1. Breve historia del cambio de uso de suelo en México.

Capítulo 2

Table 1. Landscape composition and configuration variables assessed in landscape studies of primates.

Capítulo 3

Table 1. Characteristics of the study regions in southeastern Mexico. Regions are ordered from the best preserved to the more disturbed.

Capítulo 4

Table 1. Values of model-averaged parameter estimates (*β*) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference for reproductive success and relative abundance for each landscape predictor in the two study regions (see all model sets in Supplementary Material Table A2).

Capítulo 5

Table 1. Characteristics of the study regions in southeastern Mexico. Regions are ordered from the best preserved to the more disturbed.

Table 2. Scales of effect for each landscape attribute and each response variable of howler monkeys (*Alouatta palliata* and *Alouatta pigra*) in the four study regions.

Table 3. Summary of the demographic characteristics of howler monkeys in the four study regions, Marqués de Comillas region (MC), Uxpanapa region (UR), Los Tuxtlas (LT) and the 8th North region (8N).

Table 4. Values of model-averaged parameter estimates (*β*) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference for abundance and reproductive success for the three landscape predictors in each study regions (see all model sets in Supplementary Material Table A1).

Capítulo 7

Table 1. Summary information for the eight data files comprising the database of ecological traits for the world's primates.

RESUMEN

El acelerado crecimiento de la población humana resulta en la transformación de los ecosistemas naturales en paisajes antrópicos, especialmente en los trópicos. Estos paisajes varían en estructura espacial, pero nuestro entendimiento acerca del impacto de la estructura del paisaje sobre las especies todavía es muy limitado. De hecho, los escasos estudios que utilizan una perspectiva de paisaje rara vez identifican la escala espacial más adecuada para estudiar el impacto del paisaje sobre las respuestas ecológicas (i.e. escala del efecto). Además, dichas respuestas pueden ser muy variables, ya que dependen del contexto regional en el que se encuentran los organismos, y de la función ecológica de las distintas coberturas antrópicas que dominan el paisaje.

En México, la deforestación en la última década resultó en la pérdida de 764,000 ha de bosque tropical, donde habitan las tres especies de primates mexicanos: el mono aullador de manto (*Alouatta palliata*), el mono aullador negro (*A. pigra*) y el mono araña (*Ateles geoffroyi*). Sin embargo, existen muy pocos estudios sobre la respuesta de estas especies a los cambios en la estructura del paisaje. Llenar este vacío de información es crítico para hacer predicciones confiables sobre el futuro de los primates en paisajes antrópicos y diseñar estrategias de conservación eficaces a escala de paisaje.

Esta tesis evalúa la respuesta de los primates a los cambios en la estructura de paisajes antrópicos. Para ello, primero hago una revisión del tema a nivel global (*Capítulos 1* y *2*). De los 34 estudios disponibles, el 79% no identificaron la escala del efecto, lo que puede explicar por qué la mayoría de respuestas documentadas (135 de 188 respuestas, 72%) son débiles. Sin embargo, al analizar las respuestas significativas, los primates generalmente mostraron respuestas positivas al incremento en la cobertura forestal, al índice de calidad del paisaje y a la calidad de la matriz, todas ellas variables de composición del paisaje. Las respuestas a la configuración fueron más débiles, pero la fragmentación del hábitat tendió a tener efectos positivos, subrayando el valor de conservación que tienen todos los parches de hábitat, incluso los más pequeños.

Para llenar el vacío de conocimiento existente sobre la escala del efecto del paisaje, en el *Capítulo 3* identifico algunos factores determinantes de dicha escala. Para ello, colecté datos de abundancia y relación inmaduros/hembra (un indicador del éxito reproductivo) de *A. palliata*, *A. pigra*, y *A. geoffroyi* en 4 regiones tropicales de México (Marqués de Comillas y la región 8 Norte en Chiapas, y el Valle de Uxpanapa y Los Tuxtlas en Veracruz). Estimé la estructura del paisaje (i.e. cobertura forestal, funcionalidad de la matriz, densidad de fragmentos de bosque, densidad de bordes forestales y densidad de conectores) alrededor de cada uno de los 12 sitios muestreados

por región. Las variables del paisaje fueron evaluadas en 13 buffers concéntricos de entre 100 a 1,300 m de radio para identificar el tamaño del paisaje que maximiza la asociación entre cada métrica de paisaje y cada respuesta de las especies (i.e. escala de efecto). La escala del efecto no difirió significativamente entre especies, regiones, variables de respuesta ni variables de paisaje. Sin embargo, tendió a ser menor para la densidad de conectores que para la densidad de fragmentos y la densidad de borde. Además, la escala del efecto tendió a ser mayor en las regiones más alteradas que en el resto de regiones. Por ello, debe tenerse precaución al tratar de generalizar la escala del efecto a diferentes variables explicativas y a distintas regiones.

Tras identificar las escalas del efecto, evalué el efecto relativo de tres variables del paisaje (i.e. cobertura forestal, funcionalidad de la matriz y densidad de fragmentos) sobre la abundancia y éxito reproductivo de monos araña (*Capítulo 4*) y monos aulladores (*Capítulo 5*). Los hallazgos indican que las respuestas de las tres especies de primates difieren entre regiones. La pérdida de hábitat tiene efectos negativos y más fuertes que la fragmentación del hábitat para los monos araña, particularmente en regiones más preservadas. En cambio, la funcionalidad de la matriz es importante en las regiones más alteradas, donde los monos araña pueden verse forzados a utilizar la matriz para alimentarse o desplazarse. De un modo similar, los monos aulladores responden negativamente a la pérdida de hábitat. Además, la composición de la matriz es particularmente importante en regiones con matrices más arboladas, probablemente porque este contexto espacial ofrece mayores oportunidades para la alimentación o el desplazamiento.

Para evaluar el uso de las coberturas antrópicas por parte de los primates, en el *Capítulo 6* reviso los patrones globales y los predictores del uso de dichas coberturas en 350 estudios. Encontré que al menos 147 especies de primates (de 504) utilizan coberturas antrópicas (i.e. asentamientos humanos, áreas abiertas, elementos conectores, cultivos arbóreos y vegetación secundaria). Los resultados también indicaron que los primates que toleran coberturas más alteradas tienen un 26% más de probabilidades de tener poblaciones estables o en incremento que la media para todos los primates del mundo. La mayoría de especies utilizaron coberturas arbóreas (vegetación secundaria y cultivos arbóreos), y menos especies utilizaron asentamientos humanos. Además, comparado con todas las especies de primates del mundo, las especies que utilizan coberturas antrópicas se encuentran menos amenazadas, son mayormente diurnas, con tamaños corporales medianos o grandes, no estrictamente arbóreas y generalistas de hábitat. Así, este capítulo identifica los patrones del uso de coberturas antrópicas por primates y su papel clave en la conservación y la ecología de primates.

Como resultado de la revisión elaborada en el *Capítulo 6*, en el *Capítulo 7* elaboré una base de datos global de varios rasgos ecológicos de todos los primates del mundo (i.e. ámbito hogareño, tipo de locomoción, patrón de actividad, nivel trófico, tamaño corporal, tipo de hábitat, estado de conservación, tendencia poblacional y región geográfica en la que se encuentran). Esta base de datos, fácil de utilizar y de acceso libre y gratuito, tiene una amplia aplicabilidad en los estudios de ecología con primates. Por ejemplo, puede utilizarse para evaluar la señal funcional de las respuestas de las especies a la alteración del hábitat en distintos ecosistemas. También puede servir para estudiar la influencia de las especies de primates en los servicios ecosistémicos o comparar los roles ecológicos de los primates a diferentes escalas espaciales.

Con base en los capítulos descritos arriba, el capítulo final de la tesis (*Capítulo 8*) sintetiza y discute las principales implicaciones de conservación de los resultados de la tesis. En particular, los resultados sugieren que la pérdida de hábitat es la mayor amenaza para los primates en paisajes antrópicos de México y el mundo. Sin embargo, los primates son capaces de utilizar las coberturas antrópicas para descansar, moverse, alimentarse, e incluso como hábitat temporal o permanente. En particular, los primates mexicanos parecen utilizar las coberturas antrópicas en regiones alteradas con coberturas arbóreas. Por lo tanto, mejorar la calidad de la matriz antrópica puede ser crítico para la conservación de primates. Además, dado que la principal causa del cambio de uso de suelo en los trópicos es la producción de carne, el futuro de los bosques tropicales y de los primates dependerá en gran medida de nuestra capacidad de minimizar el consumo de carne de nuestra dieta, especialmente la carne de vaca.

ABSTRACT

The accelerated growth of human population results in the transformation of natural ecosystems into anthropic landscapes, especially in the tropics. These landscapes vary in spatial structure, but our understanding about the impact of landscape structure on species is still limited. In fact, only a few studies with a landscape perspective identify the optimal spatial scale to study the impact of landscape on ecological responses (i.e. the scale of effect). Moreover, such responses can vary widely as they are dependent of the regional context where organisms occur and the ecological function of the different anthropic landscape covers.

In Mexico, deforestation in the last decade has resulted in the loss of 764,000 ha of tropical forest where the three Mexican primates inhabit: the mantled howler monkey (*Alouatta palliata*), the black howler monkey (*A. pigra*) and the spider monkey (*Ateles geoffroyi*). However, very few studies assess these species' response to changes in landscape structure. Filling this information gap is critical to make reliable predictions about the future of primates in antropic landscapes and to design conservation strategies at landscape scale.

This thesis assesses primates’ responses to anthropic landscape structure changes. With that aim, firstly I review this topic (*Chapter 1* and *2*). From the 34 studies available, 79% do not identify the scale of effect which can explain why most responses to landscape structure (135 of 188 responses, 72%) were null. Nonetheless, when analyzing the significant responses, primates mainly show positive responses to increasing forest cover, landscape quality index and matrix quality, all landscape composition variables. Responses to landscape configuration were weaker but habitat fragmentation showed mostly positive effects, stressing the conservation value of habitat patches.

To add to the scarce existing body of knowledge about the scale of landscape effect, I identify some drivers that can affect such scale in *Chapter 3*. To do so, I collected abundance and immature to female ratio data (a proxy of reproductive success) of *A. palliata*, *A. pigra*, y *A. geoffroyi* in 4 tropical regions of Mexico (Marqués de Comillas y la región 8 Norte in the state of Chiapas, y el Valle de Uxpanapa y Los Tuxtlas in the state of Veracruz). I estimated the landscape structure (i.e. forest cover, matrix functionality, forest patch density, forest edge density and connectors density) surrounding each of the 12 sampled patches in each region. Landscape variables were assessed in 13 buffers from 100 to 1,300-m radii to identify the optimal landscape size between each landscape metric and each species responses (i.e. scale of effect). The

scale of effect did not differ significantly between species, regions, response variables and landscape variables. However, the scale of effect tended to be lower for connectors' density than for forest patch density and forest edge density. Furthermore, the scale of effect tended to be higher in the more disturbed region than in the rest of the regions. Therefore, special caution should be taken when attempting to generalize the scale of effect to different explanatory variables and regions.

Once I identified the scale of effect, I assessed the relative effect of three landscape variables (i.e. forest cover, matrix functionality and patch density) on the abundance and the reproductive success of spider monkeys (*Chapter 4*) and howler monkeys (*Chapter 5*). The findings indicate that responses of the three primate species differ between regions. Forest loss had negative and stronger effects than habitat fragmentation on spider monkeys, particularly in the most preserved regions. Matrix functionality, instead, was important in most disturbed regions, where spider monkeys can be pushed to use the matrix to find food resources or to move across the landscape. Similarly, howler monkeys respond negatively to habitat loss. Also, matrix composition is particularly important in regions with more arboreal matrices, probably because this spatial context offers opportunities to move and feed from anthropic covers.

To assess primates use of anthropic landscapes, in *Chapter 6* I reviewed the global patterns and predictors of the use of anthropic land covers in 350 studies. I found that at least 147 primate species (from 504) use anthropic covers (i.e. human settlements, open areas, connectors, tree plantations and secondary forest). Results also indicated that those primates that tolerate heavily modified anthropic land covers are 26% more likely to have stable or increasing populations than the average for all primates. Most species used secondary forest and tree plantations whereas few used human settlements. Moreover, compared to all primates on Earth, species using anthropic land covers are less often threatened with extinction, but more often diurnal, medium or large-bodied, not strictly arboreal, and habitat generalists. Thus, this chapter identifies the patterns of anthropic land covers used by primates and its key role in primate ecology and conservation.

As a result of *Chapters 6*'s review, in *Chapter 7* I made a database on some important ecological traits of the world's primates, including home range size, locomotion type, diel activity, trophic guild, body mass, habitat type, current conservation status, population trend, and geographic realm. This database, easy to use and with free access, has a broad applicability in ecological and primatological research. For instance, it can be used to assess the functional signal of species' responses to habitat disturbances across ecosystems. Furthermore, this database can be used to test the influence of primate species on ecosystem function and services or to compare the ecological roles of primates at different spatial scales.

Working on the base of the chapters previously described, the last chapter of this thesis (*Chapter 8*), sums up and discusses the main conservation implications of the results founded. In particular, the results suggest that habitat loss is the main threat for primates in anthropic landscapes in Mexico and worldwide. However, primates are able to use the anthropic covers to rest, move, feed, and even as temporal or permanent habitat. In particular, Mexican primates seem to use the anthropic covers in the more disturbed regions and with more arboreal land covers. Therefore, improving matrix quality can be critical for primate conservation. Furthermore, as meat production is the main driver of land use change in the tropics, the maintenance of tropical forest and primates depend on our ability to reduce meat consumption, particularly cow meat.

Capítulo 1

Introducción general

Carmen Galán-Acedo

El cambio de uso de suelo

Entre otros cambios de uso de suelo, la conversión de los ecosistemas naturales a tierras agrícolas y ganaderas representa la mayor amenaza para la biodiversidad (Newbold et al. 2015). Durante el último siglo, esta conversión ha sido particularmente drástica en los trópicos (Song et al. 2018), donde se perdieron 129 millones de hectáreas de bosque entre 1990 y 2015 (FAO 2015). En estas regiones, la agricultura y la ganadería son las responsables del 73% de la deforestación actual (FAO 2016). Como consecuencia, cada vez más especies se encuentran forzadas a habitar paisajes modificados por el humano, donde los remanentes de vegetación original están rodeados por diferentes tipos de coberturas antrópicas (Watling et al. 2011; Taubert et al. 2018). Dado que los bosques tropicales son el principal hábitat de la mitad de la biodiversidad terrestre mundial (Dirzo & Raven 2003; Wright 2005), la pérdida de estos bosques representa su principal amenaza (Malhi et al. 2014; Newbold et al. 2016). De hecho, en las últimas décadas se ha registrado una pérdida excepcionalmente rápida de biodiversidad, lo que sugiere que enfrentamos la sexta extinción en masa de la historia (Barnosky et al. 2011; Ceballos et al. 2015). En México, el acelerado cambio de uso de suelo (Cuadro 1) cataloga al país como el quinto del mundo con más especies amenazadas (1,131 especies) en 2015 (IUCN, 2015). Sin embargo, todavía es posible desacelerar o incluso frenar la pérdida de biodiversidad si diseñamos e implementamos estrategias de conservación y manejo que sean adecuadas. Para ello, urge entender el efecto de los cambios de uso de suelo sobre las especies. Esta información es fundamental para crear un enfoque estratégico integrado en las políticas de agricultura, ganadería y actividad forestal que sea amigable con la biodiversidad.

Cuadro 1. Breve historia del cambio de uso de suelo en México

México se encuentra entre los países con mayor cobertura forestal del mundo. Es un país megadiverso que alberga entre el 10 y el 12% de todas las especies del planeta. Sin embargo, la deforestación amenaza a la mayoría de sus especies, principalmente a causa del crecimiento agrícola y ganadero. La historia del cambio de uso de suelo en México es relativamente reciente. Durante siglos, varias regiones forestales fueron ocupadas por comunidades indígenas que desarrollaban actividades tradicionales de manejo sustentable, como la rotación de áreas de cultivo que permitían la regeneración constante del bosque. Sin embargo, a finales del siglo XIX, el gobierno mexicano creó concesiones para atraer capital extranjero, abriendo las selvas de Tabasco, Chiapas, Veracruz y de la Península de Yucatán. Para regular el uso de estas selvas, después de la Revolución Mexicana, el gobierno estableció la primera ley forestal. Durante el gobierno de Lázaro Cárdenas en la década de los años 30, se creó la Reforma Agraria que incluyó la repartición de 4 millones de hectáreas de bosque a *campesinos para la formación de minifundios, que pese al esfuerzo, no fue suficiente para satisfacer las necesidades de estas familias. Más tarde, en 1943, para aumentar el crecimiento económico, se creó la ley de Unidades Industriales de Explotación Forestal, que permitió que industrias privadas tuvieran acceso a los bosques mexicanos. Esta situación creó cierta preocupación en el gobierno, prohibiendo a 11 estados la explotación de sus bosques. Su impacto, sin embargo, afectó principalmente a los habitantes de las comunidades cercanas y no tanto a las empresas. De hecho, el rol del gobierno mexicano en la industria maderera y del papel incrementó gradualmente durante los años 50 y 60.*

En la segunda mitad del siglo XX se dieron dos grandes procesos: el crecimiento demográfico y la gran mercantilización de la producción campesina. Durante la década de 1970 y principios de 1980, México creó las políticas de colonización tropical más agresivas, que resultaron en la devastación de cientos de miles de hectáreas de bosque tropical. Por ejemplo, el Programa Nacional de Desmontes fue un fondo de financiación creado para transformar los bosques en “pequeños usos económicos” agrícolas y ganaderos. Este programa fue responsable de la destrucción de cerca de 28 millones de metros cúbicos de madera en 5 años, durante los años 70.

Los datos en las últimas décadas no son más favorables. El Inventario Nacional Forestal calculó una pérdida anual de 534,707 ha de bosque entre 1976 y 2007. Lamentablemente, las tasas de deforestación siguen aumentando, particularmente en el último año, con un 36% de crecimiento según la plataforma Global Forest Watch.

La estructura del paisaje

En ecología, el concepto “paisaje” se define como una porción de tierra heterogénea en al menos un factor de interés, y que puede contener un mosaico de diferentes tipos de coberturas (Turner 2005). La estructura del paisaje se define por su composición y por su configuración espacial (Fig. 1). La composición del paisaje se refiere a los tipos y proporciones de diferentes coberturas, como el porcentaje de una determinada cobertura (e.g. bosque) en el paisaje (Dunning et al. 1992). La configuración, en cambio, se refiere a la disposición espacial y fisionomía de cada cobertura en el paisaje. Métricas como el número de fragmentos de bosque o la densidad media de los bordes forestales son típicas variables de configuración del paisaje (Dunning et al. 1992; McGarigal & Marks 2001).

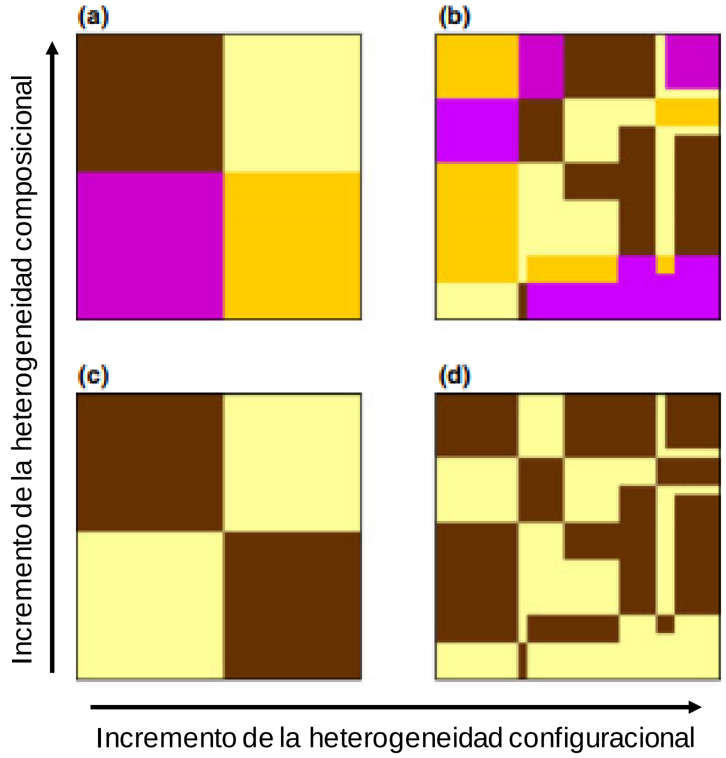

Figura 1. Ejemplo de un gradiente en heterogeneidad composicional y configuracional. Cada cuadrado representa un paisaje y los colores representan diferentes tipos de coberturas dentro del paisaje. Las flechas señalan un incremento en la heterogeneidad de la composición o la configuración del paisaje. La heterogeneidad composicional aumenta con el incremento en el tipo de coberturas y la heterogeneidad en la configuración con el aumento de la complejidad espacial de dichas coberturas. Modificado de Fahrig et al. (2011).

La importancia de la escala

Algunas teorías clásicas, como la teoría de biogeografía de islas (MacArthur & Wilson 1967) y la teoría metapoblacional (Levins 1969), proponen que el tamaño del fragmento y el aislamiento entre fragmentos son las principales variables espaciales que explican los patrones de distribución y abundancia de las especies. Sin embargo, el efecto de atributos espaciales de fragmentos no puede ser extrapolado a escala de paisaje, ya que los mecanismos que explican patrones de diversidad dependen de la escala de análisis (Fahrig 2003). Para evaluar adecuadamente el efecto de la estructura del paisaje sobre las especies es necesario utilizar una aproximación paisajística, o sea, utilizar paisajes (no fragmentos) como unidad de análisis, y así evaluar el efecto de los atributos del paisaje sobre las especies (*Capítulo 2*).

Pero, ¿qué tamaño del paisaje es el más adecuado para evaluar los efectos de la estructura del paisaje sobre las variables de respuesta? Para poder responder a esta pregunta es necesario identificar la escala del efecto. Para ello, las variables de paisaje deben medirse a diferentes escalas, es decir, en paisajes de diferente tamaño, para identificar el tamaño de paisaje que maximiza la fuerza de la relación entre cada variable del paisaje y cada variable de respuesta (Jackson & Fahrig 2012). Sin este análisis multiescalar, las inferencias acerca del efecto de la estructura del paisaje sobre las especies pueden ser erróneas. Los *Capítulos 2* y *3* de la presente tesis describen en detalle cómo se calcula la escala del efecto, sus implicaciones y algunos factores que pueden afectar dicha escala.

El papel de la composición y la configuración del paisaje sobre las especies

Importancia de la cantidad de hábitat

La cantidad de hábitat es un atributo de la composición de un paisaje. El tamaño de un fragmento de hábitat representa la cantidad de hábitat a escala local. En la década de 1960 y 1970, la teoría de biogeografía de islas (MacArthur & Wilson 1967), la teoría metapoblacional (Levins 1969) y el debate SLOSS (“single large vs. several small”; Diamond 1975) promueven el estudio del efecto del tamaño del fragmento sobre las especies. En particular, estas teorías clásicas predicen que fragmentos más pequeños y más aislados tienen una menor probabilidad de ocupación y una mayor probabilidad de extinción que los fragmentos más grandes y mejor conectados. Aunque no consideran cómo afecta el contexto del paisaje a las especies, estos modelos destacan la importancia de crear reservas de mayor tamaño para conservar la biodiversidad.

En contraste con estos modelos, la hipótesis de la cantidad de hábitat (Fahrig 2013) propone que el número de especies en un sitio de tamaño dado (i.e. densidad de especies) depende más de la cantidad de hábitat que rodea al sitio (i.e. cantidad de hábitat a escala de paisaje) que del tamaño del fragmento donde se ubica dicho sitio. De hecho, desde hace décadas sabemos que la pérdida de hábitat a escala de paisaje tiene efectos consistentemente negativos para un gran número de especies (Fahrig 2003). La pérdida de hábitat reduce la disponibilidad de recursos y la conectividad del paisaje (Findlay & Houlahan 1997; Cushman 2006; Fahrig 2013). Los paisajes con menor cantidad de hábitat están dominados por fragmentos de menor tamaño (Fahrig 2003), que pueden presentar una mayor densidad poblacional de algunos grupos taxonómicos, provocando un mayor contacto entre individuos (Marsh & Chapman 2013). Esto puede incrementar la competencia intra- e inter-específica (Stevenson et al. 2010) y la transmisión de enfermedades y parásitos (Plowright et al. 2008). Todos estos mecanismos aumentan la mortalidad de individuos, limitando la persistencia de especies y comunidades en paisajes con menor cantidad de hábitat.

Aunque pocos estudios han puesto a prueba la hipótesis de la cantidad de hábitat (revisado por Martin 2018), varios estudios encuentran evidencias a favor (e.g. Rabelo et al. 2017; Melo et al. 2017). Por tanto, la protección del hábitat a escala de paisaje debe ser una prioridad en planes de conservación. Pero, ¿qué cantidad mínima de hábitat se requiere para asegurar la persistencia de las especies en un paisaje? Algunos modelos teóricos y matemáticos sugieren que las poblaciones y su probabilidad de persistencia disminuyen drásticamente en paisajes con menos del 30-40% de hábitat remanente (‘umbral de extinción’; Fahrig 2002; Lande 1987). Este valor depende de las necesidades de hábitat de las especies y de la composición de la matriz, así como de la habilidad de las especies para utilizarla. Por ejemplo, especies con ámbitos hogareños mayores y poco hábiles para utilizar la matriz serán más sensibles a la pérdida de hábitat que especies que pueden vivir en espacios menores (Dale et al. 1994; Fahrig 2001). En cambio, si las especies son capaces de utilizar coberturas fuera de los fragmentos de hábitat, la matriz puede convertirse en un hábitat alternativo, aunque de menor calidad al original. Más recientemente, Boesing et al. (2018) demuestran que el umbral de extinción también depende del tipo de matriz. En particular, las aves del Bosque Atlántico de Brasil pueden persistir en paisajes con menor cantidad de hábitat si la matriz es arbolada (plantaciones de café) que si es abierta (pastizales). Esto sugiere que las especies no sólo dependen de la cantidad de hábitat, sino del tipo de matriz, ya que este elemento del paisaje puede ofrecer recursos complementarios y/o suplementarios (Dunning et al. 1992).

Importancia de la estructura de la matriz antrópica

El papel de la matriz antrópica ha ganado interés en los últimos años. En ecología, la matriz se define como la porción del paisaje que no es hábitat para una especie determinada (Ricketts et al. 2001). Así, este concepto es específico de los requerimientos de hábitat de cada especie. Las teorías clásicas (MacArthur & Wilson 1967; Levins 1969) típicamente consideran que la matriz es un área homogénea donde la biodiversidad no ocurre. Sin embargo, estas aproximaciones han sido ampliamente criticadas (Haila 2002; Franklin & Lindenmayer 2009) y están siendo gradualmente reemplazadas por modelos teóricos basados en paisajes heterogéneos (Dunning et al.

1992; Daily 1997; Tscharntke et al. 2012). Estos enfoques nuevos se basan en la premisa de que la matriz puede estar involucrada en procesos ecológicos clave para la persistencia de las especies en paisajes antrópicos. Por ejemplo, las especies pueden utilizar la matriz para refugiarse o desplazarse a otros fragmentos y explotar recursos adicionales como alimento (i.e. suplementación y complementación del paisaje; Dunning et al. 1992). El modelo de biogeografía rural (Daily 1997) considera que los diferentes tipos de coberturas en la matriz pueden representar hábitats de distinta calidad para las especies. Por ejemplo, Mendenhall et al. (2014) encuentran que el 60% de las especies de reptiles y el 70% de anfibios habitan en una gran variedad de coberturas antrópicas, incluyendo pastizales y campos agrícolas.

La estructura de la matriz, junto con la habilidad de las especies para utilizarla, son claves en la función que ejercen estas coberturas en el paisaje. Algunos estudios sugieren que la ocurrencia y la dispersión de los organismos en el paisaje son mayores cuando la matriz se asemeja a los fragmentos de hábitat original (Aberg et al. 1995; Prevedello & Vieira 2010). En este sentido, la vegetación secundaria es la cobertura más similar estructuralmente al hábitat de las especies especialistas de bosque. El papel de la vegetación secundaria en la conservación de las especies ha sido ampliamente estudiado (Chazdon et al. 2009; Dent & Wright 2009; Gibson et al. 2011). La funcionalidad de este tipo de vegetación depende de su edad y grado de perturbación (Newbold et al. 2015). Por ejemplo, en una revisión global, Newbold et al. (2015) encuentran que la vegetación secundaria tardía tiene mayor riqueza y abundancia de especies que la vegetación secundaria joven. Los autores también encuentran que la vegetación secundaria se asocia a una menor pérdida de especies que los cultivos, los pastizales y las áreas urbanas. Los cultivos, sin embargo, también pueden aportar recursos a las especies y ejercer un papel importante en su conservación (Zamora et al. 2007; Perfecto & Vandermeer 2010; Estrada et al. 2012). Entre ellos, algunos tipos de sistemas agroforestales parecen tener un alto potencial de conservación debido a su complejidad estructural y alta diversidad florística (Siebert 2002; Philpott & Dietsch 2003; Schroth et al. 2004). Otras coberturas en la matriz, como los elementos conectores (e.g. corredores biológicos o las cercas vivas) también pueden jugar un papel crucial en la conservación de las especies al permitir el desplazamiento, alimentación, refugio, e incluso el aumento del flujo génico (Blair 2011).

Sin embargo, el uso de la matriz antrópica también puede suponer riesgos para las especies. Por ejemplo, su uso puede incrementar la exposición de los individuos a las carreteras o las instalaciones eléctricas. El uso de carreteras puede provocar la muerte de individuos por atropello, y los expone a humanos y depredadores (Laurance et al. 2009; Taylor & Goldingay 2010; McLennan & Asiimwe 2016). Los cables eléctricos y telefónicos pueden producir quemaduras, shocks nerviosos temporales o la muerte de los individuos que los utilizan. Esto se ha encontrado especialmente en aves (Scott et al. 1972; Bevanger & Brøseth 2004; Manville 2005), pero también en otros grupos de especies (Biasotto & Kindel 2018). Además, el uso de la matriz puede incrementar los conflictos con humanos cuando las especies utilizan los cultivos como fuente de alimento. Esto puede también incrementar la transmisión de enfermedades o la exposición a depredadores y a la caza (e.g. Beisner et al. 2015; Hoare 1999; Mbora & McPeek 2009; Thirgood et al. 2005). Estas situaciones pueden aumentar el riesgo de extinción de las especies. Así, el manejo de la matriz mediante la planificación paisajística y la educación ambiental son claves para disminuir sus efectos negativos.

La fragmentación del hábitat

El debate sobre el efecto de la fragmentación del hábitat sobre la biodiversidad se inicia en los años 30 (Gause 1934; revisado por Fahrig 2017). Los primeros estudios consideraban que la fragmentación tenía principalmente efectos positivos porque un mayor número de fragmentos ofrecía refugio temporal a las presas, lo que le podía permitir escapar de sus depredadores (Huffaker 1958). Además, se consideraba que un mayor número de parches implicaban generalmente un incremento de la cantidad total de cobertura del paisaje (Fahrig 2017). En la década de 1970, a partir de la influencia de la teoría de biogeografía de islas (MacArthur & Wilson 1967), cambia el rumbo de este debate. Así, se argumenta que los efectos de la fragmentación son frecuentemente negativos y que está unida a la pérdida de hábitat (Villard & Metzger 2014). Como señala Fahrig (2017), en ambos casos la fragmentación está ligada a una ganancia o pérdida de hábitat y ambas aproximaciones expresan que la pérdida de hábitat tiene efectos negativos sobre las especies. Esta relación no es bidireccional, dado que un paisaje puede sufrir pérdida de hábitat sin verse fragmentado. En otros casos, la pérdida de hábitat puede llevar a patrones o grados muy distintos de fragmentación en un paisaje.

Entonces, ¿qué efectos tiene la fragmentación por sí misma o fragmentación *per se* (*sensu* Fahrig 2003)? Algunos autores insisten en que los efectos de la fragmentación son inseparables o indistinguibles de los efectos de la pérdida de hábitat (Didham et al. 2012; Fletcher et al. 2018). En cambio, Fahrig (2003) demuestra que podemos evaluar el efecto de la fragmentación *per se* como un atributo de la configuración del paisaje controlando experimental o estadísticamente el efecto de la pérdida de hábitat. Separar ambos efectos es fundamental para proponer estrategias de manejo y conservación más adecuadas (ver por ejemplo el debate SLOSS, Diamond 1975). Por ejemplo, si los efectos de la fragmentación son positivos, puede ser más efectivo conservar un mayor número de reservas pequeñas en el paisaje (several-small) que la misma cantidad de hábitat en una única reserva grande (single-large). Lo opuesto será mejor en un escenario donde la fragmentación tiene principalmente efectos negativos sobre las especies.

Para examinar si los efectos de la fragmentación son positivos o negativos, Fahrig (2017) revisa 118 estudios que evalúan la fragmentación independientemente de la cantidad de hábitat. La autora encuentra que el 76% de los efectos reportados fueron positivos. Algunos autores sugieren que estos efectos pueden deberse a la reducción de la expansión de fuegos, parásitos, depredadores y otras amenazas (Collinge & Forman 1998), el incremento de la conectividad del paisaje (Anzures-Dadda & Manson 2007) y la facilitación de dinámicas de complementación y suplementación del paisaje (Ethier & Fahrig 2011). Otros efectos positivos pueden estar asociados a la reducción de la competencia inter e intraespecífica (Bancroft & Turchin 2003) y el incremento en la heterogeneidad del paisaje (Hu et al. 2012) en territorios con un mayor grado de fragmentación.

Los primates en crisis de extinción

Los primates juegan un rol vital en la estructura y funcionamiento de los ecosistemas como herbívoros, dispersores de semillas y depredadores (Mittermeier et al. 2013; Estrada et al. 2017; Andresen et al. 2018). Los primates tienen una amplia distribución, desde el Neotrópico, África continental y Madagascar, hasta el sur y sureste de Asia. Residen en la mayoría de las regiones megadiversas del mundo. Habitan una gran variedad de ecosistemas (e.g. bosque húmedo, bosque seco, bosque lluvioso) y se encuentran en la mayoría de los hotspots de diversidad a nivel mundial (Lambert 2014). Por ello, conservarlos puede ayudar a proteger la biodiversidad, así como los procesos ecológicos en los que participan. Sin embargo, la mayoría de las especies de primates son especialistas de bosque, particularmente en el Neotrópico (Mittermeier et al. 2013). Por tanto, la pérdida de cobertura forestal es considerada la principal amenaza para su conservación (Estrada et al. 2017). Actualmente, de las 504 especies de primates que existen en el mundo, el 60% se encuentran en amenaza de extinción (Estrada et al. 2017).

Los primates mexicanos

México representa el límite norte de la distribución de los primates neotropicales en el continente americano. En este país ocurren tres taxa: *Alouatta palliata mexicana* o mono aullador de manto, *Alouatta pigra* o mono aullador negro, y *Ateles geoffroyi* o mono araña. En México, la destrucción del hábitat y otras amenazas como la cacería o el comercio ilegal, amenazan su supervivencia. Por ello, las subespecies *Alouatta palliata mexicana* y *Ateles geoffroyi vellerosus* se encuentran actualmente en peligro crítico de extinción y *Alouatta pigra* se encuentra en estado vulnerable (IUCN 2017). Según la Secretaría de Medio Ambiente y Recursos Naturales de México (SEMARNAT), las tres especies de primates mexicanos son consideradas especies amenazadas (Nom-059-SEMARNAT-2001) y su comercio y uso están restringidos.

Estas tres especies de primates son especialistas de bosque, diurnos, arbóreos y pasan la mayor parte de su tiempo en los estratos más altos de la cobertura vegetal (Mittermeier et al. 2013). Los primates mexicanos tienen cola prensil, que les ayuda a controlar su movimiento y mantener contacto con otros individuos (Klein 1976; Schmitt et al. 2005).

Los monos aulladores mexicanos

Los monos aulladores pertenecen a la familia *Atelidae*. Dentro del género *Alouatta* se reconocen 12 especies y 10 subespecies (ITIS 2018, www.itis.gov). Éstas se distribuyen desde el sureste del estado de Veracruz (México), a través de Centroamérica y Suramérica, hasta el norte de Argentina (Cortés-Ortiz et al. 2003). En México, la distribución de *A. palliata mexicana* se extiende desde el estado de Veracruz, pasando por Tabasco, el norte de Chiapas y Oaxaca hasta el sur de Guatemala (Rylands et al. 2005). En Tabasco *Alouatta palliata mexicana* y *Alouatta pigra* son simpátricas (Smith 1970). *Alouatta pigra* se encuentra en México, Guatemala y Belice (Rylands et al. 2005). En México, esta especie se encuentra en los estados de Quintana Roo, Campeche, Tabasco, Yucatán y Chiapas (Estrada et al. 2004).

Las dos características morfológicas dominantes son la cola prensil y el voluminoso complejo hioides/laringe. La cola es larga y desprovista de pelo en el último tercio inferior cubierta por dermatoglifos. Ésta parece tener dos funciones principales, reducir los costes de locomoción y facilitar los movimientos durante las actividades alimenticias. El hueso hioides se encuentra hipertrofiado en los machos, por lo que pueden distinguirse claramente de las hembras y es el órgano resonador y amplificador de los característicos aullidos de este género (Crockett & Eisenberg 1987). El principal rasgo distintivo de la subespecie es el pelaje claro en el dorso (Rylands et al. 2005). La cabeza, los hombros, las extremidades, la cola y ocasionalmente la región espinal son de color marrón oscuro, aunque frecuentemente se encuentran manchas de color amarillento en las patas y en la cola (Youlatos et al. 2015). El mono aullador de manto tiene un ámbito hogareño medio de 25 ha, las hembras tienen un peso corporal medio de 4.4 kg y los machos de 5.8 kg (Kelaita et al. 2011). El mono aullador negro, en cambio, tiene un ámbito hogareño medio de 27.5 ha, las hembras tienen un peso corporal de 5.7 kg y los machos de 7.6 kg (Kelaita et al. 2011). Ésta última especie posee un pelo más denso, largo y de color negro homogéneo que los monos aulladores de manto (Mittermeier et al. 2013; Estrada et al. 2017). Los machos son más grandes y pesados que las hembras en ambas especies. En *A. pigra*, los testículos se desarrollan desde la infancia, aunque en *A. palliata* son retenidos en el canal inguinal hasta la madurez sexual (Crockett & Eisenberg 1987).

En *Alouatta palliata mexicana*, el tamaño de los grupos puede variar de 3 a 44 individuos (proporción hembra/macho de 1.16 a 4.11) (Crockett & Eisenberg 1987). En *A. pigra* se han encontrado grupos formados por 2-15 individuos (Van Belle & Estrada 2006). En las dos especies los juveniles de ambos sexos migran de sus grupos natales para ingresar en otros grupos o unirse a otros individuos solitarios para formar nuevos grupos (Brockett et al. 2000). Tienen una dieta frugívoro-folívora, alimentándose de hojas, flores, semillas y frutos, particularmente hojas jóvenes y frutos maduros (Crockett & Eisenberg 1987; Crockett 1998). Ambas especies son especialistas de bosque, diurnas, arbóreas y tienen un patrón de actividad dirigido al ahorro de energía como adaptación a su dieta parcialmente folívora. Aunque su actividad puede variar mucho dependiendo de las características de la región, los monos aulladores pueden pasar entre el 64 y el 80% del día descansando, entre el 10.5 y el 23% alimentándose y entre el 9.5 y el 12% desplazándose (Rodríguez-Luna 1987).

Los monos araña

Los monos araña también pertenecen a la familia *Atelidae* (Rylands et al. 2000). Según el recuento taxonómico más actual (ITIS 2018, www.itis.gov) existen 7 especies y 8 subespecies de monos araña. *Ateles geoffroyi vellerosus* se distribuye en El Salvador, Honduras, Guatemala y México (Cuarón et al. 2003). En México, se encuentra en las selvas de Veracruz, Tabasco, Oaxaca y Chiapas (Rylands et al. 2005).

Ateles geoffroyi es una de las especies de primates más grandes del Nuevo Mundo. El peso corporal de la hembra adulta medio es de 8.3 kg y la del macho adulto de los 8.6 kg (Mittermeier et al. 2013). Su cuerpo es delgado, con brazos y piernas largos con cuatro dedos funcionales en las manos (Kellogg & Goldman 1944). El pelaje suele ser largo, la cabeza pequeña y el hocico prominente, con órbitas oculares hacia delante y fosas nasales hacia los lados separadas por un cojinete internasal (Vaughan 1988). No existe un dimorfismo sexual evidente aunque, de manera distintiva, las hembras poseen un clítoris largo en forma de péndulo, que podría ser utilizado para depositar orina y secreciones vaginales en las ramas para anunciar su presencia y estado reproductivo (Pastor-Nieto 2000).

Los monos araña tienen una organización social del tipo fisión-fusión, frecuentemente encontrándose en pequeños subgrupos de 1 a 4 individuos, pero que pueden tener hasta veinte o treinta individuos (Chapman 1990; Mittermeier et al. 2013). Los machos mayoritariamente se mueven en grupos de machos y las hembras lo hacen solas o con sus crías (Fedigan & Baxter 1984). Normalmente, las hembras migran a otros grupos y se mueven en áreas más pequeñas que los machos (Symington 1988). Los machos son más sociales, interactúan más y muestran más conductas agresivas que las hembras. Los monos araña tienen una dieta frugívora (Chapman et al. 1995; Campbell 2000). El ~70% de su dieta consiste en fruta pero también se alimentan de hojas, brotes y otras partes de la planta y ocasionalmente de hongos epífitos e incluso termitas y orugas (Cant 1990; Chapman et al. 1995; González-Zamora et al. 2009; Mittermeier et al. 2013). Su patrón de actividad depende de las características de la región, pero pueden dedicar el 38.4% de su tiempo a alimentarse, el 36.6% a descansar, y el 19.8% a desplazarse (González-Zamora et al. 2011).

Efectos de los cambios en el paisaje sobre *Alouatta* y *Ateles*

La mayoría de los estudios sobre el impacto del cambio de uso de suelo sobre los primates mexicanos, previos a esta tesis, se han realizado a escalas locales, y están enfocados en entender el efecto de las características de los fragmentos sobre una o varias variables de respuesta. A partir de los resultados de dichos trabajos, podemos predecir algunos posibles efectos de la estructura del paisaje sobre *Alouatta* y *Ateles*.

Se ha propuesto que la pérdida de hábitat o la reducción del tamaño del fragmento a escala local disminuye la disponibilidad de alimento para los primates (Arroyo-Rodríguez et al. 2017a). Esto puede provocar consecuencias negativas como la mayor competición inter- e intra-específica por los recursos o un aumento de la transmisión de enfermedades y parásitos, entre otros (Marsh & Chapman 2013). Con todo, esperamos que menores tamaños de fragmento sostengan una menor riqueza y abundancia de primates. Sin embargo, algunos estudios encuentran resultados opuestos (Harcourt & Doherty 2005). En monos aulladores (*A. palliata*, *A. pigra*, *A. seniculus* y *A. caraya*), se han encontrado mayores densidades poblacionales en más fragmentos pequeños y aislados que en zonas de bosque continuo (Arroyo-Rodríguez & Dias 2010). De hecho, los monos aulladores pueden utilizar estrategias para enfrentarse a los cambios en el paisaje, como son la adaptación de su dieta a las especies disponibles o reducir la actividad motora para gastar menos energía (Arroyo-Rodríguez & Dias 2010). Por ello, se ha propuesto que estas especies pueden ser más resistentes a los cambios en el paisaje, en especial a la disminución del tamaño del fragmento (e.g. Bicca-Marques 2003). Sin embargo, estos estudios no consideran la cantidad de hábitat en el paisaje que rodea a los fragmentos focales. De hecho, los monos aulladores pueden estar utilizando también los fragmentos de bosque vecinos u otras coberturas en la matriz para abastecer sus necesidades de hábitat (i.e. suplementación del paisaje; Dunning 1992). Por ejemplo, Zunino et al. (2007) observan cinco grupos de *A. caraya* utilizando diferentes fragmentos pequeños de bosque en el norte de Argentina para suplementar su dieta. Otros estudios han observado monos aulladores (*A. palliata*) habitando más de un fragmento en Los Tuxtas, México (Mandujano et al. 2006; Asensio et al. 2009). Por otro lado, se considera que los monos araña son más sensibles a la pérdida de hábitat que los monos aulladores, por su dieta más frugívora y sus mayores áreas de actividad. Sin embargo, varios estudios han reportado también a diferentes especies de *Ateles* utilizando coberturas antrópicas en el paisaje. Por ejemplo, Pérez-Elissetche (2015) encontró que *Ateles geoffroyi* utiliza la vegetación secundaria, campos de cultivo, cercas vivas y árboles aislados en la matriz para suplementar su hábitat en distintas regiones México, Costa Rica y El Salvador.

Por otro lado, todavía no está claro cómo afecta el aislamiento de los fragmentos a los primates dado que los estudios disponibles reportan efectos positivos, negativos y nulos (Harcourt & Doherty 2005; Arroyo-Rodríguez & Mandujano 2009). De hecho, el efecto del aislamiento del fragmento depende de muchos factores, incluyendo la cantidad de hábitat en el paisaje, la configuración espacial de las distintas coberturas en el paisaje y la habilidad de las especies para utilizar la matriz (Arroyo-Rodríguez et al. 2017a). Por ejemplo, Chaves & Stoner (2011) encontraron que los monos araña son capaces de cruzar ríos a nado para poder desplazarse a nuevos parches de hábitat en una selva alterada de México. Del mismo modo, varios estudios han reportado a monos aulladores caminando por el suelo para moverse a otros fragmentos de bosque (e.g. Pozo-Montuy & Serio-Silva 2007).

Por otro lado, los bordes de los fragmentos pueden afectar negativamente a algunas especies mientras que otras son más tolerantes y pueden incluso beneficiarse de ellos (Harcourt & Doherty 2005; Arroyo-Rodríguez & Dias 2010). En este sentido, algunos estudios han encontrado a monos araña alimentándose de la vegetación secundaria que crece en los bordes de los fragmentos (Ramos-Fernández & Ayala-Orozco 2003). Así, para estas especies, la vegetación secundaria joven que crece en los bordes de los fragmentos puede ofrecer recursos alimentarios como hojas tiernas y frutos (Lovejoy et al. 1986; Chiarello 2003). Sin embargo, aunque beneficiarse de los bordes de los fragmentos es una clara ventaja en paisajes alterados por el humano, de nuevo, los efectos de los bordes en los fragmentos dependen también de la composición y la configuración del paisaje. La mayoría de estos estudios, al no evaluar la estructura del paisaje que rodea al fragmento, no pueden ser generalizados a otros paisajes. Por ello, nuestro entendimiento sobre el impacto de la estructura de paisajes antrópicos sobre los primates mexicanos es alarmantemente escaso. Esta información es de urgente necesidad para validar modelos teóricos, resolver debates actuales (e.g. suplementación del paisaje, Dunning 1992; hipótesis de la seguridad del paisaje, Tscharntke et al. 2012; Countryside biogeography, Daily 1997) y proponer estrategias de conservación adecuadas (land sharing vs. land sparing, Phalan et al. 2011).

Objetivos de la tesis

El objetivo principal de esta tesis es evaluar la respuesta de los primates a los cambios en la estructura del paisaje. Para ello, se plantearon los siguientes objetivos específicos:

1. Revisar los estudios disponibles sobre las respuestas de los primates a los cambios en la estructura del paisaje (*Capítulo 2*).

2. Identificar el tamaño del paisaje más adecuado para evaluar el impacto de la estructura del paisaje sobre las especies de primates mexicanos (*Alouatta palliata*, *Alouatta pigra*, *Ateles geoffroyi*) en cuatro regiones del sureste de México (*Capítulo 3*).

3. Identificar los atributos del paisaje con mayor impacto sobre la abundancia relativa y la relación inmaduro/hembra de los monos araña (*Ateles geoffroyi*) en dos regiones del sureste de México (*Capítulo 4*).

4. Evaluar los efectos de la estructura del paisaje sobre la abundancia y la relación inmaduro/hembra de las dos especies de monos aulladores mexicanos (*Alouatta palliata* y *Alouatta pigra*) en cuatro regiones del suereste de México (*Capítulo 5*).

5. Evaluar el uso de las coberturas antrópicas por primates a nivel global e identificar los factores que predicen su uso (*Capítulos 6* y *7*).

Descripción de las regiones de estudio (*Capítulos 3*, *4* y *5*)

Marqués de Comillas, Chiapas: La región más conservada se encuentra en la selva Lacandona, municipio de Marqués de Comillas, estado de Chiapas (91º6’42.8”- 90º41’8.7W; 16º19’17.1” - 16º2’49.3N) (Fig. 2). La temperatura media anual es de 24ºC y la precipitación media anual es de 3,000 mm, con un periodo seco (<100 mm mensuales) de febrero a abril (van Breugel et al. 2006; Martínez-Ramos et al. 2009). La alteración antrópica de esta región empezó en la década de los años 70 del siglo XX (González-Ponciano 1996; de Vos 2002). El aumento de la inmigración y el fomento de políticas de redistribución poblacional y de colonización transformaron parte del paisaje natural en áreas de cultivo agrícola y ganadero (González-Ponciano 1996). Actualmente, la zona de estudio, comprendida entre los poblados Ixcán y Pico de Oro, conserva un 56% de bosque donde habitan el mono aullador negro y el mono araña.

Uxpanapa, Veracruz: El valle de Uxpanapa se sitúa al Sur del Estado de Veracruz, en la frontera con el estado de Oaxaca (94º50’6.809” - 94º24’30.216”W; 17º24’1.705” - 17º8’46.1”N) (Fig. 2). La temperatura media anual oscila entre los 24°C y 26°C, y las precipitaciones alcanzan valores mayores a los 3,000 mm anuales en las partes de mayor altitud (INEGI 2008). El inicio de los procesos de desarrollo económico, colonización e impactos en las selvas tropicales de esta región se inician en la década de 1950 (Hernández et al. 2013). Sin embargo, en 1970 la mayor parte de la región estaba cubierta por selvas y es entonces cuando se inicia el deterioro de sus selvas con la implementación de programas de colonización y reubicación de poblados (Vázquez 1979). La principal causa de deforestación es la ganadería, pero también la agricultura (principalmente plantaciones de hule, cítricos y mielina), actividades que todavía predominan en la región, dejando un 36% de bosque primario remanente (Chazaro 1986; Geist & Lambin 2001). En 1998 esta zona sufrió un intenso incendio, por lo que actualmente una gran parte de la cobertura vegetal es vegetación secundaria. En esta región habitan el mono aullador de manto y el mono araña.

Los Tuxtlas, Veracruz: La región de los Tuxtlas (95º03’00’’ - 98º38’00”W; 18º03’00” - 10º35’00’’N) (Fig. 2) fue decretada Reserva de la Biosfera en 1998. El clima predominante es cálido húmedo, con una precipitación media anual de 4,900 mm y con temperaturas medias de 22ºC. La deforestación en Los Tuxtlas empezó de manera intensiva entre los años 1960 y 1970, debido a la colonización, el reparto agrario y las prácticas ganaderas (von Bertrab 2010). Esta tesis se desarrolla en el volcán de San Martín Tuxtla, donde habita el mono aullador de manto y sólo el 25% de la superficie corresponde a vegetación nativa, con las coberturas dominantes de cultivos anuales y pastizales. Aunque el mono araña es nativo de esta región, en el volcán de San Martín Tuxtla está localmente extinto.

Región VIII Norte, Chiapas: La región más deforestada se sitúa en la planicie costera del Golfo de México, entre los municipios de Juárez y Reforma (93°18'20" - 93°08'00"W; 17°48'35" - 17°45'15"N) (Fig. 2). La temperatura media anual es de 25.4°C y la precipitación anual media es de 2,600 mm, con una temporada de lluvias que se extiende de mayo a diciembre (INEGI 1999). Esta región estuvo cubierta por selva tropical húmeda hasta finales de la década de 1940 (Miranda 1999). A partir de 1950 la ganadería, y en 1970 la explotación petrolera, transforman el paisaje natural dejando escasos fragmentos de selva inmersos en una matriz de pastizal (Anzures-Dadda & Manson 2007). La selva cubre aproximadamente el 10% de la superficie total donde habita el mono aullador de manto *A. palliata*. El mono araña fue nativo de esta región pero actualmente se encuentra extinto.

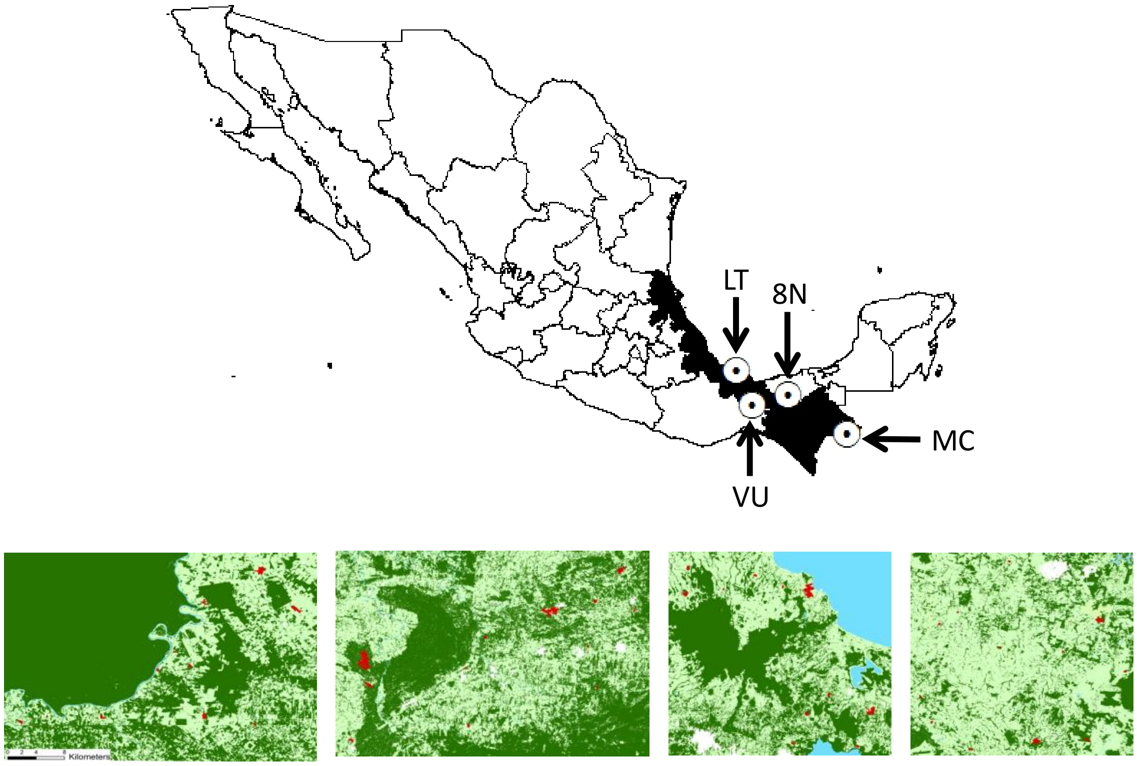

Figura 3. Localización de las zonas de estudio en México (a). Las figuras a color son las regiones donde se hizo la colecta de datos para los *Capítulos 3*, *4* y *5* de esta tesis: de izquierda a derecha, MC, Marqués de Comillas (Chiapas); VU, el valle de Uxpanapa (Veracruz); LT, la región de Los Tuxtlas (Veracruz); y 8N, la Región 8 Norte (Chiapas). En rojo se muestran los doce fragmentos seleccionados por región. Los polígonos verde

oscuro simbolizan el bosque, los verde claro las áreas abiertas, los azules los cuerpos de agua y los blancos los poblados.

Esquema de la tesis

Esta tesis consiste de 8 capítulos: la introducción (*Capítulo 1*), dos artículos de revisión (*Capítulo 2* y *6*), tres artículos basados en datos de campo (*Capítulos 3*-*5*), un artículo de datos (*Capítulo 7*), y la discusión general y conclusiones (*Capítulo 8*).

Aunque la mayoría de estudios que evalúan el efecto del cambio de uso de suelo sobre los primates se han realizado a escalas locales, cada vez más estudios están utilizando una perspectiva paisajística. El *Capítulo 2* analiza todos los estudios disponibles que evalúan el efecto de la estructura del paisaje sobre los primates. Este capítulo también discute los principales problemas asociados a este tipo de estudios y subraya algunas advertencias a la hora de realizar estudios con perspectiva paisajística. Todo ello es importante para poder alcanzar un entendimiento completo sobre la ecología y conservación de primates en paisajes modificados por el humano.

Aunque el número de estudios con perspectiva paisajística ha aumentado en los últimos años, la mayoría no evalúa la escala del efecto (Jackson & Fahrig 2012, 2015; *Capítulo 2*). Además, todavía no conocemos qué factores influyen la escala del efecto (Miguet et al. 2016). Por ello, en el *Capítulo 3* identifico la escala del efecto y evalúo cómo las especies, las respuestas biológicas, las variables del paisaje y el contexto regional influyen sobre la escala del efecto. Este tipo de estudios es fundamental para poder evaluar correctamente el efecto de los cambios en el paisaje sobre las especies.

En México, la deforestación en las últimas décadas ha resultado en la pérdida anual de 534,707 ha de superficie forestal entre 1976 y 2007 (Rosete-Vergés et al. 2014). Este proceso amenaza los primates, pero desconocemos qué variables de paisaje tienen un mayor impacto sobre estos mamíferos. Por tanto, la presente tesis también evalúa el efecto relativo de tres atributos de la estructura del paisaje sobre los monos araña (*Capítulo 4*) y los monos aulladores (*Capítulo 5*) en bosques tropicales mexicanos con diferente grado de perturbación. La información resultante de estos capítulos es fundamental para poder proponer estrategias adecuadas de conservación para los primates mexicanos.

Dado que los primates pueden utilizar otras coberturas antrópicas para desplazarse, refugiarse o alimentarse (Anderson et al. 2007a; Watling et al. 2011; Fahrig 2013), el *Capítulo 6* revisa el uso de las coberturas antrópicas por primates a nivel global, así como algunos factores que pueden ayudar a predecir dicho uso. Debido al rápido crecimiento de la población humana y la transformación del paisaje natural en paisajes modificados por el humano, este tipo de estudios es fundamental para evaluar la importancia de las coberturas antrópicas para los primates. A partir de la compilación de rasgos ecológicos de los primates del mundo realizada para el *Capítulo 6*, en el *Capítulo 7* presento una base de datos accesible y fácil de utilizar, y disponible públicamente. Esta base de datos puede ser utilizada en en estudios ecológicos y de conservación y puede ser utilizada para responder distintas preguntas de investigación a varias escalas espaciales. Finalmente, el último capítulo de la tesis (*Capítulo 8*) sintetiza los hallazgos de los capítulos anteriores y muestra las implicaciones teóricas y de conservación más relevantes de la tesis.

Capítulo 2

A global assessment of primates' responses to landscape structure

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Abstract

Land use change modifies the spatial structure of terrestrial landscapes, potentially shaping the distribution, abundance and diversity of remaining species assemblages. Non-human primates can be particularly vulnerable to landscape disturbances, but our understanding of this topic is far from complete. Here we reviewed all available studies on primates' responses to landscape structure. We found 34 studies of 71 primate species (24 genera and 10 families) that used a landscape approach. Most studies (82%) were from Neotropical forests, with howler monkeys being the most frequently studied taxon (56% of studies). All studies but one used a site-landscape or a patch-landscape study design, and frequently (34% of studies) measured landscape variables within a given radius from the edge of focal patches. Altogether, the 34 studies reported 188 responses to 17 landscape-scale metrics. However, the majority of the studies (62%) quantified landscape predictors within a single spatial scale, potentially missing significant primate-landscape responses. To accurately assess such responses, landscape metrics need to be measured at the optimal scale, i.e. the spatial extent at which the primate-landscape relationship is strongest (so-called 'scale of effect'). Only 21% of studies calculated the scale of effect through multiscale approaches. Interestingly, the vast majority of studies that do not assess the scale of effect mainly report null effects of landscape structure on primates, while most of the studies based on optimal scales find significant responses. These significant responses are primarily to landscape composition variables rather than landscape configuration variables. In particular, primates generally show positive responses to increasing forest cover, landscape quality indexes and matrix permeability. In contrast, primates show weak responses to landscape configuration. In addition, half of studies showing significant responses to landscape configuration metrics do not control for the effect of forest cover. As configuration metrics are often correlated with forest cover, this means that documented configuration effects may be simply driven by landscape-scale forest loss. Our findings suggest that forest loss (not fragmentation) is a major threat to primates, and thus, preventing deforestation (e.g. through creation of reserves) and increasing forest cover through restoration is critically needed to mitigate the impact of land use change on our closest relatives. Increasing matrix functionality can also be critical, for instance by promoting anthropogenic land covers that are similar to primates' habitat.

Key words: Habitat fragmentation, habitat loss, landscape heterogeneity, matrix composition, monkeys, multi-scale design.

I. INTRODUCTION

The advance of the agricultural frontier is rapidly converting natural ecosystems into human-modified landscapes. In recent decades, such conversion has been particularly noticeable in the tropics (Achard *et al.*, 2014; Taubert *et al.*, 2018), threatening the preservation of a large number of species (Newbold *et al.*, 2016). Yet, several factors have limited our understanding of the main drivers of species loss in human-modified landscapes. First, different species can show contrasting responses to habitat disturbance, making difficult to identify general patterns of response (Henle *et al.*, 2004). Furthermore, research has been focused primarily on a few local predictors, such as patch size (Prugh *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2013a; Haddad *et al.*, 2015) and distance to forest edges (Tuff, Tuff, & Davies, 2016; Pfeifer *et al.*, 2017). As species responses to local patterns cannot be extrapolated at the landscape scale (Fahrig *et al.*, 2018), this research bias toward local factors has limited our knowledge of the landscape-scale drivers of biological populations and assemblages. Finally, although the number of landscape studies has increased in the last decades, there are important methodological caveats in landscape research that can impair the accuracy and reliability of landscape-scale inferences (Fahrig, 2003; Arroyo-Rodríguez *et al*., 2013a). Therefore, additional studies with a landscape perspective (sensu Fahrig, 2005) are urgently needed, not only to accurately assess some important theoretical models on species' responses to landscape structure (Dunning, Danielson, & Pulliam, 1992; Tscharntke *et al.*, 2012; Villard & Metzger, 2014; Fahrig, 2017), but also for improving land planning practices for biodiversity conservation in human-modified landscapes. This knowledge is particularly urgent for strongly threatened taxa, such as primates (Estrada *et al.*, 2017).

Primates are of critical cultural and ecological importance and represent a key component of forest ecosystems (Estrada *et al.*, 2017). They are involved in numerous ecological processes, such as herbivory, seed dispersal, predation, and pest control (Stoner *et al.*, 2007; Mittermeier *et al.*, 2013; Estrada *et al.*, 2017; Andresen, Arroyo-Rodríguez, & Ramos-Robles, 2018). Most primate species are forest specialists, and hence, the rapid alteration of landscape structure caused by deforestation in tropical and subtropical regions (Taubert *et al.*, 2018) increasingly limits the distribution and abundance of primates in human-modified landscapes. This can have negative consequences for plant diversity (Stevenson & Aldana, 2008) and forest regeneration (Russo & Chapman, 2011; Marsh & Chapman, 2013; Andresen *et al.*, 2018). In fact, ~60% of the world's 504 primate species are threatened with extinction (Estrada *et al.*, 2017). Therefore, assessing the impact of landscape structure on primates is critical to improve conservation strategies, not only for primates, but also for the ecological processes in which they are involved.

Decades of research on primates' responses to habitat disturbance have been mainly focused on assessing the effects of forest patch size and isolation (Arroyo-Rodríguez *et al.*, 2013a). This bias is probably related to the deep influence of the island biogeography theory and metapopulation theory in fragmentation research (Haila, 2002). However, patch size and isolation are ambiguous predictors of landscape effects, as different landscape-scale processes (e.g. forest loss and fragmentation) can result in smaller and more isolated forest patches (Fahrig, 2003, 2013; Fahrig *et al*., 2018). Also, patch size and isolation effects may depend on matrix composition (Harcourt & Doherty, 2005; Prugh *et al.*, 2008). This ambiguity of the meaning of patch size and isolation as indicators of landscape pattern effects may help to explain why patch size and isolation are poor predictors of patch occupancy for many vertebrate species (Prugh *et al.*, 2008), including several primate species (Kowalewski & Zunino, 1999; DeGama-Blanchet & Fedigan, 2006; Benchimol & Peres, 2014).

In this sense, novel theoretical models challenge the patch paradigm, and highlight the key role played by landscape composition and configuration in moderating ecological patterns and processes (e.g. Tschartke *et al*., 2012; Fahrig, 2013; Mendenhall, Kappel & Ehrlich, 2013; Arroyo-Rodríguez *et al*., 2017). Such a role is related to the fact that habitat patches are open systems; that is, patch edges do not represent real barriers to animal movements, and hence, rather than being driven by the characteristics of single habitat patches, plant and animal assemblages usually depend on the environmental conditions present in the local landscape surrounding habitat patches (Dunning *et al*., 1992; Benton *et al*., 2002; Fahrig, 2013). In fact, the home range of primates (Arroyo-Rodríguez & Mandujano, 2009; Boyle *et al*., 2013; Estrada, Raboy & Oliveira, 2012; Almeida-Rocha *et al*., 2017) and other animals (Mendenhall *et al*., 2013; Ferreira *et al*., 2018) can be composed of several habitat patches and different land cover types (e.g. agricultural lands) and landscape elements (e.g. living fences, isolated trees), which can bring complementary and supplementary resources (Dunning *et al*., 1992). Thus, to better understand the distribution and abundance of species in these increasingly common landscapes, we need to assess primate responses to landscape-scale patterns.

The number of studies of primates that use a landscape perspective has increased in the last decade, but they also show contrasting results. For instance, the few studies that test the effect of forest fragmentation *per se* (i.e. controling the effect of forest cover; sensu Fahrig, 2003) on primates demonstrate that fragmentation can have either positive (Arroyo-Rodríguez *et al.*, 2013b), negative (Thornton, Branch, & Sunquist, 2011), or null (Ordóñez-Gómez *et al.*, 2015) effects, with different species showing contrasting responses to this variable (Thornton *et al.*, 2011). Similarly, some studies show null responses to landscape forest cover (Anzures-Dadda & Manson, 2007; Urquiza-Haas, Peres, & Dolman, 2011; Benchimol & Venticinque, 2014), whereas others demonstrate positive effects of this landscape predictor on other primate species (Blanco & Waltert, 2013; Piel *et al.*, 2015). These apparently idiosyncratic responses to landscape structure can be related to differences among primate species in ecological traits, such as diet and home range size (Boyle & Smith 2010). Nevertheless, such contrasting responses are not always explained by ecological traits (e.g. Onderdonk & Chapman, 2000), and can rather been related to differences in study designs, which can result in contradictions and results that are difficult to interpret (Fahrig, 2003; Arroyo-Rodríguez & Mandujano, 2009).

Here, we provide the first global assessment of primates' responses to landscape structure. To do this, we first discuss some important concerns with study designs to identify some potential shortfalls in primate studies on the topic. We then offer an updated summary of the literature and review all empirical evidence available to date. We describe the geographical distribution of studies and the study taxa, and assess the study designs commonly used in primate research. We finally evaluate the effect (positive or negative) of each predictor variable, separately assessing variables related to landscape composition and landscape configuration. As forest cover (i.e. a compositional variable) is usually significantly correlated with landscape configuration variables, when assessing the effect of configuration variables we separately assess the cases in which forest cover was controlled *vs.* not controlled, as the latter case may lead to ambiguous responses to landscape configuration (Fahrig, 2003).

II. CONCERNS IN LANDSCAPE STUDIES

The 'landscape perspective' and its importance in ecology and conservation has been discussed elsewhere (Fahrig, 2005), especially for the case of primate research (Arroyo-Rodríguez & Fahrig, 2014); yet, a brief overview is given here. In ecology, studies with a landscape perspective are those that asses ecological responses to landscape structure. As stated above, such a perspective is important because primates can travel in and out of the habitat patches, and thus, they can be more strongly affected by the structure of the surrounding landscape than by the spatial configuration of individual patches. Landscape structure (or heterogeneity) is defined by its spatial composition and configuration. The former refers to the types and proportions of different land covers in the landscape, such as the percentage of forest cover or the number of land cover types (Dunning *et al.*, 1992; McGarigal & Cushman, 2002). The latter describes the spatial arrangement of each land cover, such as the number of forest patches, mean patch size, or forest edge density (Dunning *et al.*, 1992; McGarigal & Cushman, 2002). Understanding the relative (independent) and interacting effect of these landscape attributes on species is an important challenge in ecology (Fahrig, 2005; Arroyo-Rodríguez & Fahrig, 2014). In this sense, we summarize below some methodological concerns that need to be considered to face such a challenge.

(1) Study design

The first and probably most important concern in studies with a landscape perspective is that the independent units of observation and analysis should be the landscapes, not the patches. Studies that measure both the ecological response (e.g. species abundance) and predictor variable (e.g. patch size) in independent habitat patches are called patch-scale studies (Fig. 1a), and should not be used to make landscape-scale inferences (Fahrig, 2003; Fahrig *et al.*, 2018). To make accurate landscape-scale inferences both the ecological response(s) and predictor variable(s) need to be measured in independent landscapes (Fig. 1b). To this end, we can use three different study designs depending on how response variables are measured, and thus on the research questions (Brennan *et al.*, 2002; McGarigal & Cushman, 2002; Arroyo-Rodríguez & Fahrig, 2014): (i) site-landscape (Fig. 1c); (ii) patch-landscape (Fig. 1d); and (iii) landscape-scale designs (Fig. 1e). Site- and patch-landscape studies measure response variables in equal-sized sample sites (e.g. transects) or habitat patches, respectively, and predictor variables (landscape attributes) are measured within a specified radius from each focal site or patch (McGarigal & Cushman, 2002), i.e. in the surrounding landscape. In landscape-scale studies, response variables are measured in several sample sites within the landscape, and a single data point for analysis corresponds to the combined response data from all sample sites within the landscape, along with the landscape composition/configuration predictor variable of that landscape (Brennan *et al.*, 2002).

Site- and patch-landscape study designs are useful to evaluate the effects of landscape context on an ecological response and are particularly recommended to assess mobile organisms such as primates (Arroyo-Rodríguez & Fahrig, 2014). Also, as the response variables are measured in focal sites/patches located in the center of study landscapes, the cost (time and money) of these study designs can be similar to patch-scale studies (Brennan *et al.*, 2002). Another advantage of these designs is that they allow one to assess the scale of effect (Jackson & Fahrig, 2012) – an important step to accurately evaluate the influences of landscape context on the ecological response of interest (see below). Landscape-scale studies, on the other hand, are particularly useful to assess ecological processes such as metapopulation dynamics and species turnover across space (Arroyo-Rodríguez & Fahrig, 2014). Note that multiple landscapes are still needed here, to answer questions about the effects of landscape structure on metapopulation dynamics or species turnover. In any case, special care should be taken when selecting the focal sample sites/patches in landscape-scale studies, because if they are located near the edge of the study landscape, they can be strongly affected by the larger landscape context outside the study landscape (Andresen *et al.*, 2018; Fig. 1e).

Figure 1 about here

(2) Constant landscape size and shape

In site- and patch-landscape study designs, the distance within which landscape variables are measured should be measured from the center of each focal site/patch (Fig. 1) and not from their patch edges (Arroyo-Rodríguez, Galán-Acedo, & Fahrig, 2017). In the latter case, different sample landscapes would have different sizes and shapes depending on the sizes and shapes of focal patches. This could lead to a confounding of landscape structure effects with landscape size and shape effects.

(3) Spatial overlap

As discussed above, a landscape approach implies that both response variables and their potential predictors are measured in independent sample landscapes. Such independence implies that the value of a variable in a given landscape does not affect the value of this same variable in other landscapes. In this sense, independence between landscapes can be violated when landscapes overlap in space at the relevant spatial extent, i.e. at the scale of effect (Eigenbrod, Hecnar, & Fahrig, 2011). The effects of such lack of independence are not well studied. There is evidence that it can decrease parameter estimates in regression models (Eigenbrod *et al.*, 2011; Jackson & Fahrig, 2012), although other studies do not find significant effects on statistical models (Zuckerberg *et al.*, 2012). In any case, to prevent potential confounding effects of overlapping landscapes on study findings, we suggest selecting sample sites that are sufficiently separated to avoid spatial overlap at the likely scale of effect, to increase the likelihood of spatial independence.

(4) Scale of effect

Species-landscape relationships depend on the spatial extent (i.e., landscape size) within which landscape variables are measured (Jackson & Fahrig, 2015; Miguet *et al.*, 2016; Martin, 2018), and this has specifically been shown in primate research (e.g. Ordóñez-Gómez *et al.*, 2015; Galán-Acedo *et al.*, 2018). Significant species-landscape relationships may be undetected if the landscape variables are measured at the incorrect scale (Fahrig, 2013; Jackson & Fahrig, 2015). Therefore, landscape studies should measure landscape variables across several spatial extents (i.e. within different-sized radii) to identify the scale(s) that yield the strongest response-landscape relationship (so-called 'scale of effect', Jackson & Fahrig, 2012). It is important to note, however, that the scale of effect usually differ among response variables (e.g. patch occupancy, species abundance, diet), as each response is related to drivers acting across different spatio-temporal scales (Thogmartin & Knutson, 2007; Bradter *et al.*, 2012; Miguet *et al.*, 2016; Martin, 2018). Thus, in practice, a multiscale approach is needed to assess the effect of each landscape variable on each ecological response. This is not trivial, as measuring landscape variables at the incorrect scale can decrease the variance explained by the models and other statistical caveats that can lead to wrong interpretations of results (de Knegt *et al.*, 2010). To accurately assess the scale of effect, the range of spatial extents tested should be selected based on species traits (e.g. vagility, home range size), because the scale of effect is thought to be a function of such species traits (Jackson & Fahrig, 2012; Miguet *et al.*, 2016). Furthermore, it is crucial to choose a wide range of scales, both smaller than and larger than the scale thought likely to contain the true scale(s) of effect (Jackson & Fahrig, 2015). When the range of scales is too narrow, studies can find that the optimal scale is the smallest or the largest scale evaluated, which suggest that the correct scale of effect is outside the selected range (Jackson & Fahrig, 2015).

(5) Confounding variables

Another important concern in landscape studies is that landscape variables can be significantly inter-correlated. In particular, forest cover (i.e. a proxy of habitat amount for forest-dependent species such as most primates) is strongly related to several landscape configuration variables (e.g. mean inter-patch distance, mean patch size, edge density, and number/density of forest patches; Fahrig, 2003; Villard & Metzger, 2014).

Studies on the effect of landscape configuration variables that do not control for the effect of forest cover may lead to ambiguous responses to landscape configuration (Fahrig, 2003, 2017). Therefore, to accurately assess the effect of landscape configuration, the effect of forest cover needs to be controlled. This is particularly important when assessing the effect of forest fragmentation on biodiversity. As the breaking apart of forest (i.e. fragmentation) is followed by forest loss, the effect of fragmentation needs to be measured independently from the effect of forest loss (i.e. so-called ‘fragmentation *per se*’; Fahrig, 2017). Such control can be done by selecting landscapes with similar forest cover but different configuration or by including forest cover as a covariate within multiple regression analyses (Fahrig, 2017). Note that, in principle, when assessing the effects of composition variables such as forest amount, we should control for correlated configuration variables. However, studies that include both composition and configuration variables generally find that composition is more important than configuration (Fahrig, 2003). This means that we are more likely to misinterpret a configuration effect when composition has not been controlled for, than the reverse. Keeping all these issues in mind, below we review the available literature on primates to assess what we know so far.

III. METHODS

(1) Literature search

We systematically reviewed all available articles on primates’ responses to changes in landscape structure. To this end, we carried out a search in the SCOPUS (www.scopus.com) and Google Scholar (https:// scholar.google.com/) databases on 21 July 2018 for research articles containing the following search terms in all reference topics: [(primate* OR monk*) AND (“radius” AND/OR “radii” AND/OR “forest cover” AND/OR “buffer” AND/OR “multiscale” AND/OR “landscape” AND/OR “multi-scale” AND/OR “landscape metric*” AND/OR “landscape variable*” AND/OR “landscape scale” AND/OR “percentage” AND/OR “forest” AND/OR “percentage of forest” AND/OR “landscape heterogeneity” AND/OR “landscape predictors” AND/OR “landscape structure”)]. We limited our review to studies that explicitly assessed the response of primates to landscape composition and/or configuration variables, excluding “grey literature”. We also excluded studies on biophysical variables, such as elevation, terrain aspect, and soil properties.

(2) Data extraction

From each article, we recorded the species' name, genus and the country where the study was conducted – which we classified in four main regions (Asia, Madagascar, Mainland Africa and Neotropics) following Estrada *et al.* (2017). We also recorded the study design considering the three major designs described above: site-landscape, patch-landscape or landscape-scale designs (Arroyo-Rodríguez & Fahrig, 2014). Regarding the spatial scale, we recorded the number of scales (buffers) included in the study, and whether the study estimated or not the scale of landscape effect. When the scale of effect was evaluated, we recorded whether the reported scale of effect was equal to the smallest or to the largest scale evaluated and we also recorded the scale range (i.e. largest scale divided by the smallest scale). To assess whether the scales were arbitrarily selected, we also recorded whether the authors offered a biological explanation for the selected scales. Finally, we recorded whether studies avoided spatial overlap between study landscapes, and thus, potential spatial dependence (i.e. pseudoreplication; Eigenbrod *et al.*, 2011).

We classified landscape variables into compositional and configurational metrics (Table 1) following McGarigal & Cushman (2002). Response variables included: abundance-related variables (i.e. encounter rate, total/mean abundance, and total/mean density), species composition, number of crossing roads, diet diversity, feeding time, resting time, travelling time, species richness, species diversity (Simpson), functional diversity, total biomass, immature-to-female ratio, number of males/females/juveniles, sex ratio, infant survival rate, group size, lambda growth rate, occurrence-related variables (e.g. presence/absence), frequency of dispersal events, and hunting pressure (usually measured through interviews). We then synthesized the results, recording if there was a significant effect or not, and the direction of significant effects (positive or negative). We did not carry out a formal meta-analysis because we are not attempting to estimate the overall effect size of each landscape variable on each response, but only summarize the number (and direction) of significant effects documented so far.

IV. RESULTS AND DISCUSSION

(1) Distribution of landscape studies

We found 34 studies of 71 primate species (24 genera and 10 families) that used a landscape perspective (Fig. 2; Table S1). Studies were distributed worldwide, but most studies (82%) were carried out in the Neotropics (Fig. 2). The most studied genera were

Alouatta (56% of studies), followed by *Callicebus* and *Ateles* (both assessed in 35% of studies), and *Sapajus* (26%), all Neotropical primates. Thus, our findings indicate that there is an important gap in research, especially regarding Asian and African primates. Filling this gap of information is urgently needed given the rapid loss and fragmentation of Paleotropical forests (Taubert *et al.*, 2018), and the threats facing primates from this geographic realm (Estrada *et al.*, 2017).

Figure 2 about here

(2) Potential methodological caveats

The vast majority of studies used either a site-landscape design (18 studies, 53% of studies) or a patch-landscape design (14 studies, 41%) (Fig. 3). One study was a review that included studies with site-landscape and patch-landscape designs (Benchimol & Peres, 2014), and only one study used a landscape-scale design (Prist, Michalski, & Metzger, 2012). Eleven of 32 site- or patch-landscape studies (34%) measured landscape variables within radii taken from the edge of focal patches, and not from the center of the site/patch where the response variables were measured. This suggests that landscape structure effects could be confounded with landscape size and/or landscape shape effects in these studies (Arroyo-Rodríguez *et al.*, 2017), although the consequences of such potential confounding effects are unclear, and need to be assessed in future studies.

Landscapes overlapped in space in 8 of 34 studies, suggesting that almost a quarter of studies may have violated the assumption of independence between replicate landscapes, and that the true parameters (slopes) may be different from those estimated in these studies (Eigenbrod *et al.*, 2011). Worryingly, fourteen studies (38%) did not show information on spatial overlap between study landscapes, suggesting that pseudoreplication problems in landscape studies of primates may be higher than recorded here. However, as stated above, the effect of such a pseudoreplication problem on statistical models is not well understood (Zuckerberg *et al.*, 2012), so this topic represents another interesting avenue for future research.

Regarding the scale of analysis, more than half of studies (21 of 34) measured landscape predictors within only a single spatial extent, two studies (6%) considered two different-sized scales, and only 11 studies (32%) included three or more scales (Fig. 3). This is alarming, as an increasing number of studies demonstrate that if landscape variables are not measured at the optimal scale, species responses to landscape predictors can be poorly estimated or missed altogether, potentially leading to erroneous conclusions about the effects of landscape structure on species (Holland, Fahrig, & Cappuccino, 2005; de Knegt *et al*., 2010; Jackson & Fahrig, 2012; Miguet *et al.*, 2016; Galán-Acedo *et al*., 2018; Gestich *et al.*, 2018).

Figure 3 about here

In this sense, 4 of 11 multi-scale studies (36%) did not test the scale of effect, but measured landscape variables across several scales to select the scale that prevented strong correlations between predictor variables (Benchimol & Peres, 2015), or simply for descriptive purposes (Pyritz *et al.*, 2010). Only seven studies (21%) provided information on the scales of landscape effects for 19 primate species. Yet, approximately half of the studies that assessed the scale of effect reported scales of effect equal to the smallest or to the largest scale, thus suggesting that the actual scales of effect were outside the range of scales tested (Jackson & Fahrig, 2015). This can be related to at least two factors: (i) the small range of scales included in the analysis; and (ii) the lack of a biological/ecological justification when selecting the range of scales (Jackson & Fahrig, 2015). In agreement with this idea, most studies that tested the scale of effect (5 of 7 multi-scale studies, 71%) used scale ranges ≤ 6, and only one study used a scale range > 10, i.e. greater than one order of magnitude (Fig. 3). In addition, only 2 of the 7 multi-scale studies (29%) offered a biological explanation for the selected scales; these were the home range requirements and dispersal distances of the study species (Ordóñez-Gómez *et al.*, 2015; Carretero-Pinzón *et al.*, 2017).

Those studies that assessed the scale of effect reported scales ranging from 0.39-km (Ordóñez-Gómez *et al*., 2015) to 5.5-km radius (Rabelo *et al*., 2017). The cause of such differences remains poorly understood, but following previous studies (e.g. Jackson & Fahrig, 2012; Miguet *et al.*, 2016) it is probably related to the huge differences in ranging behaviors and foraging-area requirements among species (e.g. home range size varies from 0.1 to > 5,000 ha; Mittermeier et al., 2013). Studies of primates also suggest that the scale of effect differs among landscape predictors, with forest cover showing larger (Gestich *et al*., 2018) or smaller (Galán-Acedo *et al.*, 2018) scale of effect, depending on the response variable and regional context. This is not surprising, as theoretical models suggest that the response variable and regional context can also drive the scale of effect (Miguet *et al.*, 2016). Thus, in practice, studies on landscape effects on primates need to use a multi-scale approach to ensure that landscape–species associations are correctly evaluated (Jackson & Fahrig, 2015).

(3) Primate responses to landscape structure

In total, the 34 studies reported 188 individual effects to 17 landscape metrics (Table 1; Supporting information Table S1). From these, 121 (64%) effects were responses to landscape composition and 39 (21%) to landscape configuration *per se* (i.e. after controlling for the effect of forest cover). We found 28 (15%) additional responses to landscape configuration, but as they come from studies that do not control for forest cover effects, we classified these effects as ambiguous responses to landscape configuration (see below). This is of key relevance as the same landscape alteration (e.g. the conversion of natural habitat to an agricultural field) may affect different composition and configuration variables (e.g. the percentage of forest and isolation) therefore confounding its effects (Fahrig *et al.*, 2011). Although 23 of 34 studies (68%) reported at least one significant effect of landscape composition or configuration on primates, null responses were most common (135 of 188 responses, 72%). This does not necessarily indicate that landscape structure has weak effects on primates, as the methodological problems indicated above may have reduced the likelihood of studies finding significant effects. For example, the percentage of significant responses to landscape compositional variables was 3.3 times higher in those studies that considered the scale of effect (69% of responses) than in those that did not consider the scale of effect (21%) (Fig. 4A). This highlights the importance of assessing the scale(s) of landscape effect on primate studies.

a. Effect of landscape composition

Only 38 of 121 responses (31%) to landscape composition were significant (Fig. 4A), probably because most studies do not assess the scale of effect (Fahrig, 2003; Arroyo-Rodríguez *et al.*, 2016). Yet, significant responses to landscape forest cover were mostly positive (69% of significant responses), including a higher probability of habitat occupancy, more individuals and species, or more time spent travelling and feeding in landscapes with more forest cover (Fig. 4B). This is not surprising, as habitat amount in a landscape is expected to be positively related to resource availability and landscape connectivity (Fahrig, 2003, 2013), potentially reducing inter and intraspecific competition and physiological stress (Arroyo-Rodríguez & Dias, 2010; Carretero-Pinzón, 2013).

Land cover richness was negatively related to primate species richness in one study (Fig. 4C), probably because, as suggested by the authors of this study, this landscape metric can lead to increasing human-primate conflicts (Adila *et al.*, 2017). Yet, different land covers in the landscape can provide complementary and supplementary resources for primates (Dunning *et al.*, 1992; Watling *et al.*, 2011; Tscharntke *et al.*, 2012; Ferreira *et al.*, 2018), thus explaining why when considering the suitability of different land covers to primates, all studies report positive responses to increasing landscape and matrix quality (Fig. 4D-E). Therefore, some primate species can benefit from moving and/or feeding in some anthropic land covers, especially in those that are more similar to the original habitat of primates (Anderson, Rowcliffe, & Cowlishaw, 2007; Watling *et al.*, 2011; Blanco & Waltert, 2013). The potential role of the agricultural covers for primates' persistence in anthropic landscapes suggests that it is needed a more holistic point of view of the landscape. In fact, several studies and theoretical approaches point out that a high heterogeneity may be the key to restoring and sustaining biodiversity in anthropic landscapes (Dunning *et al.*, 1992; Benton, Vickery, & Wilson, 2003; Tscharntke et *al.*, 2012).

Figure 4 and figure 5 about here

b. Effects of landscape configuration on primates

Regarding the effect of landscape configuration variables, we found a higher number of responses (39 responses) from studies that control for forest cover effect (Fig. 5A) than from studies that do not control such effect (28 responses, Fig. 5B). The latter group of responses can be considered ambiguous responses to configuration because landscape configuration variables are frequently correlated to forest cover (Fahrig, 2003, 2013), an thus, we suggest caution with interpretation of these results.

Considering only studies on landscape configuration *per se*, most responses (32 of 39) were not significant (Table 1; Fig. 5A). Yet, in concordance with Fahrig (2017), we found that most (3 of 4, 75%) responses to habitat fragmentation *per se* are positive (Fig. 5C). In particular, the presence and abundance of primates usually increases with increasing of the number/density of habitat patches in the landscape. This is not surprising because fragmentation *per se* decreases mean inter-patch isolation distances, and favors landscape complementation and supplementation dynamics, thus increasing resource availability for forest-dwelling species at the landscape scale (Dunning *et al.*, 1992; Fahrig, 2017). The negative effect of fragmentation can be due to an increase of roads and human presence in landscapes with more patches, leading to a higher mortality and a lower primate' occurrence (Fahrig, 2017). Supporting the importance of patch isolation for primates, one study shows that mean inter-patch distance is negatively related to population size of black howler monkeys, but positively related to population density (Arroyo-Rodríguez *et al.*, 2013b; Fig. 5E), and another study indicates that the number of vegetation corridors in the landscape is positively related to the abundance of mantled howler monkeys (Anzures-Dadda & Manson, 2007, Fig. 5D). Therefore, as most primates (84%) are canopy-dependent species, arboreal landscape elements such as corridors or arboreal crops play a key role on primates persistence in agricultural landscapes providing connectivity but also food resources and shelter (Asensio *et al.*, 2009; Tscharntke et *al.*, 2012).

V. CONCLUSIONS

1. We found a significant geographical and taxonomic bias in landscape studies of primates, which are mainly focused on Neotropical forests, and especially on the genus *Alouatta*. Therefore, our understanding of the effect of landscape structure on Asian and African primates remains extremely poor.
2. Despite this gap of information, we found an increasing number of studies on the impact of landscape structure on primates, with important theoretical and conservation implications. Nevertheless, we first need to consider some limitations in study designs, which can make interpretation of the available evidence difficult.
3. Of particular concern is the fact that the majority of the studies quantified landscape predictors within a single spatial scale, potentially missing significant primate-landscape responses. To accurately assess such responses, landscape metrics need to be measured at the optimal scale, i.e. the spatial extent at which the primate-landscape relationship is strongest (so-called 'scale of effect'). Only 21% of studies calculated the scale of effect using multiscale approaches. This may explain the large number of null responses to landscape structure, as the vast majority of studies that do not assess the scale of effect report mainly null effects of landscape structure, while most studies that optimized the scale found significant responses.
4. Significant responses to landscape structure were primarily to landscape composition variables rather than landscape configuration variables. In particular, primates generally show positive responses to increasing forest cover, landscape quality indexes and matrix permeability, whereas responses to landscape configuration were

generally weak. This is consistent with evidence from other studies (Fahrig, 2003, 2017; Garmendia *et al.*, 2013; Carrara *et al.*, 2015), and suggests that forest loss (not fragmentation) is an important threat to primates.

5. Unfortunately, half of studies showing significant responses to landscape configuration metrics did not control for the effect of forest cover. As landscape configuration variables are usually strongly correlated to forest cover (Fahrig, 2003, 2013), such impacts may be simply driven by landscape-scale forest loss. Therefore, additional studies on the effect of landscape configuration *per se* are needed to better understand the effect of these variables on primates. This represents another important gap of information that need to be filled in future research.
6. Although weaker, the impact of landscape configuration *per se* on primates should not be overlooked. For example, the efect of forest fragmentation is mostly positive, thus highlighting the very high conservation value of small habitat patches for primates in human-modified landscapes (Fahrig, 2017). Small patches can not only provide important complementary and supplementary resources for primates (Asensio *et al*., 2009; Pozo-Montuy *et al*., 2013), but they can also decrease inter-patch isolation distances, thus preventing the negative impact of habitat isolation that we found in the present review.
7. Although additional efforts need to be done to accurately assess primate's responses to landscape structure, the available findings can be used to guide conservation strategies in human-modified landscapes. First, the maintenance of native habitats for primates (e.g. through creation of reserves) and increasing habitat amount through restoration should be considered priorities in the conservation agenda for primates. Second, such conservation and restoration programs should not give a lower value to small habitat patches, as these patches can actually have a higher conservation value than the same area in a larger patch. Third, complementing this with other land-management strategies to improve overall landscape quality is also of paramount relevance. This includes matrix enrichment with food plant species and creation of wooded corridors. Finally, environmental education programs can also be critical to reduce harmful activities in the matrix (e.g. killing or hunting primates in anthropic land covers). Taken together, these management strategies can help to mitigate the negative impacts of land use change on our closest relatives.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Studies of primates’ responses to changes in landscape structure.

Figure legends

Fig. 1. Patch and landscape approaches in ecological studies. In patch-scale studies, both ecological responses and predictor variables are measured in different (and independent) focal patches distributed across the study region. Studies with a landscape approach are those that assess the effect of landscape variables on ecological responses. The responses can be measured in three ways: within equal-sized sample sites at the centre of each landscape (i.e. site-landscape design), within focal patches at the centre of each landscape (i.e. patch-landscape studies) or within several sample sites or patches across the landscape (i.e. landscape scale design). In site- and patch-landscape designs,

landscape variables are measured within a specified radius from the centre of the sites/patches. In all cases, multiple landscapes need to be sampled in order to ask questions about the influence of landscape structure on an ecological response. Note that in landscape-scale studies, the sites or patches located near the edge of the landscape can be affected by the landscape context beyond the bounds of the sample landscape. For simplicity of illustration, habitat patches (green polygons) are embedded in a homogeneous (white areas) anthropogenic matrix (modified from Arroyo-Rodríguez & Fahrig, 2014; Andresen *et al.*, 2018).

Fig. 2. Global distribution of primate studies with a landscape approach (diamonds) (A). Pink vs. orange diamonds refer to studies that assess or not the scale of landscape effect on primates, respectively. Primate species richness is represented in blue colors (based on Pimm *et al.*, 2014). The proportion and absolute number (above each column) of individual effects tested per geographic region is also indicated (B).

Fig. 3. Designs of published primate studies that use a landscape approach (n = 34 studies). The proportion (represented by the size of black vertical lines) of studies with different study designs is indicated, as is the type of buffer used to determine the extents of the replicate landscapes (site- and patch-landscape study designs only), the presence/absence of spatial overlap between landscapes, the number of scales within which landscape variables were measured, the cases in which the scale of effect (SE) was tested, and the range of scales tested. The latter was measured as the largest scale divided by the smallest scale. ‘Site and patch’ in the first column refers to a review that used both site-landscape and patch-landscape study designs. NI = no information available, which includes studies that do not specify the buffer type and one landscape-scale study where this information is not applicable.

Fig. 4. Proportions (and numbers in bars) of positive, negative and null responses (n = 121 responses from 33 studies) of primates to landscape composition variables (defined in Table 1), separately assessing studies that evaluated or did not evaluate the scale of landscape effect (SE) (A). The proportion of positive and negative significant responses is also indicated, separately showing the impact of forest cover (B), land cover richness (C), landscape quality indexes (D) and matrix permeability (E) and matrix cover (F).

Fig. 5. Proportions (and number in boxes) of positive, negative and null responses (n = 39 responses from 9 studies) of primates to landscape configuration. We separately assess studies that assess or not the scale of effect (SE). Responses from studies that

control (A) or not (B) the effect of forest cover are indicated, because the latter case may lead to ambiguous responses to landscape configuration (Fahrig 2003). Considering only the studies that assess the effect of configuration variables *per se* (A), we indicate primate responses to habitat fragmentation (C), corridor abundance (D) and mean inter-patch distance (E).

Figure 1

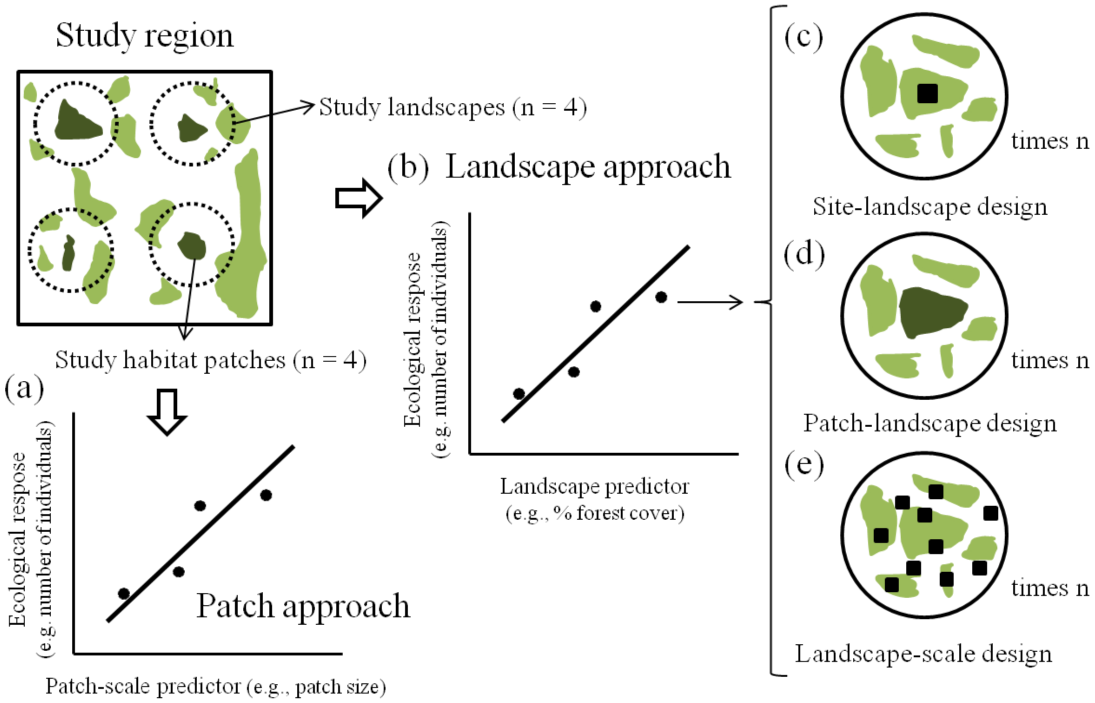
Study region
Study landscapes (n = 4)
Study habitat patches (n = 4)
(a)
Ecological respose (e.g. number of individuals)
Patch approach
Patch-scale predictor (e.g., patch size)
(b) Landscape approach
Ecological respose (e.g. number of individuals)
Landscape predictor (e.g., % forest cover)
(c)
times n
Site-landscape design
(d)
times n
Patch-landscape design
(e)
times n
Landscape-scale design

Figure 2

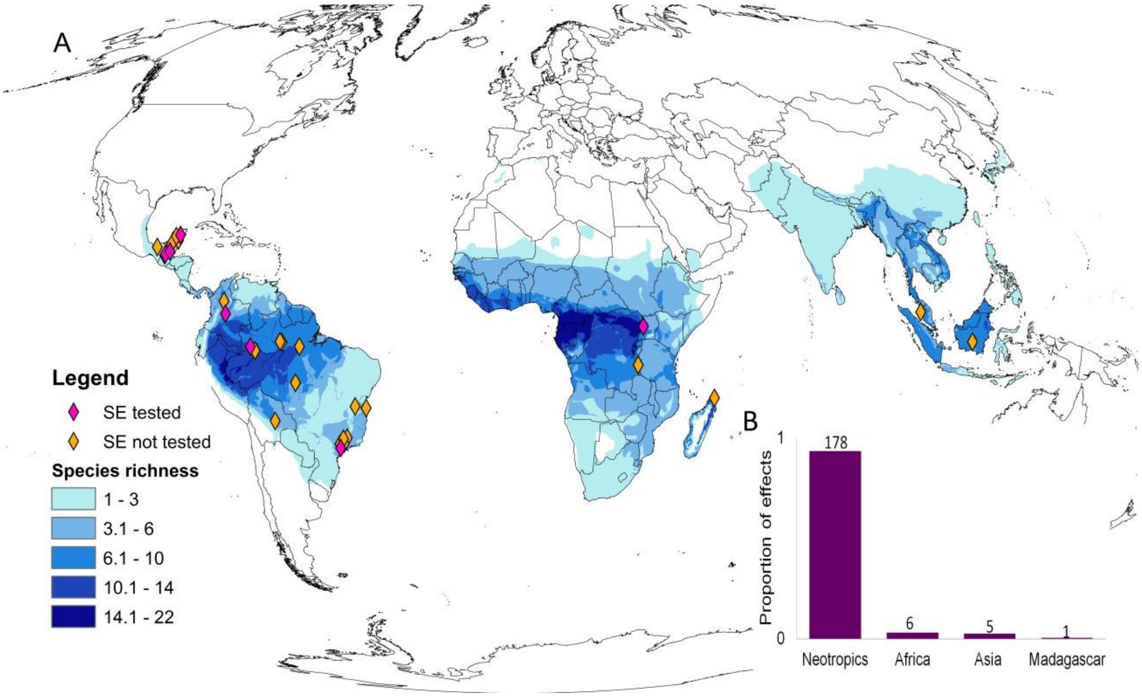
A
Legend
SE tested
SE not tested
Species richness
1 - 3
3.1 - 6
6.1 - 10
10.1 - 14
14.1 - 22
B
Proportion of effects
1
0
178
6
5
1
Neotropics
Africa
Asia
Madagascar

Figure 3

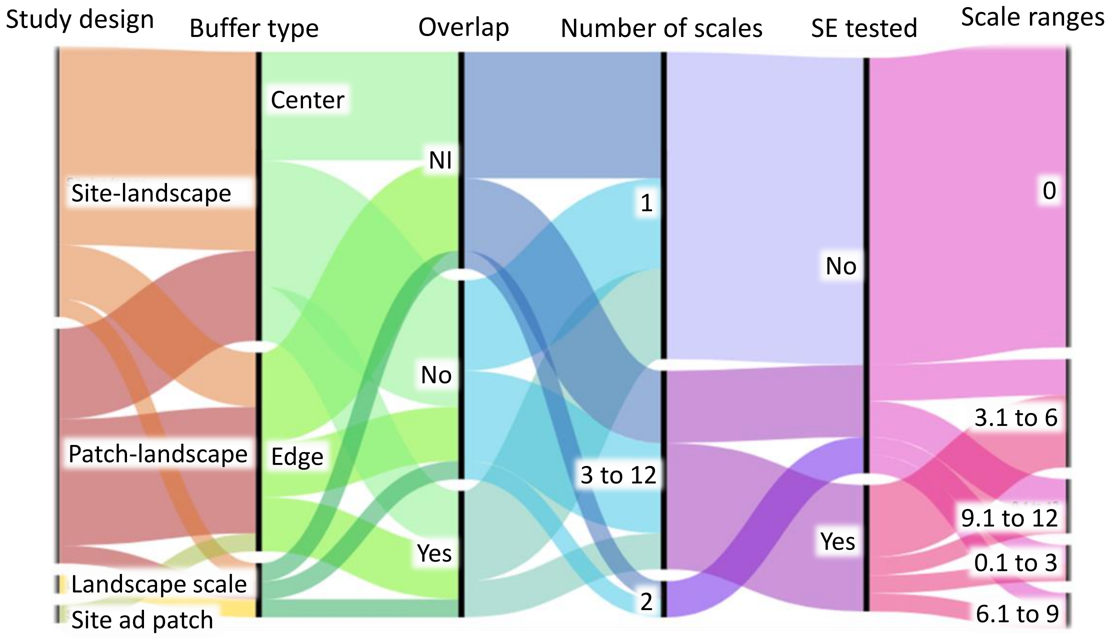
Study design
Buffer type
Overlap
Number of scales
SE tested
Scale ranges
Site-landscape
Patch-landscape
Landscape scale
Site ad patch
Center
Edge
NI
No
Yes
1
3 to 12
2
No
Yes
0
3.1 to 6
9.1 to 12
0.1 to 3
6.1 to 9

Figure 4

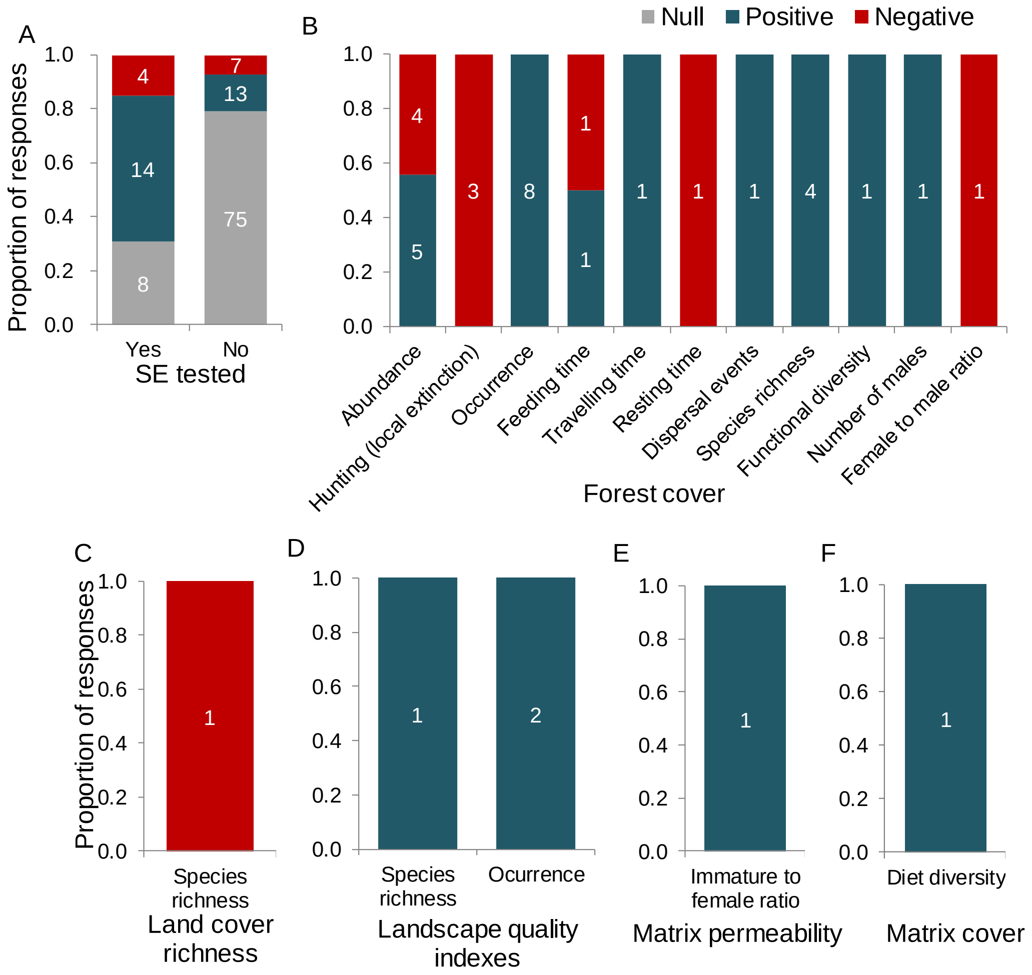
A
Proportion of responses
1.0
0.8
0.6
0.4
0.2
0.0
4
14
8
7
13
75
Yes
No
SE tested
B
Null
Positive
Negative
1.0
0.8
0.6
0.4
0.2
0.0
4
5
3
8
1
1
1
1
1
4
1
1
1
Abundance
Hunting (local extinction)
Occurrence
Feeding time
Travelling time
Resting time
Dispersal events
Species richness
Functional diversity
Number of males
Female to male ratio
Forest cover
C
Proportion of responses
1.0
0.8
0.6
0.4
0.2
0.0
1
Species richness
Land cover richness
D
1.0
0.8
0.6
0.4
0.2
0.0
1
2
Species richness
Ocurrence
Landscape quality indexes
E
1.0
0.8
0.6
0.4
0.2
0.0
1
Immature to female ratio
Matrix permeability
F
1.0
0.8
0.6
0.4
0.2
0.0
1
Diet diversity
Matrix cover

Figure 5

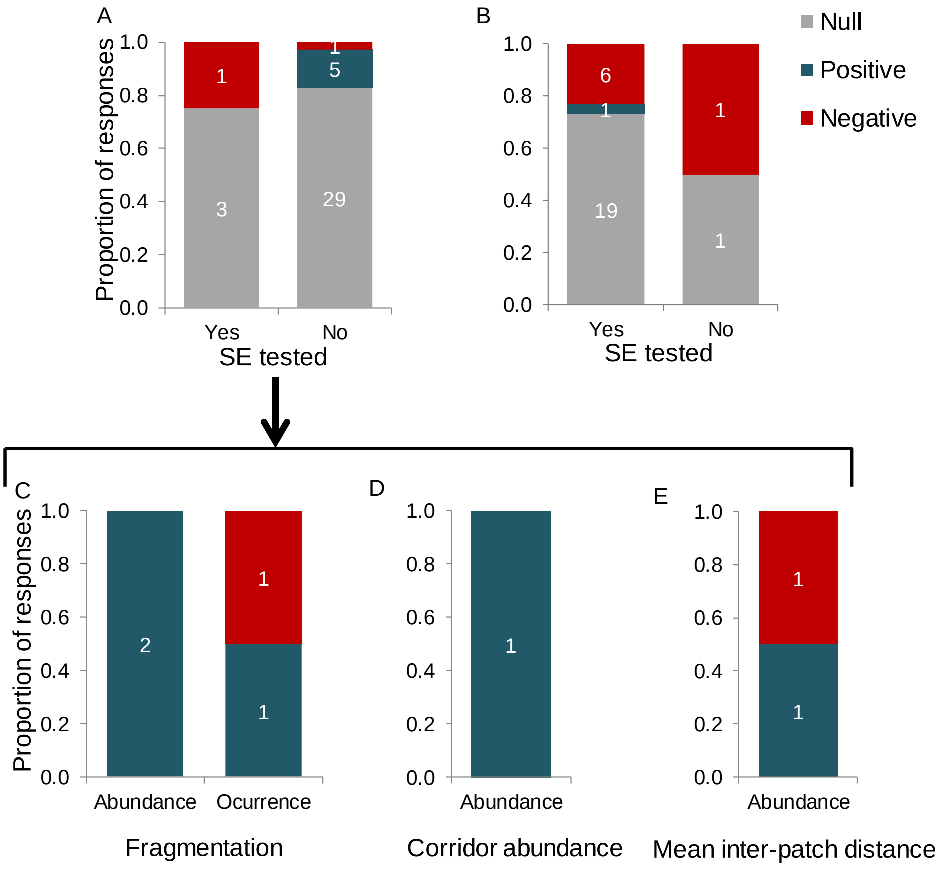
A
Proportion of responses
1.0
0.8
0.6
0.4
0.2
0.0
1
3
1
5
29
Yes
No
SE tested
B
1.0
0.8
0.6
0.4
0.2
0.0
6
1
19
1
1
Yes
No
SE tested
Null
Positive
Negative
C
Proportion of responses
1.0
0.8
0.6
0.4
0.2
0.0
2
1
1
Abundance
Ocurrence
Fragmentation
D
1.0
0.8
0.6
0.4
0.2
0.0
1
Abundance
Corridor abundance
E
1.0
0.8
0.6
0.4
0.2
0.0
1
1
Abundance
Mean inter-patch distance

Table 1. Landscape composition and configuration variables assessed in landscape studies of primates. The number of study responses per predictor is also indicated, as is the percentage of significant ones.

Predictor variables	Definition	Responses (% significant)
Landscape composition		
Agroforest cover	Percentage of agroforest in the landscape	1 (0%)
Corridor length	Sum of the lengths of wooded corridors within the landscape	2 (0%)
Forest cover	Proportion/percentage/area of forest in the landscape	99 (32%)
Land cover richness	Number of land cover types in the landscape	1 (100%)
Landscape quality indexes	Areas or numbers of pixels of different land covers in the landscape weighted by their overall suitability for primates and averaged over the landscape	8 (37%)
Logged forest cover	Percentage of logged forest in the landscape	1 (0%)
Matrix cover	Percentage of matrix habitats (i.e. open areas, secondary vegetation and riparian vegetation) in the landscape	1 (100%)
Matrix permeability	Percentage of each land cover type within the landscape matrix weighted by their suitability for primates travelling and averaged over the landscape	6 (17%)
Secondary forest cover	Proportion of secondary forest in the landscape	1 (0%)
Sugar cane cover	Percentage of sugar cane in the landscape	1 (0%)
*Landscape configuration**		
Area-weighted mean patch fractal dimension	Patch size-weighted average of the fractal dimensions of all forest patches in the landscape	2 (0%)
Corridor abundance	Corridor abundance in the landscape	2 (50%)
Edge density	Sum of forest-matrix edge length divided by landscape area	9 (11%)
Fragmentation	Number/density of forest patches, including the splitting index	33 (24%)
Mean inter-patch distance	Mean of all pairwise edge-to-edge distances between forest patches in the landscape	15 (33%)
Mean patch size	Arithmetic mean of forest patch sizes	2 (0%)
Road abundance	Road abundance in the landscape	4 (0%)

The classification of compositional or configurational variables was based on McGarigal & Marks (2001)

*These variables can be highly correlated with forest cover.

Capítulo 3

Drivers of the spatial scale that best predict primate responses to landscape structure

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Abstract

Understanding the effect of landscape structure on biodiversity is critically needed to improve management strategies. To accurately evaluate such effect, landscape metrics need to be assessed at the correct scale, i.e. considering the spatial extent at which species-landscape relationship is strongest (scale of effect, SE). Although SE is highly variable, its drivers are poorly known, but of key relevance to understand the way species use the landscape. In this study, we evaluate whether and how species traits, biological responses, landscape variables and the regional context of the study drive SE in Mexican primates. We estimated the relative abundance and immature-to-female ratio (a proxy of reproductive success) of howler monkeys (*Alouatta palliata* and *A. pigra*) and spider monkeys (*Ateles geoffroyi*) in 48 forest patches from four rainforest regions (12 patches per region) with different land-use intensity. We then assessed the composition (forest cover, matrix functionality) and configuration (forest patch density, connectors' density, forest edge density) of local landscapes considering 13 scales (100 to 1300-m radius) to identify the spatial extent at which each landscape variable best predict each response variable in each species and region. We found that SE did not differ significantly among the drivers evaluated. However, it tended to be lower for connectors' density than for forest patch density and forest edge density, probably because connectors' density is associated with local-scale processes such as supplementary dynamics. Surprisingly, SE also tended to be higher in the more disturbed region than in the rest of the regions, probably because primates in the more disturbed region used larger areas of the landscape. Our findings therefore suggest that SE depends more strongly on landscape variables and regional context than on species traits and biological responses, and hence, especial caution should be taken when attempting to generalize SE to different explanatory variables and regions.

Introduction

Land use change is threatening the maintenance of global biodiversity (Newbold et al. 2016), especially in tropical forests, which are being rapidly converted to agricultural lands and cattle pastures (Malhi et al. 2014). The remaining tropical landscapes are highly heterogeneous, as they show different composition and spatial configuration (Melo et al. 2013). Understanding the effect of these two components of landscape structure on biodiversity is critical to inform management and conservation plans (Fahrig et al. 2011, Tscharntke et al. 2012, Arroyo-Rodríguez et al. 2016). However, the spatial extent (landscape size) that should be considered to accurately assess the response of species to landscape changes is poorly known (Jackson and Fahrig 2015, Miguet et al. 2016). This issue is not trivial, as species' responses to landscape predictors can be overlooked if assessed at an incorrect scale (Wiens 1989, Holland et al. 2004). Thus, an increasing number of studies assess species-landscape relationships across multiple spatial extents to identify the scale (landscape size) that yields the strongest species–landscape relationship (scale of effect, SE) (Thornton and Fletcher 2014, Miguet et al. 2016). Unfortunately, most multi-scale studies do not measure landscape structure at the true scale of effect because they assess very few scales, usually within a narrow range (Jackson and Fahrig 2015). Furthermore, in many cases they show that the best scales are the smallest or the largest, thus suggesting that SE was located outside that range (Jackson and Fahrig 2015). Therefore, SE and its determinants are still very poorly understood (Miguet et al. 2016).

Assessing the main drivers of SE is of key relevance to understand the way species perceive and use the landscape (Jackson and Fahrig 2015). Among other drivers (reviewed by Miguet et al. 2016), SE can be affected by species traits, such as their ranging behavior and habitat specialization. For example, species with smaller home range sizes and lower vagility are predicted to be affected by spatial attributes in smaller landscapes (Jackson and Fahrig 2012, Ricci et al. 2013). Similarly, when specialization implies larger dispersal movements (e.g. frugivory), SE is also predicted to be larger for specialists than for generalists (Miguet et al. 2016). SE can also differ among response variables and landscape predictors. Regarding the response variables, the abundance of individuals is expected to depend on patterns and processes (e.g. migrations, source-sink dynamics) at larger spatial and temporal scales than reproductive success, which depend most strongly on local patterns and processes (i.e. local scales), such as resource availability (Miguet et al. 2016). Regarding the landscape predictors, SE should be larger for habitat amount (i.e. forest cover), which influences more strongly dispersal success, than for habitat fragmentation, which is expected to have higher effects on breeding and/or foraging success (Miguet et al. 2016). Finally, another important determinant of SE is the regional spatial context. SE is predicted to be lower in more disturbed regions (e.g. those with lower habitat amount and lower connectivity), where dispersal movements may be disrupted, and thus species responses mainly depend on focal patch characteristics (Delattre et al. 2013, Ricci et al. 2013). Yet, the empirical support for all these hypotheses and predictions is still very weak and not conclusive (Jackson and Fahrig 2015, Miguet et al. 2016).

Primates are particularly vulnerable to human-caused disturbances (Estrada et al. 2017, Marsh et al. 2013), including changes in landscape patterns (e.g. Arroyo-Rodríguez et al. 2013a, Benchimol and Venticinque 2014, Dias et al. 2015). Yet, the lack of landscape studies with primates has limited our knowledge about the effect of landscape structure on primates (Arroyo-Rodríguez and Mandujano 2009, Arroyo-Rodríguez et al. 2013a, Arroyo-Rodríguez and Fahrig 2014). Here, we assessed the scale of effect of landscape composition (i.e. forest cover and matrix functionality) and landscape configuration (i.e. forest patch density, forest edge density, and connectors' density) on the relative abundance (encounter rate) and immature-to-female (IF) ratio (a proxy of reproductive success) of mantled howler monkeys (*Alouatta palliata mexicana*), black howler monkeys (*A. pigra*) and spider monkeys (*Ateles geoffroyi*). We assessed such effect in four rainforest regions in southeastern Mexico with different intensity of land use change. We evaluated the strength of the relationship between each response variable and each landscape attribute in 13 different-sized landscapes (100 to 1300-m radius) to identify the spatial scale that best predicts primate responses to landscape structure (SE).

Following the hypotheses described above (detailed in Miguet et al. 2016), we predicted that SE should be higher for *A. geoffroyi* than for *A. pigra* and *A. palliata.* This is because mean home range size is lower in *A. palliata* (25 ha) and in *A. pigra* (37 ha) than in *A. geoffroyi* (~250 ha), and both howler monkeys species have a folivore-frugivore diet, whereas the spider monkey is mostly frugivore (Wallace 2008, Mittermeier et al. 2013). SE should also be higher for encounter rate than for IF ratio in all primate species and regions. Regarding the landscape predictors, SE should be higher for habitat amount (forest cover) than for habitat fragmentation (forest patch density). Finally, regarding the regional disturbance regime, SE is predicted to be higher in best preserved regions than in more disturbed regions.

Material and methods

Study areas and selected landscapes

We studied four regions in southeastern Mexico, two from the state of Veracruz (Uxpanapa region, UR; and Los Tuxtlas region, LTR) and two from the state of Chiapas (Marqués de Comillas Region, MCR; and 8th North Region, 8NR). All regions have a humid and hot climate, and the same vegetation type (rainforest), but show contrasting land-use change patterns and history (Fig. 1; Table 1). We selected patches of old-growth forest from 1 ha to 100 ha and at least 2.7 km apart from each other. Within each region we selected 12 patches: 6 patches of 1 to 10 ha, 4 of 10-50 ha, and 2 of 50-100 ha (48 patches in total).

Study species

Mexico represents the northern limit distribution of three Neotropical primate species: *Alouatta palliata mexicana* (mantled howler monkeys), *Alouatta pigra* (black howler monkeys) and *Ateles geoffroyi* (Geoffroy's spider monkeys) (Rylands et al. 2006). All these species are diurnal, arboreal, and forest specialists (Rylands et al. 2006). Mantled and black howler monkeys have a mean home range of 25 ha and 37.5 ha, respectively (Mittermeier et al. 2013). Howler monkeys have a folivore-frugivore diet and a mean body mass of 6.3 (*Alouatta palliata*) and 8.9 kg (*Alouatta pigra*) (Estrada et al. 2017). Spider monkeys, instead, are frugivorous specialists, have greater dispersal distances, with a mean home range of 250 ha (Wallace 2008) and have a mean body mass of 7.5 kg (Estrada et al. 2017). The IUCN Red List classifies *A. pigra* and *A. geoffroyi* as Endangered and *A. palliata mexicana* as Critically Endangered (IUCN RedList, consulted August 2017). *A. geoffroyi* is native from all study regions, but as described in the results, it was not present in two out of four regions. *A. palliata* is native from three out of four regions (UR, LTR and 8NR), and *A. pigra* is native from one region (MCR).

Primate surveys

For surveying primates we collected response variables from each focal patch, and measured the explanatory variables within a given radius from the geographic center of each focal patch (i.e. patch-landscape approach; *sensu* Arroyo-Rodríguez and Fahrig 2014). To determine the presence of primates, we walked slowly (~1-2 km/ha) around and inside each focal patch from 6 am to 5 pm. To avoid the difficulties in detecting and counting monkeys under heavy rain and strong wind, we worked in sunny days of the dry season (January to June 2015 and January to June 2016). Long distance vocalizations of howler monkeys helped to locate the groups within the sites. In addition, we interviewed the local people about the occurrence of primates in the area. We surveyed each site only once, but search time was relative to patch size, with 3 consecutive days dedicated to survey small patches (<10 ha), 5 days in medium-sized patches (10–50 ha), and 7 days in larger patches (>100 ha). We calculated the number of kilometers walked in each patch with a GPS (i.e. sampling effort), varying from 3.9 km to 84 km per patch, totaling 1020 km in ~1900 hours of field observations, distributed in 192 days.

Once we established visual contact, we recorded the geographical position of the group with a GPS, and we made a count of all individuals in the group. Individuals were classified into different age-sex classes (adult males and females, juveniles, and infants). As response variables we considered the encounter rate (i.e. number of individuals per km walked in each patch) (Ortiz-Martínez and Ramos-Fernández 2012) and the immature-to-female (IF) ratio, which can be considered a proxy for reproductive success and population trend (Clarke et al. 2002, Zucker and Clarke 2003).

Landscape metrics

We produced land cover maps of each landscape surrounding the focal patches using recent and high resolution Sentinel S2 satellite images (from 2015 and 2016) using ENVI 5.0 software. To better identify secondary vegetation, we monitored deforestation from last 20 years of every region using Landsat images and the CLASlite software (Asner et al. 2009). To compute the landscape metrics, we classified seven types of land covers: (i) old-growth forest cover; (ii) secondary vegetation; (iii) connectors (e.g. live fences, riparian corridors, and isolated trees of a maximum area of 0.25 ha); (iv) arboreal crops (e.g. oil palm plantations); (v) annual crops and cattle pastures; (vi) human settlements; and (vii) water bodies (Fig. 1). Our definition of connectors is based on the fact that there are no reports of patches smaller than 0.25 ha permanently occupied by Mexican primates. In other words, these patches cannot be considered habitat, but they can be used by primates as corridors and/or supplementary resources (Asensio et al. 2009, Pozo-Montuy et al. 2013).

We measured five landscape variables within 13 buffers around the geographic center of each focal patch using ArcGis 10.5 (Fig. 1). The largest landscape size was a buffer of 1300-m radius (531-ha landscape), that is twice the home range of *Ateles geoffroyi*, 21 times the home range of *Alouatta palliata* and 14 times the home range of *Alouatta pigra*. This was the largest radius until a minimum overlap between two buffers started to appear. In other words, the largest radius was selected to avoid dependence (i.e. pseudo-replication) problems in our analyses (Eigenbrod et al. 2011). The smallest radius (100-m radius) corresponds to a landscape size of ~3 ha, which is much lower than the mean home range size of all species, but larger than the smallest forest patch where howler monkeys have been found (i.e. ~1 ha; Arroyo-Rodríguez et al. 2008, Boyle and Smith 2010). We then placed 11 additional buffers at 100-m intervals between the largest and the smallest buffers: 200 m (12.6 ha), 300 m (28.3 ha), 400 m (50.3 ha), 500 m (78.5 ha), 600 m (113.1 ha), 700 m (153.9 ha), 800 m (201.0 ha), 900 m (254.4 ha), 1000 m (314.1 ha), 1100 m (380.1 ha), and 1200 (452.3 ha).

We estimated five ecologically informative landscape metrics (predictors) within each landscape size, three metrics of landscape configuration (i.e. forest patch density, forest edge density, and connectors' density) and two metrics of landscape composition (i.e. forest cover and an index of matrix functionality). These landscape metrics have demonstrated to be of key relevance for different vertebrates, including primates

(Thornton and Branch, 2011, Smith et al. 2011, Arroyo-Rodríguez et al. 2013b, reviewed by Ewers and Didham, 2006). We calculated all landscape metrics in ArcGis 10.5 software with the Patch Analyst extension (Rempel et al. 2012). Forest patch density refers to the number of forest patches within the landscape divided by landscape area (n/ha), and represents a measure of habitat fragmentation (Fahrig 2017). Forest edge density refers to the total perimeter length of all forest patches within the landscape divided by landscape area (m/ha), and is related to forest shape complexity. Connectors' density refers to the number of connectors within the landscape divided by landscape area (n/ha), and is a proxy of stepping stones availability, and thus, of landscape connectivity. Forest cover refers to proportion of landscape area covered by forest. To create the matrix functionality index (MFI) we related the percentage of each land cover type within the landscape matrix to their relative functionality. We defined matrix as the cover types that are not the original habitat of our study species (i.e. old-growth forest). Following previous studies on the topic (e.g. Garmendia et al. 2013; Arroyo-Rodríguez et al. 2013b, Marsh et al. 2016), we ranked functionality from 1 to 6 based on our understanding of the ability of monkeys to use different land covers in the matrix for feeding and/or travelling: 1 (water bodies, lowest functionality), 2 (anthropogenic cover), 3 (annual crops and cattle pastures), 4 (arboreal crops), 5 (connectors), and 6 (secondary vegetation, highest functionality). We calculated the functionality index as: MFI = [(1 x % water bodies) + (2 x % anthropogenic cover) + (3 x % annual crops and cattle pastures) + (4 x % arboreal crops) + (5 x % connectors' forests) + (6 x % secondary vegetation)]. Note that we calculated the percentage of each land cover considering the area covered by all land covers in the matrix, and not by total landscape area (Garmendia et al. 2013). MFI varies between 100 (lowest matrix functionality, 100% composed of water) to 600 (highest matrix functionality, 100% composed of secondary vegetation). Although this is a crude estimation of functionality, it can be considered an indicator of matrix permeability to primates' movements (Arroyo-Rodríguez et al. 2013b, Marsh et al. 2016). When there was no matrix in a given landscape (i.e. 100% of forest cover in the landscape), we excluded this landscape from the analyses.

Statistical analyses

We first ran Mantel tests with the package vegan for R version 3.0.1 (Oksanen et al. 2009, R Core Team 2013) to check for spatial independence of our samples. In particular, we assessed whether differences in each response variable between patches (Δ values) were related to inter-patch isolation distance within each region. All p-values were calculated using the distribution of the *R* coefficients obtained from 10,000 permutations. As all Mantel tests did not detect a significant spatial autocorrelation in none of our datasets ($R < 0.04$, $p > 0.60$, in all cases), we considered all patches as independent samples in the following analyses.

To assess SE, we used regression analyses to quantify the strength of the relationship between each landscape metric (i.e. forest cover, matrix functionality index, forest patch density, forest edge density and connector's density) and each response variable (i.e. encounter rate and IF ratio) at each scale. We statistically controlled for the effect of sampling effort (number of kilometers walked), by including this covariate in each model. We tested 520 models for howler monkeys (i.e. 4 regions × 5 landscape predictors × 2 response variables × 13 scales) and 260 models for spider monkeys (i.e. 2 regions × 5 predictors × 2 response variables × 13 scales), totaling 780 models. As the inclusion of the covariate in each model would result in collinearity problems between landscape variables and the covariate, we estimated the variance inflation factor (VIF) of each model using the car package for R. Generally, a VIF > 4 indicates possible collinearity, and a VIF > 10 indicates severe collinearity (Neter et al. 1996). We only found VIF > 4 in 7 out of 780 models (0.89%), and we did not find any VIF > 10, thus indicating that collinearity problems are negligible. Then, following Fahrig (2013), we plotted the parameter estimates (i.e. a measure of effect size) as a dependent variable against landscape size to identify the spatial extent at which the strongest associations between each response variable and each predictor were observable (i.e. SE). In particular, we estimated 60 values of SE, 40 values for howler monkeys (i.e. 4 regions × 5 predictors × 2 responses) and 20 values for spider monkeys (i.e. 2 regions × 5 predictors × 2 responses). We then calculated 95% confidence intervals to assess if SE differed between primate species. We did the same for comparing SE between biological responses (i.e. 30 values of SE for encounter rate vs. 30 values of SE for IF ratio), and among landscape variables (i.e. 12 values per landscape variable) and regions (i.e. 15 values per region). Yet, confidence intervals were calculated by excluding the cases in which SE was equal to the smallest or largest scale evaluated, as in these cases the scale of effect can be outside the study range (Jackson and Fahrig 2015).

Results

Landscape structure in four Mexican regions

Considering all landscape sizes, the percentage of forest cover tended to be lower in 8th North Region (8NR) (mean and range: 23.4%, 1.5-98.7%) than in Marqués de Comillas Region (MCR) (42.1%, 8.6-100%), Uxpanapa Region (UR) (43.5%, 14.1-99.8%) and

Los Tuxtlas Region (LTR) (41.8%, 8.9-100%) (Supplementary material Appendix 1). In all regions, the percentage of forest cover was higher in the smallest landscape size (100-m radius) and gradually decreased because of the decreasing influence of focal patch area on landscape forest cover. In all the regions, the highest average matrix functionality was observed in the smallest landscape (100-m radius landscapes), and then decreased gradually and stabilized with landscape size. Forest patch density remained relatively constant in the four regions. LTR was the region with higher forest patch density (mean = 0.5 patches/ha, range = 0.04-4.7 patches/ha), and 8NR showed the lowest forest patch density (mean = 0.06 patches/ha, range = 0-0.3 patches/ha). Similar to forest cover, edge density was higher for the smallest buffers, and gradually decreased with landscape size. Edge density was particularly lower in the more deforested region (8NR), averaging 83.4 m/ha (range = 6.2-336.3 m/ha). Finally, connectors density was higher in UR (mean = 1.7 n/ha, range = 0-3.6 n/ha) and 8NR (mean = 1.5 n/ha, range = 0-2.9 n/ha), and lower in LTR (mean = 0.9 n/ha, range = 0-2.0 n/ha) (Supplementary material Appendix 1).

Primate surveys

We only recorded spider monkeys in the two best preserved regions (MCR and UR). In MCR, spider monkeys occurred in 6 out of 12 patches, averaging 0.8 individuals per km (range: 0.1-2.2 ind/km), and mean IF ratio of 0.6 (range = 0.3-1.2). In UR, spider monkeys occurred in 5 out of 12 patches, averaging 1.06 individuals per km (range: 0.2-2.08 ind/km), and mean IF ratio of 0.3 (range: 0-0.8).

Black howler monkeys were recorded in MCR, occurring in 9 out of 12 patches. The mean number of individuals per km was 1.03 (range: 0.5-1.7 ind/km), and the mean IF ratio was 1.3 (range: 0.6-2). Mantled howler monkeys inhabited UR, LTR and 8NR. In UR, occurred in 6 out of 12 patches, averaging 0.4 individuals per km walked (range: 0.1-0.8) and mean IF ratio of 0.6 (range: 0-1). In addition, in LTR, mantled howler monkeys occurred in 5 out of 12 patches, averaging 0.5 individuals per km (range: 0.03-1.05 ind/km) with a mean IF ratio of 0.4 (range: 0.4-0.5). In the more deforested region (8NR), we found mantled howler monkeys in 9 out of 12 patches, averaging 1.2 individuals per km walked (range: 0.6-1.9) and the mean IF ratio was 0.7 (range: 0.5-1).

Scale of landscape effect on Mexican primates

Excluding the cases in which we found that SE was equal to the smallest or largest scale evaluated, SE varied between 200 and 1200 m (Figs. 2 and 3). Considering 95% confidence intervals, we did not find significant differences in SE among primate species (Fig. 4a), averaging 558 m (95%CI = 419 to 698 m) in *A. geoffroyi*, 710 m (543 to 877 m) in *A. palliata*, and 711 m (473 to 949 m) in *A. pigra*. Both response variables (encounter rate and IF ratio) also showed similar SE (Fig. 4b). Regarding the explanatory variables (Fig. 4c), SE tended to be lower for connectors' density (95%CI = 54 to 813 m) than for forest patch density (544 to 956 m) and forest edge density (633 to 1067 m). Finally, considering 95% confidence intervals the scale of effect did not differ between rainforest regions, although it tended to be higher in the more disturbed region (8NR) than in the rest of the regions (Fig. 4d).

Discussion

This study assesses four potential determinants of the scale of landscape effect (SE) on primates – a topic considered in its infancy (Miguet et al. 2016). In fact, this study is the first to empirically test the SE in the three non-human Mexican primates (*Alouatta palliata*, *A. pigra*, and *Ateles geoffroyi*), controlling sampling methods and efforts to accurately compare SE between species, regions, response variables (i.e. relative abundance and immature-to-female ratio) and explanatory variables (i.e. two metrics of landscape composition and three metrics of landscape configuration). Excluding those cases in which we found that SE was equal to the smallest or largest scale evaluated – which suggest that SE was outside that range (Jackson and Fahrig 2015) – we show that SE was highly variable, ranging from landscapes of 200-m to 1200-m radii. Although we did not find significant differences in SE among the potential determinants evaluated, our findings suggest that SE depends more strongly on landscape variables and regional context than on species traits and biological responses.

Most SE's were within the range of scales measured in our study, thus suggesting that primate-landscape relationships were adequately estimated (Jackson and Fahrig 2015). In fact, the SE found in our study were within the range reported in other studies of howler monkeys (500-m radius, Carretero-Pinzón et al. 2017) and spider monkeys (500-m radius, Thornton et al. 2011; 633-m radius, Ordóñez-Gómez et al. 2015). The fact that SE did not differ between primate species and response variables suggests that both are determined by similar patterns and processes (Fahrig 2013, Jackson and Fahrig 2015, Miguet et al. 2016). In particular, it is reasonable to expect that both the abundance of individuals and immature-to-female ratio depend on similar local patterns and processes, such as resource availability, and on similar patterns and processes at larger spatial and temporal scales (e.g. migrations, source-sink dynamics). Furthermore, as the three primate species are from the same family (Atelidae), and are diurnal, arboreal, and forest specialists (Rylands et al. 2006), the differences in diet and home range size are probably not large enough to result in significant differences in SE.

The landscape variables and the regional context of study seem to have stronger effects on SE. Regarding the effect of landscape variables, SE tended to be lower for connectors' density than for forest patch density and forest edge density. This result can be explained by the fact that connectors' elements (e.g. vegetation corridors, live fences, isolated trees) are usually used by primates for feeding – a process named "landscape supplementation" (Dunning et al. 1992). In many cases, neighboring connectors may become part of the home range of primates (reviewed by Arroyo-Rodríguez and Mandujano 2009), thus allowing primates to reduce their dispersal movements in the landscape, and consequently SE (Miguet et al. 2016). Connectors' elements can actually allow primate populations to persist in small and low quality fragments, especially when they are composed of food plant species (Arroyo-Rodríguez et al. 2017). For instance, Asensio et al. (2009) found that two groups of *Alouatta palliata* supplement their diet with flowers and fruits from *Albizia purpusii* (Fabaceae) and *Ficus lundelii* (Moraceae) located in live fences and isolated trees. Arroyo-Rodríguez et al. (2017) also found that *Ateles geoffroyi* feed from isolated trees of 22 species, and from 8 tree species in vegetation corridors. Other studies of primates have also observed events of diet supplementation in vegetation corridors, live fences, and isolated trees dispersed in the matrix (e.g. Stoner 1996, Pozo-Montuy and Serio-Silva 2007, Asensio et al. 2009, Pozo-Montuy et al. 2011, 2013, Arroyo-Rodríguez et al. 2017). Therefore, landscape supplementation dynamics may contribute to decrease SE.

In highly degraded landscapes, however, landscape supplementation may be limited, and connectors' elements can rather be used to move between forest patches to find adequate habitat and resources. Thus, the regional context within which the landscapes are embedded has a strong effect on SE. Interestingly, SE tended to be highest in the more deforested region (8NR). Based on previous studies we predicted that SE should be lower in more disturbed regions, where dispersal movements may be limited and species responses should mainly depend on local characteristics, such as patch size (Delattre et al. 2013, Ricci et al. 2013, Miguet et al. 2016). Yet, there is evidence that primates' persistence in 8NR region depends on metapopulation dynamics. For instance, Anzures-Dadda and Manson (2007) recorded several inter-patch animal movements in this region during a 3-years period, and a higher abundance of howler monkeys in those patches surrounded by a higher density of connectors within a 1-km radius. The value of connectors for inter-patch primate movements in highly degraded landscapes is well documented (e.g. Green 1978, Braza et al. 1981, Arroyo-Rodríguez et al. 2013b, Andriamandimbiarisoa et al. 2015). As 8NR is the most deforested region and is dominated by very small forest patches, the very high density of connectors in this region (Supplementary material Appendix 1) may 'force' primates to disperse more often and farther to find supplementary habitat, thus increasing SE. This is in agreement with Miguet et al. (2016), which suggest that when connectivity is not disrupted, animals may use larger areas of the landscape, thus increasing SE.

We can therefore conclude that SE depends more strongly on landscape variables and regional context than on species traits and biological responses. Thus, especial caution should be taken when attempting to generalize the SE to different explanatory variables and regions. These findings are 'good news' for conservation planning, as they suggest that we can plan management strategies for both species and biological responses at the same spatial scale (Smith et al. 2011). However, the fact that species-landscape associations can be wrongly estimated if assessed at the incorrect scale (Holland et al. 2004, Jackson and Fahrig 2015), future studies on the effect of landscape structure on primates should use a multi-scale approach to ensure that landscape-species relationships are evaluated at the correct scale. This is of critical importance to better understand the impact of landscape structure on primates and other species, and thus improve management and conservation strategies in human-modified landscapes.

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Table 1. Characteristics of the study regions in southeastern Mexico. Regions are ordered from the best preserved to the more disturbed.

	MCR	**UR**	**LTR**	**8NR**
Mean annual temperature (ºC)	22-26	24-26	22	25
Mean annual precipitation (mm)	2,143	3,640	4,900	2,600
Land-use history	1970's	1950's	1960's	1950's
Dominant anthropogenic land covers	Cattle pastures and agriculture	Cattle pastures and agriculture	Cattle pastures	Cattle pastures
Remaining forest cover (%)	~36%[1]	~30%[2]	~17%[3]	~5%[4]
Primate species	*Alouatta pigra* *Ateles geoffroyi*	*Alouatta palliata* *Ateles geoffroyi*	*Alouatta palliata*	*Alouatta palliata*

References: [1]Carabias et al. (2009); [2]Hernández et al. (2013), [3]Castillo-Campos and Laborde (2004); [4]Anzures-Dadda and Manson (2007)

Capítulo 4

Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests

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Aceptado en Landscape Ecology

Abstract

Context

Understanding population responses to landscape structure is critical to improve landscape planning. Yet, large uncertainty remains about how such responses vary among regions with different disturbance intensity. This knowledge is particularly important for forest-specialist species, such as spider monkeys.

Objectives

Assessing the effect of landscape composition and configuration on the abundance and reproductive success of spider monkeys (*Ateles geoffroyi*) in two fragmented rainforests with different land-use intensities.

Methods

We calculated the encounter rate (relative abundance) and immature-to-female ratio (reproductive success) of spider monkeys in two Mexican rainforest regions (12 forest patches per region, ~1140 h of field observations), and assessed their responses to three landscape predictors (forest cover, matrix functionality, and forest patch density) considering the scale of effect in each region.

Results

Spider monkeys showed different responses to landscape structure in each region. Encounter rate increased strongly with matrix functionality in the more disturbed region, and tended to be negatively impacted by patch density in the best-preserved region, but this latter association was weak. Forest cover was positively related to immature-to-female ratio in both regions, but such association was stronger in the best-preserved region.

Conclusions

Our findings suggest that forest loss has stronger negative effects on spider monkeys than forest fragmentation, especially in best-preserved rainforests. Matrix composition is relatively more important in more disturbed regions, where monkeys may be pushed to use the matrix more frequently for feeding and/or traveling. Preventing forest loss and improving matrix quality should be a priority for the conservation of this endangered species.

Keywords: Forest loss · Forest specialist · Functional heterogeneity · Land-use change · Mexico · Multi-scale assessment · Spider monkeys

Introduction

Land-use change is a main threat to global biodiversity (Malhi et al. 2014; Newbold et al. 2016). Production activities such as agriculture and cattle ranching are increasingly altering landscape structure (Hansen et al. 2013; Melo et al. 2013), that is, landscape composition and configuration (Dunning et al. 1992). Understanding the effects that these landscape changes may have on biodiversity is urgently needed to improve conservation strategies at the landscape scale (Fahrig et al. 2011; Tscharntke et al. 2012), especially in the tropics, where the remaining forests are highly fragmented (Taubert et al. 2018). Unfortunately, most studies are implemented at local scales (McGarigal and Cushman 2002; Arroyo-Rodríguez et al. 2013a), and the majority of studies that use a landscape perspective do not assess the scale of effect (i.e. the spatial extent at which species-landscape relationship is strongest; Jackson and Fahrig 2012, 2015; McGarigal et al. 2016). Moreover, although population responses to landscape changes can vary widely among regions, the vast majority of studies are implemented at one single region, thus limiting our ability to adequately generalize the observed findings across habitats and ecological conditions (Villard and Metzger 2014). Therefore, landscape studies at the optimal scale (i.e. considering the scale of effect) and comparing population responses to landscape changes among regions with different land-use intensity are urgently needed to better understand the effect of landscape structure on species.

Forest fragmentation is often considered a process that involves both the loss and the breaking apart of forest (Didham et al. 2012). Yet, as a given amount of forest cover (i.e. landscape composition) can be broken apart into different numbers of forest patches, forest fragmentation may be better thought of as a pattern (not a process) describing the configuration of a given landscape (McGarigal & Cushman 2002; Fahrig 2003). In this sense, evidence on the relative effect of forest loss and fragmentation indicates that forest loss shows stronger negative effects on biodiversity than fragmentation per se (i.e. after controlling for the effect of forest cover; Fahrig 2003). In contrast, the effects of forest fragmentation are generally weak, and when significant, they are mostly positive (Fahrig 2017). The negative effect of forest loss is not surprising, as both resource availability and landscape connectivity are limited in landscapes with lower forest cover, especially when considering forest-dependent species (Fahrig 2013). The significant positive responses to fragmentation per se are also not surprising when we consider that habitat homogenization, competitive exclusion, spreading of risk, among other threatening ecological processes, can decrease with increasing forest fragmentation (Fahrig 2017). Yet, our understanding on this topic is far from complete, as previous studies on this topic are focused on few taxa (mostly birds) and ecosystems (mostly temperate forests).

The anthropogenic matrix in which forest patches are embedded can be composed of different land covers, including secondary forests, tree plantations, cattle pastures and human settlements. Each of these land covers can have different functions for species, including foraging, dispersal and reproduction (Prevedello and Vieira 2010; Fahrig et al. 2011). In fact, an increasing number of studies demonstrate that different species of birds, frogs, mammals, and ants are able to use supplementary and complementary resources from the matrix (Dunning et al. 1992; Gascon et al. 1999; Anderson et al. 2007; Estrada et al. 2012; Boesing et al. 2018). However, the impact of matrix composition on forest-dwelling species is still poorly known, especially for endangered and forest-specialist species, such as most primates (Estrada et al. 2017).

Primates are particularly susceptible to land-use changes (Marsh et al. 2013; Arroyo-Rodríguez et al. 2017a). Of the 504 primate species in the world, ~60% are threatened with extinction, mainly due to human-induced habitat loss (Estrada et al. 2017). Primates have a wide distribution and inhabit most megadiverse regions of the world in a great variety of ecosystems (e.g. moist lowland forest, dry forest, mangrove, savanna) (Mittermeier et al. 2013; IUCN 2017). They play a vital role in the structure and functioning of the ecosystems where they occur as herbivores, seed dispersers, and as predators of insects, small mammals, birds and reptiles (Mittermeier et al. 2013; Estrada et al. 2017; Andresen et al. 2018). Because primates inhabit many of the most diverse and threatened ecosystems in the world (i.e. diversity hotspots; Myers et al. 2000), their conservation may help to preserve many other species, as well as the ecological processes in which they participate, with a potentially positive effect on rural people’s livelihoods (Estrada et al. 2017). Therefore, understanding the effect of landscape structure on primates has critical ecological and applied implications.

Studies of primates in human-modified landscapes have been focused on assessing species responses to patch-scale attributes, such as patch size (Arroyo-Rodríguez et al. 2013a, 2017a). Yet, we assessed in a recent study the scale of effect of different landscape structure variables on the relative abundance of all three Mexican primates (*Alouatta palliata*, *A. pigra,* and *Ateles geoffroyi*; Galán-Acedo et al. 2018). We found that the scale of effect tended to be larger in the more disturbed region, probably because under this regional context primates are pushed to use larger areas of the landscape (Galán-Acedo et al. 2018). However, as we evaluated univariate models, we do not know the relative importance of each landscape variable in predicting primate abundance. Here, we used the optimal spatial scales identified by Galán-Acedo et al. (2018) to evaluate the relative impact of three independent landscape metrics on the Geoffroy's spider monkey (*A. geoffroyi*) using a multimodel averaging approach. In particular, we assessed the effect of landscape composition (i.e. forest cover and matrix functionality) and configuration (i.e. forest fragmentation) on the relative abundance and reproductive success of spider monkeys in two rainforest regions of southeastern Mexico: the relatively well-preserved Marqués de Comillas rainforest (Chiapas) and the more disturbed but highly heterogeneous Uxpanapa rainforest (Veracruz).

We focused on spider monkeys because it is a forest specialist and endangered primate species (IUCN, 2017). We predict that forest cover is positively associated with monkey relative abundance and reproductive success because forest loss decreases resource availability for this forest-dependent species (Chaves et al. 2012) and increases inter-patch isolation distances (Fahrig 2013), thus limiting animal movements. Following Fahrig (2017), we also predict weaker responses to fragmentation than to forest loss, but if significant, responses to fragmentation will be mostly positive. This prediction is reasonable if we consider that with increasing the number/density of forest patches in the landscape, mean inter-patch isolation distance decreases, thus increasing resource availability for forest-dwelling species at the landscape scale (Dunning et al. 1992; Fahrig 2017). Regarding the effect of matrix functionality, which was given by the dominance of tree land covers in the matrix, we predict positive effects on spider monkey abundance and reproductive success. Such positive responses to matrix functionality can be particularly evident in the more disturbed and heterogeneous region (Uxpanapa), because under this regional context primates may be pushed to use more frequently the matrix for feeding and traveling (Anderson et al. 2007; Watling et al. 2011; Estrada et al. 2012; Blanco and Waltert 2013; Arroyo-Rodríguez et al. 2017b).

Methods

Study species

The Geoffroy's spider monkey is a large-sized primate (mean body mass = 7.5 kg; Estrada et al. 2017), strictly arboreal, mostly frugivorous (> 67% of feeding time consuming fruits; González-Zamora et al. 2009), and with large spatial requirements (home range size is usually > 200 ha; Wallace 2008) – ecological traits that can increase the susceptibility of this species to landscape changes (Marsh and Chapman 2013). This species extends over much of Central America, from Mexico to Panama. Spider monkeys have a high degree of fission-fusion dynamics, where members of a large group fission and fuse into smaller subgroups (van Roosmalen and Klein 1988). Therefore, subgroup size and composition can vary widely over time (Ramos-Fernández et al. 2009). Adult females spend more time alone than males or with an infant (Symington 1988). In this sense, reproductive lifespan can continue beyond 20 years of age, interbirth interval is ca. 32 months and nursing can take > 2 years (Milton 1981). However, populations of spider monkeys are declining mainly due to habitat loss (Cuarón et al. 2008). Currently, this species is classified as Endangered (IUCN 2017).

Study regions

We surveyed spider monkeys in two rainforest regions from southeastern Mexico that encompass most of the species range in the country (see Calixto-Pérez et al. 2018): the relatively well-preserved Marqués de Comillas region (91º6'42.8"- 90º41'8.7W; 16º19'17.1" - 16º2'49.3N) in the state of Chiapas, and the more disturbed Uxpanapa region (94º50'6.809" - 94º24'30.216"W; 17º24'1.705" - 17º8'46.1"N), in the state of Veracruz (Fig. 1). Two regions (i.e. the Los Tuxtlas rainforest, and the 8th North Region) assessed in our previous study (Galán-Acedo et al. 2018) were excluded from the present one because the spider monkey has been extirpated from these regions. The climate in Marqués de Comillas is warm (i.e. mean annual temperature varies between 22 and 26 ºC) and humid (i.e. mean annual rainfall is 2,143 mm; Toledo 2003). Deforestation in this region started in the early 1970's, and we estimated that nowadays ~56% of old-growth forest cover remains embedded in a matrix of agricultural lands (e.g. annual crops such as maize and chili, and tree plantations such as oil palm plantations), cattle pastures and human settlements (Carabias et al. 2009). The Uxpanapa rainforest also has a warm and humid climate (mean annual precipitation = 3640 mm; mean annual temperature = 24 to 26 °C). Here, deforestation started between 1950s and 1970s, when the Mexican government established new communities of poor peasants in the tropics. In 1998 the region suffered an intense forest fire that affected a large extent of tropical forest, mostly converted to secondary vegetation dominated by light-demanding species from genera *Ficus*, *Cecropia*, *Bursera*, *Miconia*, *Heliocarpus*, *Piper*, and *Ochoma* (Hernández et al. 2013). We estimated that ~35% of old-growth forest covers remains (Fig. 1), with a highly heterogeneous matrix composed of secondary vegetation, rubber plantations, citric and Gmelina plantations, cattle pastures or human settlements (Hernández et al. 2013).

Study forest patches and response variables

In each region, we randomly selected 12 old-growth forest patches with a minimum distance between each other of 2.7 km to avoid the overlapping of the landscape metrics (see below). Patches were selected considering three size classes: 6 patches of 1 to 10 ha, 4 of 10-50 ha, and 2 of 50-100 ha (24 patches in total). We surveyed primates in each forest site following standardized protocols (see details in Galán-Acedo et al. 2018). From 6 am to 5 pm, we walked slowly (~1-2 km/hr) inside and around each focal patch. To avoid bias related to adverse climatic conditions, we only worked in sunny days of the dry season (July to December) and part of the wet season (January to June 2015, and January to June 2016). We surveyed each site once, with search time being proportional to patch size. In particular, we spent 3 consecutive days surveying monkeys in smaller patches (<10 ha), 5 days in medium-sized patches (10–50 ha), and 7 days in larger patches (>50 ha). In total, we worked 104 days (~1140 hours of field observations) and we walked 523 km (9 to 84 km per patch). When we made visual contact with primates, we recorded the geographical position of the individual/subgroup with a GPS, and we counted all individuals in the subgroup. Following Carpenter (1935) and Ramos-Fernández et al. (2009), individuals were classified as adult males and females (i.e. with darker faces and sexual maturity), juveniles (i.e. with smaller body sizes and intermediate dependence of their mothers) and infants (i.e. with the smallest body sizes and always traveling with their respective mothers). We then calculated the encounter rate (i.e. number of individuals per km walked in each patch; Setchell and Curtis 2003) and the immature-to-female ratio as proxies of relative abundance and reproductive success, respectively.

Landscape metrics

We measured all landscape metrics within 13 different scales (i.e. local concentric landscapes of 100- to 1300-m radius, at 100 m intervals) from the geographic center of each focal forest patch (i.e. patch-landscape approach, sensu Arroyo-Rodríguez and Fahrig 2014). To this end, we first produced land cover maps of each landscape surrounding the focal patches using high resolution (10 x 10-m pixels) Sentinel S2 satellite images from 2015 and 2016. To compute the landscape metrics, we classified seven types of land covers: (i) old-growth forest cover; (ii) secondary vegetation; (iii) connectors (e.g. live fences, riparian corridors, and isolated trees); (iv) tree plantations (e.g. oil palm plantations); (v) annual plantations and cattle pastures; (vi) human settlements; and (vii) water bodies. We used control points of all land cover types taken directly from the field with a GPS to conduct a supervised classification using ENVI 5.0 software. Overall classification accuracy was very high (Kappa index ≥ 0.9, based on 100 ground truth points per land cover class). To identify secondary vegetation, we monitored deforestation from 1997 to 2017 in the two regions using Landsat images and the CLASlite software (Asner et al. 2009). We defined ‘connectors’ as any patch < 0.25 ha because they cannot be considered habitat (i.e. these patches are probably used as corridors and/or as supplementary resources, but not as permanent habitat; Asensio et al. 2009; Pozo-Montuy et al. 2013; Arroyo-Rodríguez et al 2017b).

We used ArcGis 10.5 software with the Patch Analyst extension (Rempel et al. 2012) to calculate three landscape variables: two metrics of landscape composition (i.e. forest cover and matrix functionality) and one metric of landscape configuration (i.e. forest patch density). These landscape predictors have demonstrated to be of key relevance for different vertebrates (Fahrig 2003, 2013; Smith et al. 2011), including primates (Thornton et al. 2011; Arroyo-Rodríguez et al. 2013b, 2017b). Forest cover refers to the percentage of old-growth forest cover in the landscape, and it is positively related to landscape connectivity (Fahrig 2013). To calculate matrix functionality, we first ranked the functionality of all land cover types that are not the original habitat (i.e. old-growth forest) of spider monkeys, from 1 (lowest functionality) to 6 (highest functionality). Such a ranking was based on our understanding of the ability of spider monkeys to use different land covers in the matrix for feeding and/or travelling (Arroyo-Rodríguez et al. 2017b): 1 = water bodies, 2 = human settlements, 3 = open areas, 4 = tree plantations, 5 = connectors, and 6 = secondary vegetation. The matrix functionality index was calculated as follow: MFI = [(1 × % of water bodies) +

(2 × % of human settlements) + (3 × % of open areas) + (4 × % of tree plantations) + (5 × % of connectors) + (6 × % of secondary vegetation)]. To make this index independent of forest cover, we calculated all percentages considering the area covered by all land covers in the matrix, and not by total landscape area (Garmendia et al. 2013). This index varies between 100 (100% composed of water) and 600 (100% composed of secondary vegetation), and is therefore positively related to resource availability in the matrix and to matrix permeability (Garmendia et al. 2013). Finally, forest patch density refers to the number of forest patches within the landscape divided by total landscape area (n/ha). This widely used landscape metric is an accurate descriptor of forest fragmentation, which is particularly faithful to the definition of forest fragmentation (i.e. the breaking apart of forest; Fahrig 2003, 2017), and has been used in other studies of primates (e.g. Arroyo-Rodríguez et al. 2013b; Ordóñez-Gómez et al. 2015; Gestich et al. 2018).

Scale of landscape effect

Species-landscape relationships depend on the spatial extent (i.e., landscape size) at which landscape variables are measured (Jackson and Fahrig 2015). Thus, landscape variables need to be measured across different extents to identify the one that yield the strongest species-landscape relationship (i.e. so-called ‘scale of effect’; Jackson & Fahrig, 2012; McGarigal et al. 2016). We therefore assessed all landscape structure variables considering their respective scales of effect based on a previous study on this topic (Galán-Acedo et al. 2018). In particular, we followed the protocol proposed by Jackson and Fahrig (2015) and others (e.g. Fahrig 2013; Ordóñez-Gómez et al. 2015; Gestich et al. 2018) to identify the scale of effect of each landscape variable on each response in each region. In particular, we ran linear regressions between each landscape metric and each response variable, and we used the parameter estimate (slope) as a metric of the strength of each relationship. Such regressions were carried out for each of the 13 landscape sizes, to then plot the parameter estimate (as a dependent variable) against landscape size to identify the spatial extent at which the strongest associations between each response variable and each predictor were observable. The final optimal scales are detailed in Supplementary Table A1, and were used in the statistical analyses that are described below.

Statistical analyses

We first tested for spatial independence among samples with Mantel tests using the package *vegan* for R version 3.0.1 (R Core Team 2013; Oksanen et al. 2016). In particular, we evaluated if the differences in each response variable between patches (i.e. a matrix of Δ values for relative abundance, and another matrix of Δ values for reproductive success) were related to inter-patch distances within each study region. All p-values were calculated using the distribution of the R coefficients obtained from 10,000 permutations. All Mantel tests showed no spatial autocorrelation in our datasets ($R < 0.04$, $p > 0.60$, in all cases), thus suggesting that all patches can be considered independent samples.

To evaluate the effects of landscape variables on each response variable we built generalized lineal models including all three landscape predictors (i.e. forest cover, matrix functionality and patch density) measured at the scale of effect (Table A1). To avoid multicollinearity among spatial attributes we estimated their variance inflation factors (VIF) using the car package for R version 3.0.1 (Fox et al. 2012). We did not detect significant collinearity between predictors, as all VIF values were < 2.7 (Neter et al. 1996). Then, we used an information-theoretic approach and multimodel inference to assess the relative effect of each predictor on each response variable (Burnham and Anderson 2002). For each response variable we constructed 8 models, representing all combinations of three explanatory variables plus the null model, which includes only the intercept. For each model we computed the Akaike's information criterion corrected for small samples (AICc), and we ranked the models from the best to the worst (Table A2). We used Akaike weights (w_i) to evaluate the empirical support for each predictor and to produce model-averaged parameter estimates (Anderson 2007). Hence, we summed w_i of ranked models until the total was >0.95 (Whittingham et al. 2005). The set of models for which $\sum w_i$ was 0.95 represents a set that had 95% probability of containing the true best model (Burnham and Anderson 2002).

Results

Spider monkeys in the Marqués de Comillas region were recorded in 6 of 12 patches (50%). In this region, we recorded 164 individuals, averaging 0.8 individuals per km (range: 0.1-2.2 ind/km), and mean immature-to-female ratio was 0.6 (range = 0.3-1.2). In Uxpanapa, we recorded spider monkeys in 5 out of 12 patches (42%), totaling 229 individuals. The mean encounter rate in this region was 1.06 individuals per km (range: 0.2-2.08 ind/km), and the mean immature-to-female ratio was 0.3 (range: 0-0.8).

Considering the largest landscape size (i.e. 1,300 m radius) used to identify the scale of landscape effect on spider monkeys, the mean percentage of forest cover surrounding the focal forest patches ranged from 12.5% to 64.5% in Marqués de Comillas, and from 17.3 to 70.8% in Uxpanapa. The range of variation of forest patch density was also similar in the Marqués de Comillas (0.05-0.31 patches/ha) and Uxpanapa regions (0.02-0.24 patches/ha). Matrix functionality also showed a similar range of variation in both regions, although slightly higher in Uxpanapa (343.1 to 564.7) than in Marqués de Comillas (320.4 to 443.2).

In both regions, we found strong associations between landscape metrics and response variables (>48% of explained deviance by each complete model; Fig. 2). In Marqués de Comillas, the encounter rate decreased mainly with increasing forest patch density ($\sum w_i = 0.8$; Fig 2a), but the unconditional variance was greater than the model-averaged parameter estimate (Table 1), which suggests caution in the interpretation of this parameter estimate. Also, in this region the immature-to-female ratio was strongly and positively related to forest cover ($\sum w_i = 0.9$; Fig 2c). Regarding the Uxpanapa region, matrix functionality was positively related to both response variables, but this association was stronger when assessing the encounter rate ($\sum w_i = 0.9$; Fig. 2b) than when assessing the immature-to-female ratio ($\sum w_i = 0.5$; Fig. 2d) (Table A2).

Discussion

To our knowledge, this is the first assessment of the impact of landscape composition and configuration on the relative abundance and reproductive success of a primate species, comparing regions with different degree of land-use intensity. In particular, we found that forest loss shows stronger negative effects on spider monkey populations than fragmentation per se, thus supporting previous studies with other biological groups (Fahrig 2003, 2017). This finding was especially evident in the best-preserved rainforest (Marqués de Comillas). Yet, as expected, matrix composition seems to play a more important role in the more disturbed region, being positively related to both the encounter rate and immature-to-female ratio in the Uxpanapa region. Although the encounter rate of spider monkeys tended to be negatively impacted by forest fragmentation (patch density) in the best-preserved region, as expected from previous empirical evidence (Fahrig 2003, 2017), this effect was weak. Our findings therefore support the idea that conservation actions should be focused on managing landscape composition, such as preventing forest loss and increasing matrix quality.

Consistent with previous studies of birds, insects and mammals (Fahrig 2003, 2013), forest loss (not fragmentation) seems to be the most important threat to spider monkeys in our study regions (see also Ordóñez-Gómez et al. 2015). Forest cover was positively and consistently related to the encounter rate and immature-to-female ratio of spider monkeys in both regions, with stronger effects on reproductive success in the best-preserved region. Thus, our results suggest that in regions with a relatively high forest cover, spider monkeys mainly respond to landscape-scale forest loss, which supports the fragmentation threshold hypothesis (Andrén 1994; Villard and Metzger 2014). Forest loss decreases the availability of food for forest-specialist species (Fahrig 2013; Marsh and Chapman 2013), and can also decrease primate survival rate (Altmann et al. 1985; Marsh and Chapman 2013). Furthermore, forest loss decreases landscape connectivity, thus limiting individual movements in the landscape (Fahrig 2003; Arroyo-Rodríguez et al. 2008; Carretero-Pinzón et al. 2017). This can be particularly evident for forest-dependent primates, such as the spider monkey, which depend on large tracts of old-growth forest for feeding and traveling (Marsh and Chapman 2013). In fact, Ordóñez-Gómez et al. (2015) demonstrate that in the Marqués de Comillas region, leaf consumption by spider monkeys increases with decreasing forest cover, probably because of the reduced availability of fruits in strongly deforested landscapes. Nevertheless, as described below, in regions with lower forest cover, primates can also supplement their diet with food resources from the matrix (Arroyo-Rodríguez et al. 2017b), thus increasing the importance of matrix composition for primates in these regions.

Consistent with our hypothesis, matrix functionality showed a stronger positive effect on the encounter rate and immature-to-female ratio of spider monkeys in the Uxpanapa region than in Marqués de Comillas. This suggests that matrix composition plays a more important role in more disturbed regions, probably because under this regional context primates can be pushed to use more frequently the matrix for feeding and traveling (Anderson et al. 2007; Watling et al. 2011; Blanco and Waltert 2013; Arroyo-Rodríguez et al. 2017b). This can be particularly plausible in the Uxpanapa region, which is composed of a higher amount of secondary forests and tree plantations in the matrix. Spider monkeys are able to use different tree covers in the matrix as supplementary resources (Ramos-Fernandez et al. 2013; Arroyo-Rodríguez et al. 2017b). This process is called “landscape supplementation” (sensu Dunning et al. 1992) and can contribute to increase the abundance and reproductive success of monkeys in patches surrounded by higher tree cover in the matrix (i.e. secondary vegetation and tree plantations).

As expected, forest patch density showed a weak effect on spider monkeys in both regions. In fact, the unconditional variance was higher than the model-averaged parameter estimate (i.e. slope), suggesting caution with interpretation of this parameter (Burham and Anderson 2002; Anderson 2007). This result is, however, consistent with Fahrig (2003, 2017), who has reviewed the overall effect of habitat fragmentation on biodiversity and has documented that such effect is generally weak. A possible explanation of the lack of a significant effect of fragmentation in the present study is the fact that both regions have a relatively high amount of forest (35-56% of forest cover) and a large number of forest patches (Fig. 1), which decrease inter-patch isolation distances, and thus favor animal movements and resource availability (Fahrig 2003, 2013). However, additional studies with other landscape configuration variables are needed to draw stronger conclusions about the effect of landscape configuration on this primate.

Taken together, our findings highlight the importance of landscape composition for maintaining primate populations in human-modified rainforests. Spider monkeys-landscape associations were generally strong in both regions (i.e. high explained deviance by the models), probably because spider monkeys are forest specialists. In particular, forest cover and matrix composition appear to be key drivers of spider monkey populations in fragmented rainforests. Therefore, to preserve spider monkey populations and their important ecological roles in the ecosystem (e.g. seed dispersal, Chaves et al. 2011; González-Zamora et al. 2012), conservation initiatives should be focused on preventing forest loss, increasing forest cover (e.g. forest restoration projects) and improving the quality of the anthropogenic matrix by increasing tree land covers outside the remaining forest patches (Prevedello and Vieira 2010; Estrada et al. 2012; Arroyo-Rodríguez et al. 2017b).

Compliance with ethical standards

This research was approved by the Secretary of Environment and Natural Resources (SEMARNAT) of Mexico (No. SGPA/DGVS/10837/14). No animals were captured or handled, so the research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and the legal requirements of Mexico. All study patches are private lands, and we obtained all required permits to work on them from the landowners.

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

Table 1 Values of model-averaged parameter estimates (*β*) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference for reproductive success and relative abundance for each landscape predictor in the two study regions (see all model sets in Supplementary Material Table A2).

Region/Predictors	Reproductive success		Relative abundance	
	β	UV	*β*	UV
Marqués de Comillas Region				
Forest cover	0.016	0.00002	0.002	0.00005
Matrix functionality	-0.0004	0.0000007	-0.0006	0.000002
Patch density	-0.07	0.19*	-4.08	7.99*
Uxpanapa Region				
Forest cover	0.003	0.00002	0.001	0.00002
Matrix functionality	0.001	0.000003	0.01	0.000005
Patch density	-0.06	0.47*	-0.28	1.14*

*Values with asterisk indicate the cases where the unconditional variance was higher than the model-averaged parameter estimates. This means that the parameter estimates is very spread out around the mean and that this variable may have positive, negative or null effects, suggesting caution with interpretations (Burnham and Anderson 2002; Anderson 2007).

Figure legends

Fig. 1 Location of the two study regions, focal forest patches (in red) and their respective surrounding local landscape in southeastern Mexico. An example of a focal patch and their respective landscape is also indicated. For simplicity, we do not add all classified land covers in each region, but only those with higher contrast (forest cover is indicated with dark green, cattle pastures and annual plantations with light green, water bodies in blue, and white polygons represent human settlements).

Fig. 2 Predictor variables included in 95% set of models (bars) for the two study regions, Marqués de Comillas region and Uxpanapa region. The importance of each variable is shown by the sum of Akaike weights ($\sum w_i$, panels). We assessed the impact of forest cover (FC), matrix functionality (MF) and forest patch density (PD). The percentage of deviance explained by each complete model (goodness-of-fit of each complete model) is also indicated. Positive (+) or negative (-) effects of each landscape predictor on each response variable are indicated next to the parameter estimates.

Figure 1

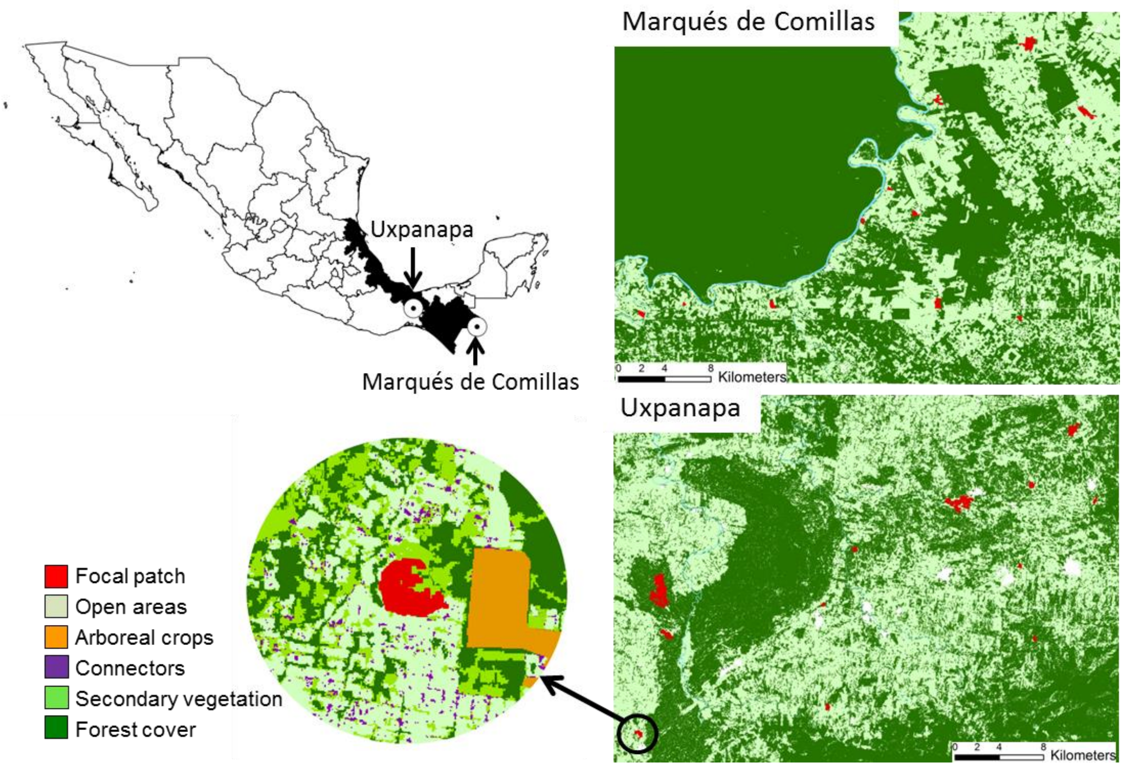
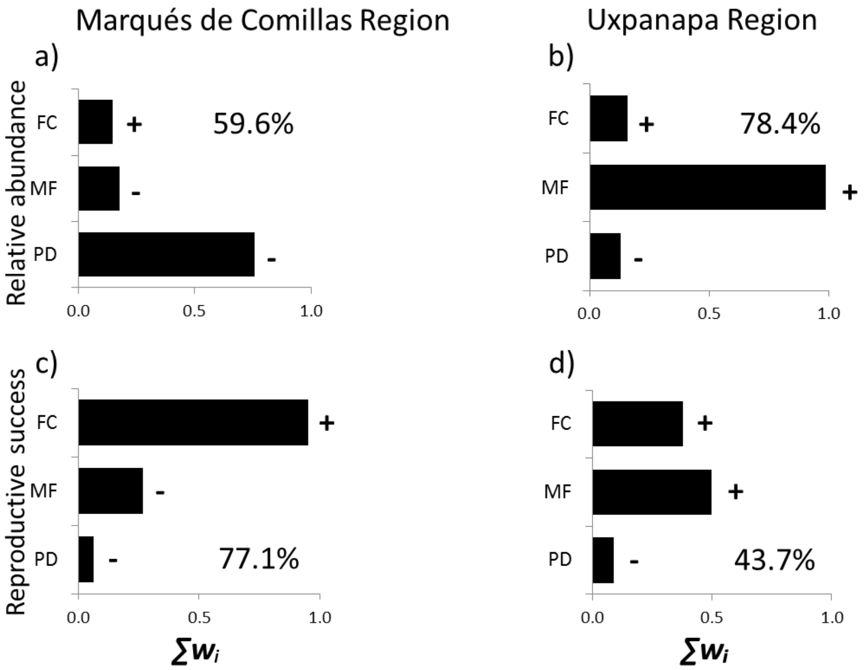

Marqués de Comillas
Uxpanapa
Uxpanapa
Marqués de Comillas
0 2 4 8 Kilometers
Uxpanapa
0 2 4 8 Kilometers
🟥 Focal patch
🟩 Open areas
🟧 Arboreal crops
🟪 Connectors
🟩 Secondary vegetation
🟩 Forest cover

Figure 2


Marqués de Comillas Region
Uxpanapa Region
a)
b)
c)
d)
Relative abundance
Reproductive success
FC
MF
PD
+
-
59.6%
78.4%
77.1%
43.7%
0.0
0.5
1.0
∑wᵢ

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Capítulo 5

Impact of landscape structure on two endangered primates across rainforest regions with different land-use intensity

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Abstract

Land-use change is a major threat to species persistence worldwide, but the landscape-scale drivers of biotic populations and assemblages remains poorly understood. In fact, such drivers can vary across regions with contrasting land-use intensity, thus limiting the effectiveness of conservation strategies across human-modified landscapes. The present study is the first in assessing the impact of landscape structure (i.e. forest cover, matrix functionality, and forest patch density) on the abundance and immature-to-female ratio (IFR, a proxy of reproductive success) of two endangered howler monkeys (*Alouatta palliata mexicana* and *A. pigra*) in four Mexican rainforests with different degree of land-use intensity (12 landscapes per region, ~1900 hours of field observations). Surprisingly, the abundance of *A. palliata* was 3.3 times higher in the most deforested region, probably because individuals are pushed to take refuge in the remaining forest patches, concentrating there. Yet, *A. pigra* populations in the Lacandona rainforest where between 1.5 and 4.8 times larger than *A. palliata* populations in other rainforests. Most primate responses to landscape structure differed among regions. Forest loss generally had negative effects on abundance and IFR, but was positively related to IFR in the most deforested region. Matrix functionality had strong positive effects on IFR in regions with more arboreal matrices. Only in the best preserved region, patch density was negatively related to monkey abundance. Therefore, preventing forest loss should be a conservation focus, particularly in the best preserved rainforests. Increasing matrix quality is also important in regions with arboreal matrices, probably because this regional context allows monkeys to use matrix covers for feeding and/or travelling.

Keywords: habitat fragmentation, habitat loss, landscape heterogeneity, landscape perspective, matrix composition, multi-scalar approach, spatial scale

Introduction

Human activities transform natural ecosystems into landscapes with different degrees of disturbance and structural heterogeneity (Newbold et al., 2015; Song et al., 2018; Taubert et al., 2018). In the tropics, agriculture and cattle ranching are responsible for 73% of habitat loss (FAO, 2016), threatening species persistence in anthropic landscapes. In fact, in the last decades, biodiversity has been lost at such dramatic rates that our planet is believed to be experiencing the sixth mass extinction in its geologic history (Barnosky et al., 2011; Ceballos et al., 2015).

Understanding the effects that landscape structure has on species responses is critical to propose adequate management and conservation strategies for species persistence in human modified landscapes. Nonetheless, studies that assess species responses to landscape structure are still scarce (Fahrig, 2005). Furthermore, the existing studies generally do not identify the scale of effect (i.e. the scale at which the relationship between landscape predictors and species responses is stronger; Jackson and Fahrig 2012), which can lead to inaccurate or biased conclusions (Fahrig, 2003; Arroyo-Rodríguez & Fahrig, 2014; Jackson & Fahrig, 2015). Also, there is a paucity in studies assessing the effect of the regional context, (i.e. comparing species responses among regions), thus limiting our ability to adequately generalize the observed findings across similar regional characteristics (e.g. deforestation degree, matrix type, anthropic pressure) (Pardini et al., 2010; Villard & Metzger, 2014). Obtaining these types of data is particularly urgent for species strongly threatened with extinction, as is the case of most primates (Estrada et al., 2017).

Primates play key roles in ecosystem function, acting as herbivores, seed dispersers, predators, and even ecosystem engineers (Stoner et al., 2007; Stevenson & Guzman-Caro, 2010; Mittermeier et al., 2013; Estrada et al., 2017; Andresen, Arroyo-Rodríguez, & Ramos-Robles, 2018). The loss or decline of primate populations will likely trigger cascading effect with long-term negative consequences for plant diversity (Stevenson & Aldana, 2008), forest regeneration and ecosystem resilience (Russo & Chapman, 2011; Marsh & Chapman, 2013; Andresen, Arroyo-Rodríguez, & Ramos-Robles, 2018). Unfortunately, as most primates are forest-dependent species (Mittermeier et al., 2013), forest degradation is increasingly limiting their distribution and abundance. As a consequence, ~60% of primate species are currently threatened with extinction, as is the case of forest-dwelling howler monkeys (Almeida-Rocha, Peres, & Oliveira, 2017; Estrada et al., 2017).

Habitat loss is considered the main threat to primates persistence in human modified landscapes worldwide (Arroyo-Rodríguez, Galán-Acedo, & Fahrig, 2017). For instance, it has been widely found that patch size (i.e. habitat amount at the local scale) seems to be the main threat for howler monkeys populations in anthropic landscapes (Arroyo-Rodríguez & Dias, 2010). Habitat loss limits resource availability and connectivity, which may in turn alter primate foraging behavior and cause increases in the incidence of disease and parasites, inter- and intraspecific competition, and physiological stress, ultimately having negative effects on primate abundance, diversity and distribution (Honess & Marin, 2006; Marsh & Chapman, 2013; Carretero-Pinzón et al., 2017; Nagy-Reis et al., 2017; Rabelo et al., 2017; Gabriel, Gould, & Cook, 2018). Contrary to habitat loss, habitat fragmentation *per se* (i.e. the number or density of fragments in a landscape), has generally no effect on primates (Thornton, Branch, & Sunquist, 2011; Galán et al. 2019a). This can be explained, in part, due to the fact that several primate species can use the anthropic matrix for travelling, resting and/or foraging (Watling et al. 2011; Galán et al. 2019b), supplementing the resources they obtain in forest patches (Dunning, Danielson, & Pulliam, 1992). This also explain why patch isolation is not a strong predictor of howlers patch occurrence or population size, as individuals of howler monkeys can move across the landscape to supplement their habitat (Arroyo-Rodríguez & Dias, 2010).

Changes in landscape structure are not only a result of landscape-scale practices but also of larger spatial scales (Schweiger et al., 2005; Knop et al., 2006). Regions might differ regarding the patterns of land-use, human pressure, climate or soil conditions. This may have an impact on species responses to landscape structure (Lindenmayer et al., 2008; Pardini et al., 2010; Villard & Metzger, 2014). Hence, primate species may need different conservation strategies depending on the regional context where they occur. However, to our knowledge, only one study has assessed primates’ responses to landscape structure in different regions (Galán-Acedo et al. 2019a). They found that forest cover was strongly and positively related with spider monkeys’ reproductive success in two regions with different amounts of remaining forest (~56% and ~35%). However, abundance increased strongly with matrix functionality in the more disturbed region and was negatively impacted by fragmentation in the less disturbed region.

Here, we evaluated the effects of landscape structure (forest cover, matrix functionality and forest patch density) on the abundance and reproductive success (IFR) of Mexican howler monkeys (*Alouatta palliata* and *Alouatta pigra*). We tested such effects in four rainforest regions of southeastern Mexico, for which we first identified the scale of effect of each landscape predictors on the response variables (Galán-Acedo et al., 2018). Howler monkeys are forest-specialist species (Mittermeier et al., 2013) and thus, landscape forest cover is predicted to be positively related to the abundance and reproductive success of both species, although such response can be stronger in the most conserved region, i.e. where there is more forest remaining at the regional scale (Fahrig, 2013). We also predicted that in regions with more arboreal covers in the matrix , matrix functionality will be positively related to the response variables because primates may use a highly functional matrix for feeding and travelling (Anderson et al. 2007; Fahrig et al. 2011; Watling et al. 2011; Estrada et al. 2012; Tscharntke et al. 2012; Galán-Acedo et al. 2019b). In concordance with previous studies of primates (Thornton et al. 2011, Ateles) and other taxa (Fahrig, 2003; Fahrig, 2017), we also expected that fragmentation would have weak or even positive effects on howler monkeys' responses. Finally, following the 'extinction threshold' hypothesis (Lande, 1987), which proposes that a population's persistence probability dramatically decreases in regions with < 30-40% of remnant habitat, we expected decreased abundance of howlers in the more deforested region.

Methods

Study regions

We worked in four regions in southeastern Mexico: Marqués de Comillas (MC) and the 8th North region (8N) in the state of Chiapas, and the Uxpanapa region (UR) and Los Tuxtlas (LT) in the state of Veracruz (Fig. 1). The primary vegetation type in all regions is tropical rainforest, and climate is hot and wet (Table 1). Deforestation began the earliest in 8N (early 1950s), then in UR (late 1950s), followed by LT (1960) and MC (1970). This history correlates with the amount of forest cover remaining (Table 1): MC (~56%), UR (~35%), LT (~26%) and 8N (~10%). MC and UR are the regions with most arboreal matrix covers regions. UR suffered a fire in 1998 and is currently composed by patches of primary forest embedded in a matrix of secondary vegetation, arboreal and some annual crops and pastures. LT and 8N are, instead, regions with less suitable matrices for arboreal-dependent species composed mainly by open areas (i.e. pastures and annual crops).

The four regions were selected due to their similarity in climate and vegetation, because they have anthropic matrices composed of agriculture and/or cattle pastures, while having different land use change histories, as well as different degrees of forest loss and fragmentation. Thus, regions can be placed along a disturbance gradient, from least to most disturbed: MC, UR, LT and 8N (Table 1).

Table 1

Figure 1

Study species

Howler monkeys are diurnal, arboreal and forest specialists (Rylands et al., 2006). In Mexico, their northern limit distribution, inhabit the Mexican mantled howler monkey (*Alouatta palliata mexicana*) and the black howler monkey (*Alouatta pigra*) (Rylands et al. 2006). Mantled howler monkeys have a mean home range of 25 ha and a body mass of 6.3 kg, whereas black howler monkeys have a mean home range of 27.5 ha and a body mass of 8.9 kg (Mittermeier et al., 2013; Estrada et al., 2017). Due to deforestation in Mexico howler monkey populations are declining these species are classified as Engandered (*A. pigra*) and Critically Endangered (*A. palliata mexicana*) by the IUCN (IUCN, 2017). Currently, *Alouatta pigra* inhabits only MC, and *Alouatta palliata* can be found in UR, LT and 8N.

Forest patches and primate surveys

In each region, we defined a window of ~116,000 ha as study region size. We then randomly selected 12 old-growth forest patches separated by ≤ 2.7 km from each other within three size class categories: 6 patches of 1-10 ha, 4 of 10-50 ha, and 2 of 50-100 ha (48 patches in total). To determine the presence of primates in each forest patch, we walked slowly (~1-2 km/ha) inside and around each focal patch from 6 am to 5 pm. We only worked during sunny days of the dry season (January to June in 2015 and 2016) to avoid the difficulties of detecting and counting monkeys under bad weather conditions. Long distance vocalizations helped us locate groups within the patches. When we had visual contact with a group, we recorded its position with a GPS, and counted all individuals in it. Individuals were classified as adult males, adult females, juveniles and infants.

We surveyed each patch once, but search time was relative to patch size, with 3 consecutive days dedicated to survey small patches (1-10 ha), 5 days in medium-sized patches (10–50 ha), and 7 days in large patches (50-100 ha). In total, we sampled during 192 days (~1900 hours of field observations) and we walked 1020 km (3.9 km to 84 km/patch). As response variables we considered the abundance (i.e. total count) and the reproductive success evaluated as immature-to-female ratio (IFR). Immatures are the sum of juveniles and infants and the ratio was calculated considering the total number of immatures and females in a focal patch.

Landscape metrics

We produced land cover maps of each circular landscape surrounding the focal patches using recent and high resolution Sentinel S2 satellite images (from 2015 and 2016) and ENVI 5.0 software (Fig 1). The classifications performed well, with 90% of accuracy (Kappa index ≥ 0.9). To identify secondary vegetation, we monitored deforestation from 1997 to 2017 in the four regions using Landsat images and the CLASlite software (Asner et al. 2009). In each region, we classified seven types of land cover: (i) old-growth forest ; (ii) secondary vegetation; (iii) connectors (e.g. live fences, riparian corridors, and isolated tree patches of a maximum canopy area of 0.25 ha); (iv) arboreal crops (e.g. rubber plantations); (v) annual crops and cattle pastures; (vi) human settlements; and (vii) water bodies (Fig. 1). Our definition of connectors is based on the fact that patches ≤0.25 ha cannot be considered habitat because they are only used by primates as corridors and/or as supplementary resources (Asensio et al. 2009; Pozo-Montuy et al. 2013).

We analyzed the effects of 3 landscape predictors, two metrics of landscape composition (forest cover and an index of matrix functionality) and one metric of landscape configuration (forest patch density) using the scales of effect. These landscape predictors were calculated using ArcGis 10.5 software with the Patch Analyst extension (Rempel, Kaukinen, & Carr, 2012). Forest cover refers to the percentage of old-growth forest cover in the landscape, and it is positively related to landscape connectivity (Fahrig, 2013). To calculate matrix functionality, we first ranked the functionality of all land cover types that are not the original habitat of spider monkeys (i.e. old-growth forest), from 1 (lowest functionality) to 6 (highest functionality). Such a ranking was based on our understanding of the ability of spider monkeys to use different land covers in the matrix for feeding and/or travelling (Arroyo-Rodríguez et al., 2017): 1 (water bodies), 2 (human settlements), 3 (open areas), 4 (tree plantations), 5 (connectors), and 6 (secondary vegetation). The matrix functionality index was calculated as follow: MFI = [(1 × % of water bodies) + (2 × % of human settlements) + (3 × % of open areas) + (4 × % of tree plantations) + (5 × % of connectors) + (6 × % of secondary vegetation)]. To make this index independent of forest cover, we calculated all percentages considering the area covered by all land covers in the matrix, and not by total landscape area (Garmendia et al., 2013). This index varies between 100 (100% composed of water) and 600 (100% composed of secondary vegetation), and is therefore positively related to resource availability in the matrix and to matrix permeability (Garmendia et al., 2013). Finally, forest patch density refers to the number of forest patches within the landscape divided by total landscape area (n/ha). This widely used landscape metric is an accurate descriptor of forest fragmentation (Lenore Fahrig, 2017). Overall, these landscape predictors have demonstrated to be of key relevance for different vertebrates (Ewers & Didham, 2006; Smith, Fahrig, & Francis, 2011), including primates (Thornton, Branch, & Sunquist, 2011; Arroyo-Rodríguez et al., 2013).

We followed the protocol proposed by Jackson and Fahrig (2015) to identify the scale at which the relationship between a landscape predictor and a species' response is strongest (i.e. scale of effect). We did this separately for each predictor-response combination in each region (Galán-Acedo et al. 2018). Using regression analyses we tested 13 scales, varying the radius of the circular landscapes (measured from the center of the focal patch) in 100 m increments, with the smallest radius being 100 m and the largest 1300 m at 100 m. The scale of effect was the landscape size at which the strongest associations between each response variable and each predictor were observed (Supporting Information Table S1). More detailed information about this assessment can be founded in Galán-Acedo et al. (2018).

Statistical analyses

We first tested for spatial independence among samples with Mantel tests using package 'vegan' (Oksanen et al. 2016) for R version 3.0.1 (R Core Team 2013). None of these tests detected a significant spatial autocorrelation in our datasets ($R < 0.04$, $p > 0.60$, in all cases). To assess collinearity among landscape predictors we estimated their variance inflation factors (VIF) using the 'car' package for R. We did not detect significant collinearity between predictors, as all VIF values were < 2.71 (Neter et al., 1996).

To evaluate the effects of landscape variables on each response variable we built generalized lineal models including all three landscape predictors (forest cover, matrix functionality and patch density). All models were built using the package glmulti for R (Calcagno & de Mazancourt, 2010). We used an information-theoretic approach and multimodel inference to assess the relative effect of each predictor on each response variable (Burnham & Anderson, 2002). For each response variable we constructed 4 models, representing all combinations of explanatory variables. For each model we computed the Akaike's information criterion corrected for small samples (AICc), and we ranked the models from best to worst (Supporting Information Table S2). The set of models with a difference in AICc (ΔAICc) <2 was considered to have strong empirical support and similar plausibility, explaining most of the variation in the response variable (Burnham & Anderson, 2002). Finally, we used Akaike weights (w_i) to evaluate the empirical support for each predictor and produce model-averaged parameter estimates (Anderson, 2007). Hence, we summed w_i of ranked models until the total was >0.95 (Whittingham et al., 2005). The set of models for which $\sum w_i$ is 0.95 represents a set that has 95% probability of containing the true best model (Burnham & Anderson, 2002). Models for IFR were tested using a Gaussian error structure. When we analyzed howlers' abundance we constructed generalized linear models with a Poisson error and a log-link function. We corrected overdispersion associated with Poisson models using QAICc values instead of AICc (Calcagno & de Mazancourt, 2010).

Results

In total, we recorded 579 individuals of howler monkeys in the four regions. In MC we recorded 244 individuals of black howler monkeys in 44 groups, inhabiting 9 out of the 12 patches. In UR we recorded 51 individuals of mantled howler monkeys in 6 groups that inhabited 6 out of 12 patches. In LT we found 116 individuals spanned in 11 groups inhabiting 5 out of 12 patches, and the 8N region was inhabited by 168 individuals of mantled howler monkeys separated in 13 groups inhabiting 9 out of 12 patches (Table 2).

Table 2

Most associations between landscape metrics and response variables were relatively strong (>37.5% of deviance explained by each complete model, excluding abundance in UR and the 8N region; Fig. 2). In MC, abundance was strongly and positively related to forest cover ($\sum w_i = 0.9$) and decreased with increasing forest patch density ($\sum w_i = 0.9$; Fig 2a). Also, in this region immature-to-female ratio (IFR) increased with matrix functionality ($\sum w_i = 0.7$; Fig 2b). In UR, the association between landscape metrics and abundance was relatively weak (11.1% of explained deviance). Forest patch density was the variable more strongly related to abundance in this region ($\sum w_i = 0.2$; Fig 2c), but the unconditional variance was greater than the model-averaged parameter estimate (Table 3), suggesting that caution is needed in the interpretation of this parameter estimate. In the same region, matrix functionality was positively related to IFR ($\sum w_i = 0.5$; Fig 2d). In LT forest cover was strongly and positively related to both response variables, but this association was stronger when assessing abundance (abundance: $\sum w_i = 0.8$, Fig 2e; IFR: $\sum w_i = 0.6$; Fig 2f). Finally, in the most deforested region (8N) we found that abundance was positively, though weakly, associated to matrix functionality ($\sum w_i = 0.3$; Fig 2g). In the same region, IFR was negatively related to all the landscape predictors, especially to forest cover ($\sum w_i = 0.6$; Fig 2h).

Figure 2

Table 3

Discussion

To our knowledge, this is the first study that assesses the impact of landscape structure on the abundance and immature-to-female ratio (IFR) of two endangered primates, comparing such impact among regions with different land-use intensity. Our findings indicate that forest cover is positively related to primate abundance and IFR in most regions. Yet, contrary to our expectations, in the most deforested region forest cover was negatively related to IFR. As we expected, matrix functionality has a relatively strong positive effect on IFR in regions with more suitable (arboreal) matrices (MC and UR). Patch density (a metric of forest fragmentation) generally shows weak effects on all responses, but contrary to our hypothesis, in the best preserved region this landscape predictor was negatively related to monkey abundance. Finally, contrary to our expectations, the most deforested region (8N) has high abundance of howler monkeys but landscape predictors have mostly negative effects on howlers' abundance and reproductive success.

Forest cover was positively related five of eight models in the different regional contexts. This effect was particularly strong to howlers' abundance in the most conserved region (MC), thus suggesting that in regions with relatively high forest cover, species abundance depends on habitat amount. Forest cover increases the availability of food for forest-specialist species and increase landscape connectedness, thus favoring animal movements across the landscape (Fahrig, 2003; Fahrig, 2013; Marsh & Chapman, 2013; Carretero-Pinzón et al., 2017). Forest cover was also strongly and positively related to abundance and reproductive success in LT, a more disturbed region (26% of old-growth forest) with a homogeneous matrix composed of pastures and annual crops. As these land covers have very low functionality for forest-dwelling species (Prevedello & Vieira, 2010; Fahrig et al., 2011), howlers can be more strongly dependent on forest cover under this regional context. Nonetheless, contrary to our expectations, forest cover was strongly and negatively related to the reproductive success in the most deforested region.

As forest cover, fragmentation had negative effects on black howler monkeys' abundance in the most preserved region (MC). This result is opposite to the fragmentation threshold idea (Lande, 1987), according to which one expects stronger negative responses to habitat fragmentation when habitat amount is low (approximately 20–30% of the area). However, in conserved regions, primates inhabiting landscapes with high forest cover could not be used to some types of anthropic alteration (such as fragmentation) moving to other areas without perturbation in the landscape. Also, more fragmented regions can imply a high degree of human presence and hunting in the landscape, decreasing howler monkey abundance. Except the abundance model in MC, we found that the unconditional variance of fragmentation was higher than the model-averaged parameter estimate, suggesting caution with the interpretation of this parameter (Burham and Anderson 2002; Anderson 2007).

Consistent with our hypothesis, matrix functionality showed strong and positive effects on howler monkeys' reproductive success in the more heterogeneous regions, (MC and UR). However, in these regions matrix functionality had a negative but weak effect in howlers' abundance. These regions have a matrix composed by secondary vegetation, arboreal crops (rubber, citrics, oil palm), annual crops and pastures, compared to LT and 8N, that are mainly composed by pastures and annual crops. Therefore, in regions with more functional matrices (i.e. structurally more similar to their natural habitat; Prevedello and Vieira 2010; Fahrig et al. 2011) primates can use these covers more easily for feeding, which increases individuals (and immatures) survival (Watling et al., 2011; Blanco & Waltert, 2013; Arroyo-Rodríguez et al., 2017). This process is called ‘landscape supplementation’ (Dunning, Danielson, & Pulliam, 1992) and presumably plays an important role on primates’ persistence in altered landscapes (Galán-Acedo et al. 2019b). Also, because arboreal matrices provide opportunities for dispersal, primates’ abundance can decrease in landscapes with more functional matrices because individuals are moving across the landscape. Thus, heterogeneous landscapes provide higher resilience and stability to human-modified landscapes (landscape-moderated insurance hypothesis; Tscharntke et al. 2012).

Contrary to our expectations, population primate regional abundance does not decrease in regions with less than 30-40% of habitat. In fact, *Alouatta palliata* is more abundant in the most degraded region and decreased with the increasing of forest cover. This result can suggest that in more disturbed areas howlers are easier to identify and that this primate species cope and even could benefit from disturbed habitats. In this sense, the habitat-amount threshold, which proposes that a population’s persistence probability dramatically decreases in areas with < 30-40% of remnant habitat, likely varies depending on species habitat requirements and their ability to use the anthropic matrix (Fahrig, 2001; Morante-Filho et al., 2015). Howler monkeys are frequently considered to have high behavioral flexibility that allows them to cope with degraded habitats (Bicca-Marques, 2003; Arroyo-Rodríguez & Dias, 2010). For instance, it has been found that howlers can change their home range size, diet composition and activity budget in response to habitat disturbance (Arroyo-Rodríguez & Dias, 2010). All these behavioral changes can increase howlers’ ability to inhabit strongly anthropic landscapes.

Concluding, this study highlights the influence of the regional context for maintaining primate populations in anthropic degraded landscapes. Primate-landscape associations were mostly strong (i.e. high explained deviance by the models), probably because howler monkeys are forest specialists. Our findings suggest that landscape composition has relatively stronger impacts on primates than landscape configuration. Also, our results points out that preventing forest loss should be a conservation action, particularly in the most conserved regions and in homogeneous regions with relatively high degrees of deforestation (26% of remnant forest). Increasing matrix functionality is also important to increase howlers' reproductive success, particularly in regions with more arboreal matrices. Moreover, limiting forest fragmentation in conserved regions is necessary to avoid decrements in howlers' abundance. Finally, studies considering other variables such as anthropic pressure, movement behavior across the landscape, diet or variables at local scales (e.g. basal area) are needed to understand what is affecting to howler monkey populations in severe deforested regions.

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Table 1. Characteristics of the study regions in southeastern Mexico. Regions are ordered from the least to most disturbed.

	Marqués de Comillas	**Uxpanapa region**	**Los Tuxtlas**	**8th North region**
Coordinates	90º41’8.7”W 16º2’49.3”N	94º24’30.216”W 17º8’46.1”N	98º38’00”W 18º03’00”N	93º08’00”W 17º45’15”N
Mean annual temperature (ºC)	22-26	24-26	22	25
Mean annual precipitation (mm)	2,143	3,640	4,900	2,600
Start of deforestation	1970’s	1950’s	1960’s	1950’s
Dominant anthropic land covers in matrix	Agriculture and cattle pastures	Agriculture and cattle pastures	Cattle pastures	Cattle pastures
Remaining forest cover (%)	~56%	~35%	~26%	~10%

Table 2. Demographic characteristics of howler monkeys in each study region.

	Marqués de Comillas	**Uxpanapa región**	**Los Tuxtlas**	**8th North region**
Primate species	*Alouatta pigra*	*Alouatta palliata*	*Alouatta palliata*	*Alouatta palliata*
# Occupied patches	9	6	5	9
# Individuals	244	51	116	168
# Groups	44	6	11	13
IFR	0.98 (range = 0-2)	0.30 (range = 0-1)	0.11 (range = 0-0.29)	0.51 (range = 0-1)

Table 3 Values of model-averaged parameter estimates (*β*) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference for both response variables (abundance and reproductive success) for the three landscape predictors in each of the study regions (see all model sets in Supporting Information Table S2). Asterisks indicate cases in which the unconditional variance (UV) is higher than the model-averaged parameter estimates (β), suggesting caution with interpretation of this parameters.

Region/Predictors	Abundance		Immature to female ratio	
	B	UV	*B*	UV
Marqués de Comillas				
Forest cover	0.024	0.00006	-0.004	0.0001
Matrix functionality	-0.0008	0.000004	0.003	0.000009
Patch density	-10.098	7.503	-0.383	2.031*
Uxpana region				
Forest cover	0.0004	0.00002	0.002	0.00002
Matrix functionality	-0.0003	0.0000008	0.002	0.000005
Patch density	1.373	8.681*	0.366	1.366*
Los Tuxtlas				

Forest cover	0.040	0.0004	0.002	0.000007
Matrix functionality	-0.006	0.0001	-0.0003	0.000001
Patch density	0.539	1.346*	-0.027	0.014
8th North region				
Forest cover	-0.006	0.0002	-0.019	0.0004
Matrix functionality	0.0008	0.000001	-0.0004	0.000005
Patch density	-2.533	34.694*	-2.420	26.768*

Figure legends

Figure 1. (a) Location of the four study regions in southeastern Mexico. (b) Study regions are ordered from the least to the most disturbed: MC = Marqués de Comillas, (c) UR = Uxpanapa region, (d) LT = Los Tuxtlas and (e) 8N = 8th North region. Red marks represent the selected study forest patches. For simplicity, we do not add all classified land covers in each region, but only those with higher contrast (forest cover is indicated with dark green, open areas with light green, water bodies in blue, and white polygons represent human settlements).

Figure 2. Predictor variables included in 95% set of models (bars) for the two response variables, abundance and reproductive success of howler monkeys, and for the four study regions (MC = Marqués de Comillas, UR = Uxpanapa region, LT = Los Tuxtlas, 8N = 8th North region). Black howler monkeys (*Alouatta pigra*) inhabit MC, while mantled howler monkeys (*Alouatta palliata mexicana*) inhabit the other three regions. The importance of each variable is shown by the sum of Akaike weights ($\sum w_i$). We assessed the impact of three landscape predictors: forest cover (FC), matrix functionality (MF) and forest patch density (PD). The percentage of deviance explained by each complete model (i.e. goodness-of-fit of each complete model) is indicated in each panel. Positive (+) or negative (-) effects of each landscape predictor on each response variable are indicated. When the unconditional variance was higher than the model-averaged parameter estimates we do not indicate the sign (+/-) of effect, because such patterns suggest caution with interpretation of parameter estimates (see Table 3).

Figure 1

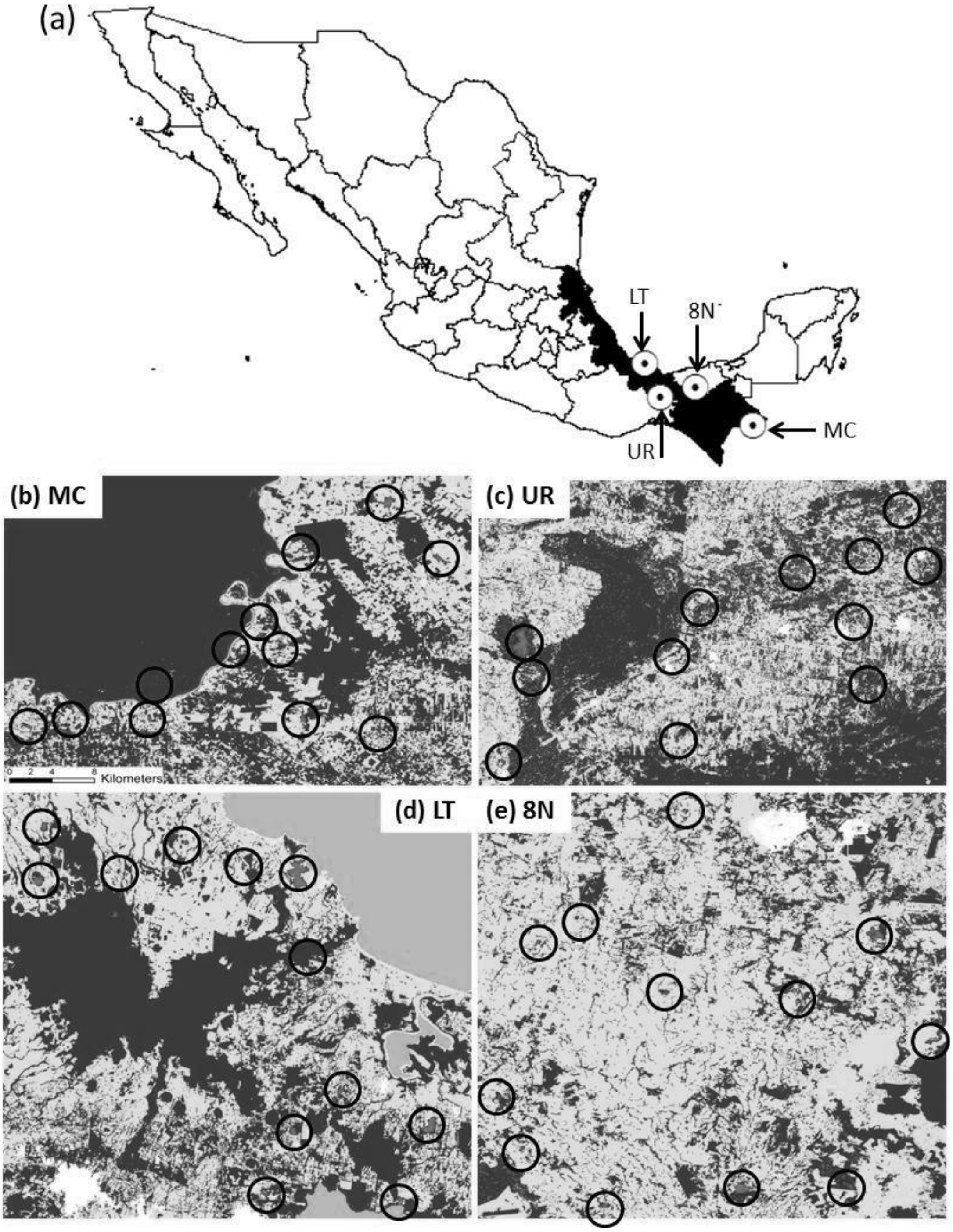
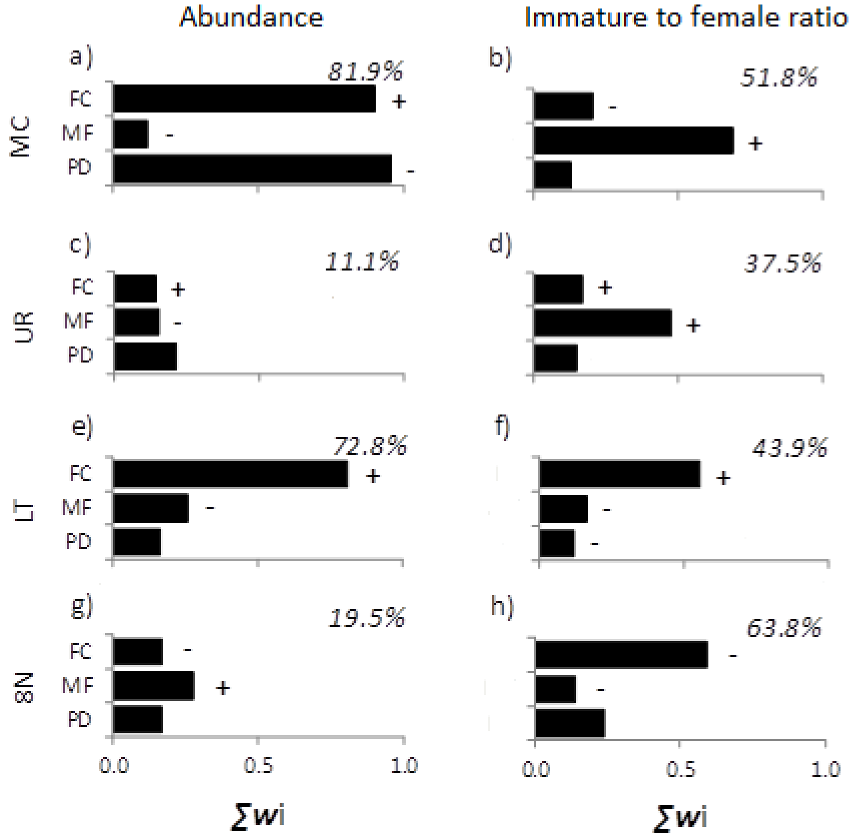


Figure 2


Abundance
Immature to female ratio
a)
81.9%
FC
MF
PD
+
-
-
MC
b)
51.8%
-
+
c)
11.1%
FC
MF
PD
+
-
UR
d)
37.5%
+
+
e)
72.8%
FC
MF
PD
+
-
LT
f)
43.9%
+
-
-
g)
19.5%
FC
MF
PD
-
+
8N
h)
63.8%
-
-
0.0
0.5
1.0
∑wi
0.0
0.5
1.0
∑wi

Capítulo 6

The conservation value of human-modified landscapes for the world's primates

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Abstract

Land-use change pushes biodiversity into human-modified landscapes, where native ecosystems are surrounded by anthropic land covers (ALCs). The ability of species to use these emerging covers remains poorly understood. We quantified the use of ALCs by 147 primate species worldwide, and analyzed species' attributes that predict such use. Most species use secondary forests and tree plantations, while only few use human settlements. ALCs are used for foraging by at least 86 species with an important conservation outcome: those that tolerate heavily modified ALCs are 26% more likely to have stable or increasing populations than the average for all primates. There is no phylogenetic signal in ALCs use. Compared to all primates on Earth, species using ALCs are less often threatened with extinction, but more often diurnal, medium or large-bodied, not strictly arboreal, and habitat generalists. These novel findings provide valuable quantitative information for improving management practices for primate conservation worldwide.

Introduction

With ~70% of all terrestrial ecosystems currently altered by human activities[1], the preservation of biodiversity and ecosystem functions is challenging[2], particularly in the tropics[3]. As a consequence of land use change, an increasing number of species are being 'forced' to inhabit human-modified landscapes, which are constituted by a mosaic of different land covers, both natural and anthropic. The ability of organisms to use anthropic land covers (ALCs) is rapidly becoming a key determinant of their persistence in human-modified landscapes[3,4]. Therefore, a better understanding of how and why some species use different types of ALCs is urgently needed to better predict and manage biodiversity in the Anthropocene[5].

Traditionally, the ALCs surrounding remnants of natural vegetation are referred to as "the matrix"[4,6]. However, rather than being regarded as a homogeneous land cover of unsuitable habitat, as assumed in early classical models[7,8], the anthropic matrix should be viewed as collection of different ALCs, many of which can be used by species for different purposes, including foraging, dispersal and reproduction[6,9]. In fact, there is evidence for birds, frogs, small mammals, and ants showing that the higher the ability of a species to use ALCs, the lower their probability of becoming extinct in fragmented landscapes[9-11]. In other words, patch-dependent species typically have higher extinction thresholds[12], meaning they require larger amounts of unmodified habitat to avoid extinction[13]. Unfortunately, for many species, studies mostly focus on their ecology within their primary habitat, especially in protected areas[14], thus limiting our understanding of their use of and tolerance to ALCs. This information is urgently needed to shed light on many theoretical debates about the main drivers of biodiversity patterns in human-modified landscapes.

The predominance of the habitat–matrix paradigm (i.e. binary landscapes comprised of either habitat or non-habitat) in landscape ecology has been strongly criticized[15,16] and is gradually being replaced by novel approaches based on heterogeneous landscapes[17,18]. Emerging ecological approaches, such as ‘countryside biogeography’[19] and different theoretical models[20,21] and debates (e.g. land-sharing vs. land-sparing debate[22,23]) are based on the premise that the matrix is in fact heterogeneous, and that each ALC type may span a spectrum of species-specific ecological value. To better understand species’ responses to landscape changes we need to assess the ecological role of each land cover (e.g. provision of food, refuge, nesting sites) to be able to design “functional landscapes”[18]. This information can be used to improve management and conservation strategies. For instance, if species are relatively resilient to changes in their habitat and able to use resources in ALCs, they will fare better with a land-sharing approach that limits land-use intensification at the potential cost of increased habitat conversion[24]. Alternatively, if species are highly sensitive to habitat changes and are unable to use ALCs, a land-sparing approach will be more effective as it maximizes natural habitat conservation whilst concentrating production elsewhere[22].

Non-human primates (primates, hereafter) are particularly susceptible to land-use changes[25], which threaten ~60% (n = 278 species) of the world’s 504 species with extinction[26]. As most primate species are forest specialists, particularly in the Neotropics[27] forest loss is considered a main threat to primate conservation[28]. There are, though, many local and landscape characteristics that may help reduce the impact of habitat loss on primate survival in human-modified landscapes[29]. However, most research has focused on assessing the effects of the characteristics of natural vegetation remnants on primate diet, behavior, and demography[30]. While primates are known to use some types of ALCs[31–33], the available evidence is widely scattered and the global patterns of use remain unknown beyond a qualitative level. Further, no comprehensive effort exists to link primates’ ecological traits to the extent of use of specific ALCs, greatly limiting our ability to predict the impact of specific landscape-management strategies on these mammals.

Our main goals were to assess quantitative patterns regarding which types of ALCs are most frequently used by primates and for what activities, and to determine whether there are certain characteristics of the species, such as conservation status, ecological traits, and/or phylogenetic relationships, that may help us predict their use of ALCs. We addressed these questions by reviewing 468 records of ALC use by primates. We focused on the most common ALC types in human-modified landscapes, including human settlements, open areas (i.e. annual crops and cattle pastures), tree plantations, connectors (i.e. isolated trees and linear landscape elements such as live fences and hedgerows), and secondary forests (i.e. regenerating forests following the removal of native vegetation). We compared the characteristics of species using these ALCs with the expected values based on all of the world's primates. The primate characteristics considered were: conservation status (IUCN conservation category and population trends), ecological traits (diel activity, locomotion, trophic guild, body mass, and forest specialization) and phylogenetic relationships.

Results

Figure 1

Primates' global use of ALCs

We found positive evidence that at least 147 primate species (~30% of 504 primate species on Earth) use one of the five ALC types, with 60 genera (out of 82 genera in the world, ~75%) and all 15 families represented. Use of ALCs was evident worldwide (Fig. 1a), but the percentage of species was significantly higher than expected by chance in mainland Africa, and lower than expected in Madagascar ($\chi^2 = 15.78$, $P = 0.001$; Fig. 1b). Different ALC types varied in the number of species using them ($\chi^2 = 20.64$, $P < 0.001$; Fig. 1c): secondary vegetation was used by the highest number of species (79) and human settlements were used by the lowest (34). This is not surprising, as these two types of ALC represent two extremes in a gradient of habitat modification. This pattern was particularly evident in the Neotropics and in Madagascar (Fig. 1d), where most species are strictly arboreal. On the other hand, a higher proportion of primates from mainland Africa were recorded using human settlements and open areas and a higher proportion of primates from Asia used tree plantations, human settlements and open areas such as annual crops and cattle pastures (Fig. 1d). This is probably because many primate species in these two biogeographic realms have both arboreal and terrestrial locomotion modes. In some regions of these realms this pattern can also be caused by peoples' perception of primates as sacred animals, which favours their persistence in human-dominated environments[35,36].

All ALC types were used for foraging, resting, and travelling (Fig. 2). Human settlements and secondary forests were mostly used for either foraging or all activities combined, suggesting that these ALCs can be used as temporary or permanent habitats under certain conditions. Although most studies did not report if the species were using ALCs as habitat, at least 86 species (17% of all primates on Earth) are actively obtaining food resources from ALCs, highlighting their importance for primate conservation[32,37]. In the case of forest-specialist primates, which represent 70% of the studied species, these results suggest that they can supplement their diet by foraging in ALCs – a process referred to as "landscape supplementation"[20]. Connectors, such as living fences and isolated trees, supported primate foraging for 24 species, but almost half of the records were for travel alone, demonstrating the important role of these ALCs in increasing landscape connectivity[32,38,39]. An important next step will be to assess which species can maintain their populations solely in ALCs, which species are strongly dependent on their natural habitats, and which ones may survive in natural habitat patches with some degree of landscape supplementation in ALCs.

Figure 2

Conservation signal in ALCs use

We found a significant, positive relationship between the use of ALCs and both conservation status and population trend (IUCN red list[40]; Fig. 3).The proportion of species classified as Least Concern was significantly higher in the group of primates recorded using ALCs, compared to all primates, particularly in human settlements ($\chi^2 = 18.95$, $P < 0.001$). Nearly half of all species recorded using ALCs were classified as Vulnerable, Endangered or Critically Endangered by IUCN (Fig. 3a), suggesting that ALC use alone does not necessarily prevent endangerment. Although use of ALCs may favor primate persistence in human-modified landscapes, it is important to recognize that their use also exposes primates to important threats, such as hunting, road kills, predation and infectious diseases[41–43].

Primate species that use human settlements, the most modified ALC type we examined, were more likely to have stable or increasing populations than the global average, showing the implications of behavioral tolerance to human presence for conservation. About 80% of all species using ALCs showed declining population sizes (Fig. 3b). Nonetheless, ALC use seems to soften this pattern, as we found a lower proportion of species with decreasing populations using ALCs than would be expected based on the world's primates. The latter pattern was particularly strong for primates using human settlements ($\chi^2 = 25.52$, $P < 0.001$) and open areas ($\chi^2 = 10.67$, $P = 0.005$). These results suggest that species able to use highly modified ALC types have a higher probability of persisting in anthropogenic tropical landscapes.

Figure 3

Ecological traits that predicts ALCs use in primates

We also found significant associations between the ecological traits of primates and their use of ALCs (Fig. 4). In particular, nocturnality was less frequent among species using ALCs, especially in open areas ($\chi^2 = 13.88$, $P < 0.001$), secondary forest ($\chi^2 = 11.58$, $P = 0.003$), connectors ($\chi^2 = 9.62$, $P = 0.008$) and human settlements ($\chi^2 = 8.52$, $P = 0.014$; Fig. 4a). We would have expected a higher (not lower) incidence of nocturnality among species using ALCs because nocturnal primates are less likely to encounter humans, and thus, they could perceive ALCs as less dangerous, compared to diurnal primates[44]. Yet, nocturnal primates are all forest specialists, arboreal and with small-to-medium body mass – ecological traits that together seem to limit the use of ALCs. In this regard, strictly arboreal species were less frequent in the group of primates using ALCs, particularly among those using human settlements ($\chi^2 = 19.66$, $P < 0.001$) and open areas ($\chi^2 = 13.95$, $P < 0.001$; Fig. 4b). Similarly, there was also a lower proportion of small-bodied species using ALCs than expected by chance, particularly, once again, among those using human settlements ($\chi^2 = 12.43$, $P = 0.002$) and open areas ($\chi^2 = 19.01$, $P < 0.001$; Fig. 4c). The latter result is not surprising as large-bodied species are more likely to be terrestrial, which facilitates their movement into treeless areas. Also, small primates, which tend to have small home ranges[45], may be able to persist in habitat remnants for a longer time period, compared to larger primates with larger home ranges; this may lower the probability of observing them in ALCs, especially in landscapes with a relatively recent history of anthropic land use (e.g. < 30 y). Even though forest-specialists were less frequent among ALC-tolerant species (χ^2 = 11.19, P = 0.003), particularly in human settlements (χ^2 = 31.53, P < 0.001) and open areas (χ^2 = 11.76, P = 0.003) (Fig. 4d), they were present in all land cover types. Taken together, these results suggest that the more generalist a species is in terms of habitat and/or locomotion, the more resilient it is to habitat disturbance[46]. Surprisingly, primate trophic guild was not related to the use of ALCs, although there was a weak trend towards a higher proportion of omnivorous species in human settlements than expected (Supplementary Fig. 1).

Figure 4

Phylogenetic signal in ALCs use

Figure 5

We found a very weak phylogenetic signal in the use of ALCs (Fig. 5), where it was neither clustered nor randomly distributed across the phylogenetic tree (D = 0.83; P [D = 0] < 0.001; P [D = 1] = 0.001). The sensitivity analyses revealed that removing Cercopithecidae, the primate family with the largest number of species analysed, did not influence the estimates of phylogenetic signal. However, the removal of sportive lemurs (family Lepilemuridae) significantly influenced our estimates of phylogenetic signal, despite having a similar number of species to most other families (see Supplementary Note 1). In particular, our results indicate that most species in this primate family do not use ALCs, i.e. non-use of ALCs is a phylogenetically conserved characteristic for this clade. The highly conserved morphology and shared ecological traits (e.g. arboreal locomotion, nocturnal activity, forest specialization) within this family[48] could explain this pattern. In contrast, the behavioral and ecological traits that could make a species tolerant to ALC conditions vary in their degree of phylogenetic conservatism[49]. This, together with the widespread alteration of primates' habitats, leads to a pattern in which the use of ALCs is unpredictable in relation to species' evolutionary relationships.

Discussion

Given the ongoing loss and alteration of primates' natural habitats, knowledge about how and why some species are able to use anthropic land covers is essential to propose effective conservation strategies in human-modified landscapes. For the first time, we provide a comprehensive quantification of the use of five dominant types of ALCs by primates worldwide. We also provide a global assessment of the relationships between primate use of ALCs and primates' ecological traits, conservation status and phylogenetic relationships. Our findings highlight the fact that ALCs can play important roles for the conservation of many primate species in anthropogenic landscapes, providing food resources, refuge and opportunities for dispersal. We note, however, that for 70% of the primates on Earth, we found no evidence of ALC use, suggesting that benefits associated with ALCs are limited to some species, in which case they are unlikely to prevent the extinction crisis of the world's primates[26]. While some poorly studied species might also be able to exploit ALCs, many other species are likely to depend on remnants of their primary habitat for their long-term conservation. Also, the use of ALCs can have negative effects on primates' populations, as it increases both exposure to several threats and occurrence of conflicts with humans due to crop raiding, aggression or disease transmission[41–43]. Thus, although priority conservation actions should focus on the maintenance of primary habitats for primates and other vertebrate taxa[9], they can be complemented with other land-management strategies such as replacing highly modified ALCs by more functional land covers that provide resources for wildlife or facilitate their movement between habitat patches. Such an integrative approach will enhance the conservation value of increasingly modified landscapes for our closest relatives.

METHODS

Evidence of ALC use by primates

We systematically searched for articles published up to November 2nd, 2016, using the following search term sequence in ISI Web of Knowledge (www.isiwebofknowledge.com), SciVerse SCOPUS (www.scopus.com) and Google Scholar (https:// scholar.google.com.br/) databases: [(primate* OR monk*) AND (“plantation” OR “crop” OR “agroecosystem” OR “cultivation” OR “agriculture” OR “regenerating forest” OR “regenerating vegetation” OR “secondary forest” OR “secondary vegetation” OR “second growth” OR “clear cut” OR “live fence” OR “isolated trees” OR “scattered trees” OR “remnant trees” OR “corridor” OR “fencerow” OR “corridor line” OR “bridge” OR “stepping stones” OR “fence” OR “connectivity” OR “hedgerow” OR “strip” OR “city” OR “urban” OR “human settlement” OR “village” OR “settlement” OR “pasture” OR “grazing line” OR “ground” OR “cattle” OR “ground”) AND/OR (“fragmentation” OR “landscape”)]. These keywords were searched across all reference topics, except in Web of Knowledge where searches were restricted to title, abstract and keywords of articles. We then conducted additional searches in Google Scholar using keywords translated into both Portuguese, Spanish and French, including the “grey literature” (e.g. MSc and PhD theses and unpublished reports). We classified all hits obtained into five groups, depending on the type of ALC used by primates: (i) human settlements (i.e. any kind of urban environment such as cities, towns or villages), (ii) open areas (i.e. annual crops and cattle pastures), (iii) tree plantations (including all types of agroforestry systems), (iv) connectors (i.e. isolated trees and linear landscape elements, such as vegetation corridors, live fences and hedgerows), and (v) secondary forests (i.e. regenerating forests following regrowth after an acute disturbance event, such as logging and deforestation, at any stage of succession). We excluded review articles and studies with captive or reintroduced animals. Because for some ALCs the available literature is scarce, we selected the most recent 60 studies per each type of ALC. Nevertheless, as some studies included information about more than one ALC type, the final database included 258 independent studies (Supplementary Table 1) containing 468 records of 147 primate species using ALCs. Such records span 44 countries from four biogeographic realms: mainland Africa (17 countries), Madagascar, Asia (13 countries), and the Neotropics (13 countries).

From each study, we obtained, for each primate species, the scientific name and family, geographic coordinates and country, and the activity recorded within the ALC (i.e. travelling, resting, foraging, or all activities). Travelling refers to movements within and between ALC types. Resting refers to short/long diurnal/nocturnal rests, and foraging refers to the procurement, acquisition and/or ingestion of food. We assumed that resting and foraging require travel to reach any given destination. Therefore, the category of 'all activities' included studies that reported observations on all three main activities, or resting and foraging, in an ALC. As most studies did not report extended information about the use of each ALC, we cannot know if primates are using it as habitat. Information about the surrounding landscape, such as distance to the nearest edge, proportion of remaining primary habitat, were not reported in the vast majority of studies, thereby precluding analyses related to these types of information. Furthermore, although studies reported general coordinates of the study sites, most did not report the coordinates where the individuals were recorded in a ALC, limiting our capacity to assess the landscape context.

Conservation and ecological predictors

For each primate species we obtained the conservation status, the population trend, and whether they are forest-specialists or not, from the International Union for Conservation of Nature (IUCN) database in the 'letsR'[50] package for R, version 3.0.1.[51]. Regarding ecological traits, we considered: locomotion mode (i.e., arboreal, terrestrial or both), diel activity (i.e., diurnal, nocturnal or cathemeral), body mass and trophic guild. Although body mass is a morphological trait, we considered it as an ecological trait because of its very high ecological significance. For instance, it is positively related to home range size, thus affecting the way species interact with their environment[52,53]. Body mass was categorized into three classes: small (<2 kg), medium (2-10 kg), and large (>10 kg). Trophic guilds included six general groups: frugivorous (>60% of fruits in diet), folivorous (>60% leaves in diet), folivorous-frugivorous (diet comprised of both fruits and leaves in similar proportions), omnivorous (both plants and animals in diet), insectivorous (diet dominated by arthropods) and gummivorous (diet dominated by plant exudates). Ecological trait data was primarily extracted from Mittermeier *et al.*[27]. When some of the ecological traits were not reported in this encyclopedia, we actively searched for information in the literature. When the trait was reported in other scientific articles or databases, we searched for 1-3 references (depending on availability) and we used mean or modal values (Supplementary Table 2). In total, we reviewed 370 studies, most of them published in peer-reviewed scientific journals and books. For each specific datum we included the corresponding reference. The database was carefully checked for possible errors. When a specific datum was considered non-reliable (e.g., very extreme or contradictory values, and values obtained with questionable methodology) we did not include it in the database. To assess relationships between primate characteristics and ALC use, we used goodness of fit Chi-square tests. We selected this analysis because it is particularly recommended to compare observed vs. expected frequencies. In particular, we compared the number of species with each trait between those species that were observed using ALCs and the expected values based on all of the world's primates. We excluded from analyses species for which there was no available information.

Phylogenetic signal

To quantify phylogenetic signal in ALCs use, we used published phylogenetic relationships and divergence times from a molecular timetree built using 79 gene segments for 372 species (367 primates and 5 outgroup species) and 8 fossil-calibrated nodes[54]. Specifically, we used the timetree built considering autocorrelated rates of molecular evolution (identified by Bayesian model selection as fitting the data better than a model with independent rates), and a conservative interpretation of both the age and the placement of key fossils with the living primate radiation. Of the 367 species included in this phylogeny, we retained 352 after standardizing synonyms and dropping infraspecific taxa.

To explore how phylogeny might capture species differences in ALCs use, we calculated the D statistic[55]. D measures phylogenetic signal strength in binary traits. Values of D are scaled to set points of 0.0 (trait values phylogenetically conserved as expected under a Brownian Motion threshold model) and 1.0 (trait values distributed randomly across the phylogeny). For significance testing, the observed distribution of trait values at the tips of the tree was compared to both randomly shuffled values and the expected values from a Brownian Motion threshold model. For all tests of phylogenetic signal, we used the *phylo.d* function in the R package 'caper'[56]. We used 9999 permutations to estimate the probability of the observed value of D under null models of both no phylogenetic structure and Brownian Motion.

To investigate the non-random but weak result we found for the Order as a whole, we tested whether certain clades were driving relatively large changes in our estimates of phylogenetic signal. We adapted the framework provided in the ‘sensiPhy’ package to perform sensitivity analyses and tested how excluding families (with ten or more species) from the analyses would influence the estimates of phylogenetic signal. When the removal of a clade leads to a large change in the estimate of D, it can be considered to be influential. To correct for clade size, we used randomization tests to determine if the change in parameter estimates is significantly different from a null distribution created by randomly removing the same number of species as the focal clade (Supplementary Table 3, Supplementary Fig. 2).

Data availability. All data generated or analysed during this study are included in this published article or its Supplementary Information files.

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Supplementary Information is available in the online version of the paper.

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Contributions

C.A.-G. and V.A.-R. designed the research project, with advice from E.A. and L.V.A. C.A.-G. reviewed literature and collected the data. C.A.-G., L.V.A., and V.A.-R. analysed data. C.A.-G., V.A.-R. and E.A. led the writing of the manuscript. All authors offered important feedback on the manuscript.

Competing interests

The auhors declare no competing interests.

Figure legends

Figure 1 | Geographic distribution of studies reporting the use of different anthropic land covers (ALCs) by primates. Geographic distribution of studies reporting the use of different anthropic land covers (ALCs) by primates. Spatial location of each study (**a**). Proportion of species using ALCs (n = 147 species) compared to the total proportion of species (n = 504 species) in each biogeographic realm (**b**). African primates were classified in two groups, those from mainland Africa and those from Madagascar, because these two land masses span the distribution of two highly divergent taxa of primates (catarrhines and strepsirrhines, respectively). Number of primate species recorded using each of five ALCs (**c**). Proportion of primate species using each ALC type in each realm (**d**). ALCs are categorized as human settlements (HS), open areas (OA), tree plantations (TP), connectors (CO), and secondary forests (SF). Species richness data in (**a**) was extracted from Pimm *et al.* (2014).

Figure 2 | Activities of primates in each anthropic land cover (ALC) type. Activities of primates in each anthropic land cover (ALC) type. The proportion (and total numbers above each column and within column sections) of records for travelling, resting, foraging or all activities in different ALC types is indicated. ALCs include human settlements (HS), open areas (OA), tree plantations (TP), connectors (CO), and secondary forests (SF). The total number of records varies because some studies report activities for more than one primate species whereas others do not report any primate activity.

Figure 3 | Conservation status and population trends of primate species using anthropic land covers (ALCs) compared to all the world's primates. The proportion (and total number above bars) of primate species within each IUCN threat category (**a**), and population trend (**b**), are shown. We tested for differences in frequencies with Chi-square tests of goodness of fit (*$P \leq 0.05$, **$P \leq 0.01$) between primates using ALCs and all the world's primates, by separately assessing primate species that used different types of ALCs (HS = human settlements, OA = open areas, TP = tree plantations, CO = connectors, and SF = secondary forest). From higher to lower extinction risk, threat categories include: Critically endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT) and Least Concern (LC). We excluded species classified as Data Deficient and Not Evaluated in (**a**), and those whose population trends are unknown in (**b**).

Figure 4 | Ecological traits of primate species that have been recorded using anthropic land covers (ALCs). The proportions (and total number above bars) of primate species exhibiting different diel activity patterns (**a**), modes of locomotion (**b**), body mass classes (**c**) and forest specialization or not (**d**). We tested for differences in frequencies with Chi-square tests of goodness of fit ($*P \leq 0.05$, $**P \leq 0.01$) between primates using ALCs and all the world's primates, by separately assessing primate species that used different ALC types (HS = human settlements, OA = open areas, TP = tree plantations, CO = connectors, and SF = secondary forest). Body mass (BM) was classified as small (< 2 kg), medium (2-10 kg) or large (>10 kg). We excluded from analyses those species for which we found no information.

Figure 5 | Distribution of the use of anthropic land covers (ALCs) across the primate phylogeny. Use of ALCs (present/absent) is indicated for each of the 352 species with phylogenetic data, based on the molecular timetree of Dos Reis *et al.*[47]. All genera with ≥2 species are labeled, and branches are color-coded by realm.

Capítulo 7

Ecological traits of the world’s primates

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En revisión en Scientific Data

Abstract

Ecosystems largely depend, for both their functioning and their ecological integrity, on the ecological traits of the species that inhabit them. Non-human primates have a wide geographic distribution and play vital roles in ecosystem structure, function, and resilience. However, there is no comprehensive compilation of information on ecological traits of all primate species to accurately assess such roles at a global scale. Here we present a database on some important ecological traits of the world's primates (504 species), including home range size, locomotion type, diel activity, trophic guild, body mass, habitat type, current conservation status, population trend, and geographic realm. We compiled this information through a careful review of 370 studies published between 1941 and 2018, resulting in a comprehensive, easily accessible and user-friendly database. This database has broad applicability in primatological studies, and can potentially be used to address many research questions at all spatial scales, from local to global.

Background & Summary

Ecological traits of species determine their contributions to ecosystem properties and their tolerance to environmental changes, including human-induced disturbances[1,2]. Non-human primates show a large variation in ecological traits (e.g., body mass varies from 0.03 kg to 130 kg)[3]. They play key roles in the structure and functioning of the ecosystems where they occur, acting as herbivores, seed dispersers, and predators[3–5]. Primates have a wide distribution, inhabiting a great variety of the Earth's ecosystems, in both tropical and temperate latitudes[6]. However, to our knowledge, no study to date has assessed the ecological roles of primates at a global scale, probably due to the lack of a global database of ecological traits. Also, despite the current conservation crisis of the world's primates[4], there is little information on the ecological traits that can make primate species more prone to extinction in human-modified landscapes[7,8]. Because primates inhabit many of the most diverse and threatened ecosystems in the world[3], understanding the relationships between the ecological traits of species and their responses to habitat disturbance is of key relevance. This information is not only needed for primate conservation, but also to preserve the many other species of organisms with which primates interact and thus the ecological processes in which they are involved[4].

Despite some efforts to compile ecological information on primate species, available databases are usually restricted to specific geographic regions (e.g., Madagascar[9]) or are not up-to-date with recent information[10]. Also, information is widely scattered in different types of sources, including hard-to-access publications[3], and user-restricted web pages (e.g., www.alltheworldsprimates.com). Furthermore, most resources include large amounts of information for some species, making it difficult to find specific ecological traits for many species. Thus, our main objective is to provide for the scientific community a comprehensive, easily accessible and user-friendly database of some traits with ecological significance for the world's primates (Fig. 1). The database includes information on primates' home range size (352 out of 504 species), locomotion type (497 species), diel activity (504 species), trophic guild (410 species), body mass (467 species), habitat type (480 species), current conservation status (504 species), population trend (393 species) and geographic realm (504 species). The structure of the database allows for different levels of organization (e.g., by taxon and trait).

Potential uses of this database include ecological research on (1) the functional structure of primate communities, (2) the influence of primate species on ecosystem function and services, (3) the functional signal of species' responses to habitat disturbances across ecosystems, and (4) the relationship between primate conservation efforts and ecosystem conservation. The database can also be used to (5) estimate various diversity indices to assess relationships between these and other ecosystem attributes, including functioning and resilience, and to (6) compare the ecological roles of primates at different spatial scales. For instance, we have used this database to test, at a global scale, which ecological traits of primates correlate more strongly with the use of the anthropogenic matrix in human-modified landscapes (Galán-Acedo *et al.*[11] under review).

Methods

Ecological traits included in the database are: home range size, locomotion type, diel activity, trophic guild, body mass, habitat type, current conservation status, population trend, and geographic realm. We selected these variables because of their well-known ecological significance[12]. For instance, body mass is correlated to many life-history traits that can affect the structure and dynamics of ecological networks[13,14] and is recognized as a variable that can have profound impact across multiple scales of organization, from the individual to the ecosystem level[13,15–17]. We followed the most up-to-date primate taxonomic nomenclature published in Estrada *et al.*[4], which is mostly based on the International Union for Conservation of Nature (IUCN).

We collected data from 370 studies published between 1941 and 2018, including scientific articles, books, reports, dissertations, and web pages. The literature search included publications in English, Spanish, French, German and Portuguese. Current conservation status and population trend of each species were obtained from the IUCN database, using the 'letsR'[18] package for R, version 3.0.1.[19]. Habitat type was obtained from this source as well, but when there was no information for a given primate species, we used the information in Mittermeier *et al.*[3]. We also used Mittermeier *et al.*[3] as the primary source for several ecological traits (i.e., geographic realm, home range, locomotion type, diel activity and trophic guild). When a given trait was not available in this source, we actively searched for the missing information in the World Wide Web (public domain and scientific publications). When different sources yielded different information for a given species and trait, we recorded information from 2-3 sources. This procedure allowed us to have a more comprehensive, accurate and objective database.

Information on home range sizes is given in hectares. When a study reported more than one home range sizes we averaged all the values reported. Locomotion type refers to arboreal, terrestrial or both types of locomotion. The category both refers to primates that carry out daily activities on the ground as well as on the trees. Diel activity categories include diurnal, nocturnal and cathemeral. In terms of trophic guild we consider six general groups: frugivore (>60% of fruits/seeds in diet), folivore (>60% leaves in diet), folivore-frugivore (diet comprised of both fruits and leaves in similar proportions), omnivore (diet comprised of both plants and animals in similar proportions), insectivore (>50% of arthropods in diet) and gummivore (diet dominated by plant exudates). Body mass is expressed in kilograms; values for this variable can represent reported individual values, reported averages, or, when a study included more than one body mass datum, calculated mean. When available, we separately report the body mass of adult males and females. Regarding habitat type, we include seven categories of natural habitats: (1) forest, includes ecosystems such as tropical wet forest, cloud forest, dry forest, montane forest, temperate forest and semidecidious forest; (2) savannah, includes savannah forest and savannah mosaics; (3) shrubland, includes ecosystems dominated by shrubs, such as scrub, brush and bush; (4) grassland, includes ecosystems mainly composed of grasses (Poaceae family); (5) wetlands, includes ecosystems such as swamps, flooded forest, swampy forest, wetlands and mangroves; (6) rocky areas, includes ecosystems such as inland cliffs and mountain peaks; and, (7) desert.

IUCN threat categories include Critically endangered, Endangered, Vulnerable, Near Threatened, Least Concern, Data Deficient and Not Evaluated. Population trend includes increasing, stable and decreasing populations. Finally, we considered four main geographic realms: Asia, Mainland Africa, Madagascar and Neotropics. African primates were classified in two groups, those from mainland Africa and those from Madagascar, because these two land masses span the distribution of two highly divergent primate suborders (catarrhines and strepsirrhines, respectively). These methods are expanded versions of descriptions in our related work under review Galán-Acedo *et al.*[11]. Data files are stored in Zenodo [Data Citation 1: Zenodo. http://doi.org/10.5281/zenodo.1342459].

Code Availability

Code for the technical validation can be found on Zenodo archived repository “Test_validation” [Data Citation 1: Zenodo. http://doi.org/10.5281/zenodo.1342459].

Data Records

The complete database for the ecological traits of primates consists of seven different data files with descriptive names (Table 1). Data files are stored in Zenodo [Data Citation 1: Zenodo. http://doi.org/10.5281/zenodo.1342459]. We also include a text file “References.txt” [Data Citation 1: Zenodo. http://doi.org/10.5281/zenodo.1342459] that contains all the references included as numbers in the data files. The first row of each data file is the header containing the variables’ names; each of the following rows presents data for a single primate species and a single information source. A given species can appear in more than one row because in some cases we included ecological traits from more than one source.

Table 1. Summary information for the eight data files comprising the database of ecological traits for the world's primates.

Data file name	N species	Abbreviations	N rows	N columns	File size
HomeRange.csv	352	NA = No information	792	7	57 KB
Locomotion.csv	497	NA = No information AR = Arboreal T = Terrestrial BOTH = Arboreal and terrestrial locomotion	505	6	35 KB
DielActivity.csv	504	D = Diurnal N = Nocturnal CA = Cathemeral	505	6	34 KB
TrophicGuild.csv	410	NA = No information	542	6	41 KB
BodyMass.csv	467	NA = No information	572	10	50 KB
Habitat.csv	480	NA = No information	505	14	44 KB
IUCN_Poptrend_Realm.csv	504	NE = Not evaluated DD = Data deficient LC = Least concern NT = Near threatened VU = Vulnerable EN = Endangered CR = Critically endangered NA = No information I = Increasing D = Decreasing S = Stable M_Africa = Mainland Africa	505	9	42 KB

Technical Validation

Most of the records included in the database are based on published material in peer-reviewed scientific journals and books, and thus we have confidence in their accuracy. Also, for each specific datum we include the corresponding reference in the database, allowing users to both assess the validity and consult the original sources. Moreover, the authors have carefully checked the database for possible redundancies and errors. When a specific datum was considered non-reliable (e.g., very extreme or contradictory values, and values obtained with questionable methodology) we did not include it in the database. We also used the 'validate'[20] R package to check the database for structural integrity (i.e., its internal organization). Data will be corrected and updated if any errors are detected and reported to the corresponding author.

Usage Notes

We would appreciate if researchers cite the database stored in Zenodo [Data Citation 1: Zenodo. http://doi.org/10.5281/zenodo.1342459] in the specific version used, as well as this publication, when using all or part of the database.

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Author contributions

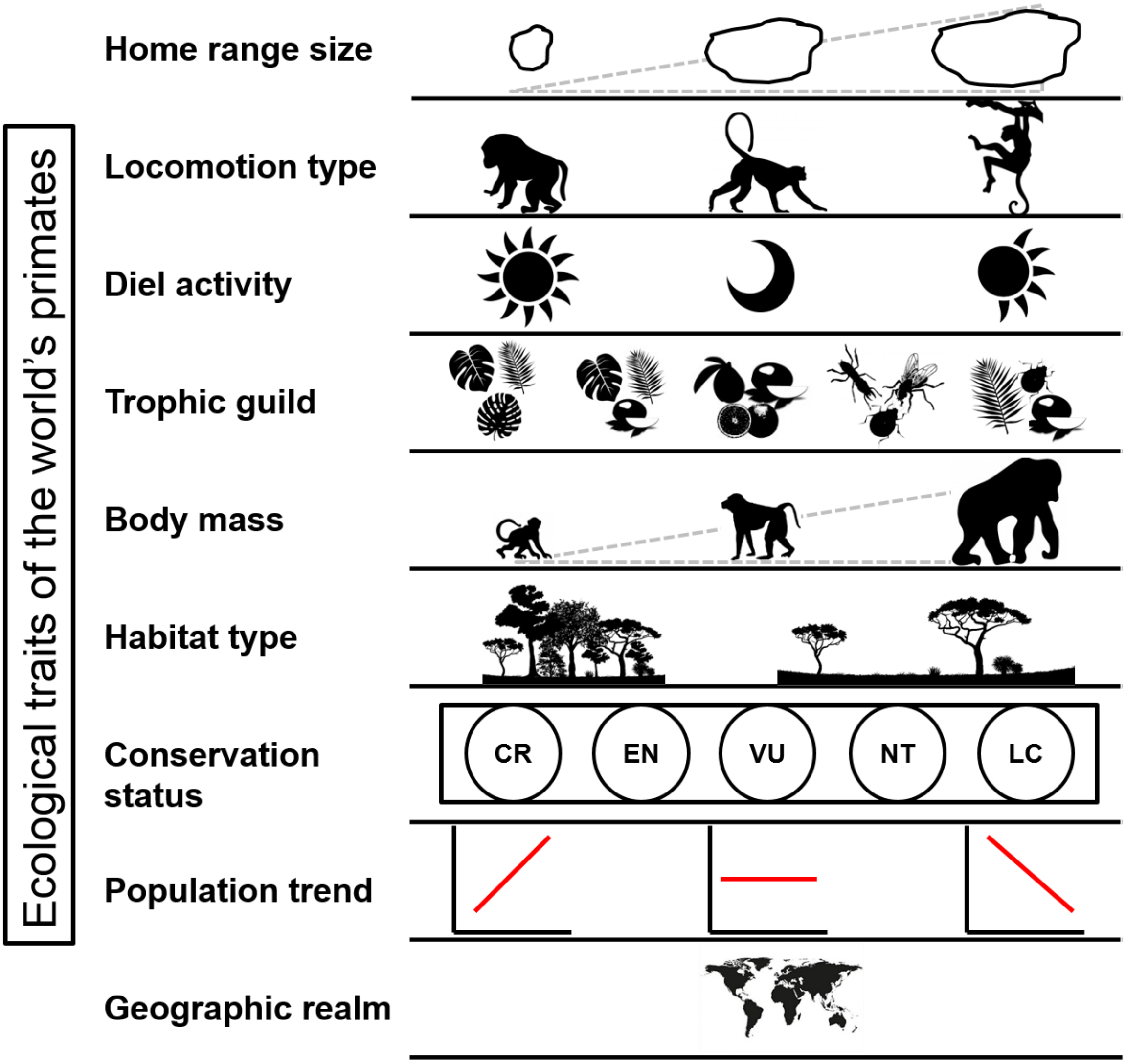
C.A.-G., V.A.-R. and E.A. designed the database and wrote the manuscript. C.A.-G. reviewed the literature and collected the data, and V.A.-R carefully reviewed the database.

Competing interests

The authors declare no competing interests.

Figure Legend

Figure 1. Summary of the ecological traits of the word's primates included in the database. From left to right pictures represent: home range size gradient from small to large; locomotion types are terrestrial, both locomotion types, and arboreal; diel activity includes diurnal, nocturnal and cathemeral; trophic guild includes folivore, folivore-frugivore, frugivore, insectivore, omnivore, and gummivore (the latter not depicted); body mass gradient from small to large; habitat type includes seven categories (see text) but only two are depicted as examples (forest and savannah); IUCN conservation status includes seven categories, with five depicted here CR critically endangered, EN endangered, VU vulnerable, NT near threatened and LC least concern; population trend is represented by three graphs indicating increasing, stable and decreasing populations; geographic realm is represented by a global map. Images used with permission from Microsoft.


Ecological traits of the world's primates
Home range size
Locomotion type
Diel activity
Trophic guild
Body mass
Habitat type
Conservation status
CR
EN
VU
NT
LC
Population trend
Geographic realm

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Data citations

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Capítulo 8

Discusión general y conclusiones

Carmen Galán-Acedo

Efecto de la estructura de paisajes antrópicos sobre los primates

El cambio de uso de suelo es considerado la principal amenaza para los primates en paisajes antrópicos (Marsh et al. 2013; Estrada et al. 2017). Sin embargo, como muestra el *Capítulo 2* de la presente tesis, nuestro entendimiento acerca de los atributos del paisaje que determinan la abundancia y diversidad de primates es todavía muy limitado. Esto se debe, por un lado, al reducido número de estudios con primates a escala de paisaje (34 estudios), y por otro, a varias limitaciones metodológicas presentes en los estudios existentes. Entre otras (ver *Capítulo 2*), cabe destacar que la mayoría de los estudios (79%) evalúan la estructura del paisaje a una sola escala espacial, sin identificar la escala del efecto. Este hallazgo es preocupante, ya que puede limitar el alcance de las conclusiones de estos estudios (Jackson y Fahrig 2015). En particular, como se muestra en el *Capítulo 3* para el caso de los primates mexicanos, la fuerza de la asociación entre cada atributo del paisaje y cada variable de respuesta depende del tamaño del paisaje seleccionada para medir dicho atributo (Galán-Acedo et al. 2018). Por tanto, en la práctica, es importante evaluar los atributos del paisaje considerando varias extensiones espaciales para identificar aquella que maximiza la asociación entre cada atributo del paisaje y cada respuesta (i.e., la denominada 'escala del efecto del paisaje'; Jackson y Fahrig 2015). En este sentido, el hecho de que la mayoría de los estudios con primates a escala de paisaje no consideren la escala del efecto, puede explicar por qué la mayoría de las respuestas de primates a los cambios en el paisaje tienden a ser débiles (*Capítulo 2*). Por tanto, un primer mensaje de esta tesis es que necesitamos incrementar el número de estudios que consideren la escala del efecto para entender mejor las respuestas de los primates a los cambios espaciales en el paisaje.

El *Capítulo 2* también demuestra que aquellos estudios que documentan efectos significativos del paisaje sobre los primates sugieren que las respuestas a la cantidad de hábitat son más fuertes que las respuestas a la fragmentación del mismo. Este hallazgo no es sorprendente, ya que revisiones globales sobre el efecto relativo de la cantidad de hábitat (i.e. composición de paisaje) y la fragmentación (i.e. configuración) indican que la pérdida de hábitat tiene un impacto mayor sobre las especies que la fragmentación (Fahrig 2003, 2013). Ésto también es consistente con el *Capítulo 4*, que sugiere que la pérdida de hábitat (no la fragmentación) es la mayor amenaza para los monos araña en las regiones de estudio. Así, no es de extrañar que el mono araña esté extinto en las dos regiones más perturbadas (i.e. zona norte de Los Tuxtlas, Región VIII Norte de Chiapas). De un modo similar, en el *Capítulo 5* encuentro que los monos aulladores se ven más afectados por la pérdida de hábitat que por la fragmentación. Sin embargo, los monos aulladores parecen ser más resistentes a la alteración del hábitat, dado que se encuentran presentes en las cuatro regiones evaluadas en esta tesis. Esto puede deberse a que éstas nespecies de primates muestran una alta flexibilidad comportamental en paisajes o regiones con alto grado de perturbación (Bicca-Marques 2003; Arroyo-Rodríguez & Dias 2010). Así, el segundo mensaje de esta tesis es que la pérdida de cobertura forestal parece ser la principal amenaza para los primates en paisajes antrópicos.

Otro atributo de la composición del paisaje que puede jugar un papel crítico en el mantenimiento de poblaciones de primates es la composición de la matriz antrópica (ver *Capítulos 2*, *4* y *6*). Por ejemplo, el *Capítulo 2* demuestra que matrices de mayor calidad (i.e. aquellas más similares al hábitat original de la especie) tienen efectos positivos en la dieta y el éxito reproductivo de los primates. Este hallazgo apoya estudios previos con otros animales en paisajes antrópicos (Anderson et al. 2007; Watling et al. 2011). De hecho, en México, los monos araña que habitan regiones tropicales más degradadas pueden verse forzados a usar más frecuentemente la matriz para moverse y alimentarse. Esto puede explicar por qué la abundancia de monos araña incrementa en paisajes rodeados de una matriz más funcional, i.e. más arbolada (Galán-Acedo et al. 2019a; *Capítulo 4*). Igualmente, en el *Capítulo 5* la funcionalidad de la matriz tiene una asociación fuerte y positiva con el éxito reproductivo de los monos aulladores en las regiones con coberturas más arboladas. De nuevo, esto implica que en regiones con coberturas de mayor calidad (Prevedello & Vieira 2010; Fahrig et al. 2011), es más probable que los primates utilicen la matriz. Finalmente, el *Capítulo 6* (Galán-Acedo et al. 2019b) muestra que al menos el 30% de las especies de primates del mundo han sido reportadas utilizando algún tipo de cobertura antrópica y que por lo menos 86 especies las utilizan para suplementar su dieta (Dunning et al. 1992). Por tanto, un tercer mensaje importante de la presente tesis es que las coberturas antrópicas pueden ser usadas por algunos primates para suplementar el paisaje e incluso como hábitat temporal o alternativo.

El *Capítulo 2* también sugiere que la fragmentación tiene efectos positivos sobre los primates. Este hallazgo es consistente con Fahrig (2017), quien encuentra que la fragmentación tiene principalmente efectos positivos sobre las especies. Sin embargo, los *Capítulos 4* y *5,* muestran efectos principalmente nulos de la fragmentación sobre los monos araña y los monos aulladores. Además, contrario a los esperado, en el *Capítulo 5* se encuentran efectos negativos para *A. pigra* en la región más conservada. Por otro lado, el *Capítulo 2* también demuestra que la abundancia de conectores tiene efectos positivos sobre la abundancia de primates, indicando de nuevo que los primates pueden utilizar las coberturas de la matriz para suplementar el hábitat (Dunning et al. 1992). No obstante, la mayoría de variables de configuración del paisaje evaluadas en este capítulo tienen efectos nulos, por lo que, consistente con previos estudios (Fahrig 2003), estos resultados apoyan la idea de que la configuración del paisaje tiene efectos más débiles que la composición.

La presente tesis también demuestra que la respuesta de las especies depende del contexto regional de cambio de uso de suelo (*Capítulos 3, 4* y *5*). Por un lado, la escala del efecto tiende a ser mayor en las regiones más alteradas que en el resto de regiones (*Capítulo 3*). Esto puede deberse a que en regiones más degradadas, las especies pueden verse forzadas a utilizar áreas mayores para abastecer sus necesidades de hábitat. Por otro lado, los *capítulos 4* y *5* indican que las respuestas de los monos mexicanos a la estructura del paisaje varían según el contexto regional. Por ejemplo, en la región más degradada, la funcionalidad de la matriz juega un papel más importante para la tasa de encuentro y el éxito reproductivo de los monos araña, mientras que la cantidad de cobertura forestal es la variable más importante en la región más conservada (*Capítulo 4*). De un modo similar, el *Capítulo 5* muestra que en regiones con matrices más arboladas, la funcionalidad de la matriz tiene efectos positivos en el éxito reproductivo de los monos aulladores. Además, la fragmentación tiene efectos negativos para la abundancia de monos en la región más preservada. Así, otro mensaje de esta tesis es que los efectos de la estructura del paisaje sobre los primates en un cotexto regional particular no son generalizables a regiones con características diferentes.

Finalmente, otra aportación novedosa de la presente tesis es que demuestra que diferentes especies de primates pueden tener respuestas contrastantes a los cambios en la estructura del paisaje (*Capítulos 2, 4, 5 y 6*). Por ejemplo, los monos araña parecen estar más fuertemente afectados por la pérdida de hábitat que los monos aulladores (*Capítulos 4* y *5*). Esto puede deberse a que los monos araña tienen una dieta más frugívora y ocupan mayores áreas de actividad. Los monos aulladores, en cambio, parecen ser capaces de adaptar su dieta (e.g. comiendo más hojas) y su patrón de actividad (i.e. dedicando más tiempo al descanso) en regiones altamente degradadas (Arroyo-Rodríguez & Dias, 2010). El *Capítulo 6* también indica que las especies que utilizan coberturas antrópicas comparten ciertos rasgos que las hacen menos susceptibles a estos ambientes. De hecho, los primates que utilizan las coberturas antrópicas se encuentran menos amenazados de lo esperado (IUCN 2017) y tienen poblaciones más estables o en incremento. Estas especies son mayormente diurnas, con tamaños corporales medianos o grandes, no estrictamente arbóreas y generalistas de hábitat. Por lo tanto, otro mensaje importante de esta tesis es que los efectos de la estructura del paisaje sobre una especie de primate determinada no son extrapolables a especies con rasgos ecológicos distintos.

Aportaciones teóricas

Esta tesis aporta información valiosa que puede alimentar debates teóricos e hipótesis sobre la respuesta de las especies a los cambios espaciales en el paisaje (Tabla 1).

1) Aunque esta tesis no pone a prueba *la teoría metapoblacional* (Levins 1969; Hanski 1998), sí cuestiona el uso de paisajes binarios (hábitat vs. no hábitat) que es comúnmente aplicado en estudios que ponen a prueba esta teoría. Por ejemplo, el *Capítulo 6* sugiere que diferentes coberturas antrópicas que rodean a los remanentes de hábitat pueden ser usadas por los primates para alimentarse, e incluso como hábitat temporal. Por ello, considerar que la matriz antrópica es homogénea e inutilizable por las especies es poco realista, lo que puede limitar la capacidad predictiva de esta teoría. Por tanto, aproximaciones teóricas más recientes, como la biogeografía del campo (Countryside biogeography; Daily 1997) pueden tener mayor capacidad predictiva en este tipo de contextos paisajísticos.
2) Las *dinámicas de suplementación del paisaje* (Dunning 1992) ayudan a explicar patrones de distribución y abundancia de especies en paisajes antrópicos. En concreto, predicen que la presencia y abundancia de un organismo en un parche de hábitat es mayor cuando dicho parche se encuentra cercano a otras coberturas

que contienen recursos suplementarios. En concordancia con esto, el *Capítulo 2* demuestra que la calidad del paisaje (i.e. índice de calidad del paisaje) tiene una relación positiva con la ocurrencia y la riqueza de especies de primates. Del mismo modo, en los *Capítulos 4* y 5, también encuentro que la funcionalidad de la matriz tiene efectos más fuertes y positivos sobre la abundancia relativa y reproducción del mono araña en la región más heterogénea (*Capítulo 4*) y sobre el éxito reproductivo de los monos aulladores en las dos regiones más heterogéneas (*Capítulo 5*). Además, en el *Capítulo 6* encuentro que, a nivel global, los primates utilizan las coberturas antrópicas para desplazarse, refugiarse y alimentarse.

3) El *debate sobre la pérdida de hábitat vs. fragmentación* (Fahrig 2003, 2017). El efecto de la pérdida de hábitat parece ser consistentemente negativo para diferentes grupos taxonómicos (Fahrig 2003). En contraste, el impacto de la fragmentación per se (i.e. controlando el efecto de la pérdida de hábitat) es mayormente débil, y positivo cuando es significativo (Fahrig 2017). Consistente con estos hallazgos, los *Capítulos 2, 4* y *5* sugieren que la pérdida de hábitat tiene efectos negativos más fuertes sobre los primates que los efectos de la fragmentación. Por tanto, la conservación de primates parece depender más de la preservación de hábitat en el paisaje, que del arreglo espacial del mismo.

4) La *hipótesis del umbral de extinción* (Lande 1987) postula que existe una cantidad de hábitat crítica por debajo de la que el tamaño de una población disminuye drásticamente, aumentando así su probabilidad de extinción. Los estudios sobre esta hipótesis sugieren que el umbral de extinción se sitúa entre el 10 y el 40% de hábitat remanente (Bascompte & Solé 1996; Fahrig 1997; Swift & Hannon 2010). La presente tesis sugiere que para el caso de los monos araña, el umbral de extinción debe ubicarse cercano al 25% de cobertura forestal remanente, o sea que pérdidas de más del 75% de cobertura forestal pueden causar el colapso de las poblaciones de estos animales (Galán-Acedo et al. 2019). Sin embargo, no encontramos un umbral claro para los monos aulladores, pues incluso la región más degrada, con tan sólo 10% de cobertura remanente, presentó un gran número de monos, incluso mayor al de regiones más conservadas. Este resultado puede deberse a la flexibilidad comportamental de esta especie (Arroyo-Rodríguez & Dias 2010), aunque son necesarios más estudios en otras regiones del país para entender mejor estos umbrales en ambas especies.

Implicaciones de esta tesis para la conservación de primates en paisajes antrópicos

Los resultados de esta tesis indican que la pérdida de hábitat es la mayor amenaza para la supervivencia de los primates en paisajes antrópicos (*Capítulo 2*, *Capítulo 4*, Galán-Acedo et al. 2019a y *Capítulo 5*). Así, las principales estrategias de conservación a seguir son la prevención de la deforestación y el aumento de la cobertura forestal (restauración). Estos resultados son consistentes con estudios previos (e.g. Fahrig 2003, 2017; Ordóñez-Gomez et al. 2015). Por ejemplo, será fundamental **el establecimiento de áreas de conservación comunitarias.** Dos estudios muestran que la abundancia de primates incrementa después de la conservación de áreas de bosque implementada por comunidades locales (Aveling & Aveling 1987; Horwich & Lyon 1998). Además, **proteger los fragmentos de bosque remanentes en paisajes perturbados** es fundamental**.** Por ejemplo, Horwich & Lyon (1998) compara la abundancia de monos aulladores antes y después de la protección de parches de bosque en Belice, y encuentra mayor abundancia de monos aulladores después de su protección. Otra acción de manejo es **el aumento de la cantidad de cobertura forestal mediante la restauración de hábitat.**

Otro resultado clave de esta tesis es el papel positivo que las coberturas antrópicas pueden jugar en la conservación de primates en paisajes antrópicos. Por ello, es importante **aumentar la calidad ecológica de estas coberturas para las especies, incrementando particularmente la abundancia y diversidad de árboles que puedan ser usados por estas especies para moverse y alimentarse.** Además, se pueden **incorporar o proteger corredores arbolados en zonas deforestadas.** Por ejemplo, en un estudio en Belize con monos aulladores negros se encontró que la protección de un corredor biológico incrementó la población en un 138%, entre otras intervenciones (Horwich & Lion 1998). En la misma línea se pueden **instalar sitios de paso verdes o estructuras colgantes para evitar los atropellos de primates en carreteras.** Estas iniciativas, aunque escasas, han demostrado tener efectos positivos para los primates (e.g. Valladares-Padua et al. 1995). También se pueden **substutir cercas de alambre**

por cercas vivas. Por ejemplo, Estrada et al. (1994) encuentran que las cercas vivas tienen mayor biomasa y especies de mamíferos no voladores que los pastos y fueron similares a los bosques y a los cultivos a la sombra. Otra acción de manejo en las coberturas antrópicas es **la promoción de agroecosistemas mixtos con cultivos bajo sombra.** Por ejemplo, en una amplia revisión sobre el tema, Estrada et al. (2012) reportan que 57 especies de primates son capaces de utilizar 38 tipos de cultivos para suplementar su dieta o desplazarse, pero también como refugio, residencia temporal o residencia permanente en cultivos mixtos o bajo sombra.

Además de estas acciones de manejo, ¿hay algo más que podamos hacer para evitar el declive y extinción de los primates a nivel global? Como se ha comentado a lo largo de esta tesis, el acelerado crecimiento de la población humana, así como las prácticas de consumo que se llevan a cabo globalmente, son las principales causas de la deforestación a nivel global. De hecho, la agricultura y la ganadería son las culpables del 73% de la deforestación actual, particularmente en los trópicos (FAO, 2016). Es interesante saber, además, que el 80% de la agricultura actual se dedica a producir alimento para el ganado. Por la tanto, podemos decir que el consumo de carne es la principal amenaza para supervivencia de los primates. Así, es importante reconocer el papel que ejercemos individualmente como consumidores. De hecho, acciones pequeñas y que no comportan un riesgo para la salud, como un cambio en la dieta que reduzca el consumo de carne y de productos provenientes principalmente de la vaca son fundamentales para frenar la crisis de extinción global a la que hoy nos enfrentamos (Springmann et al. 2017; Poore & Nemecek 2018).

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Material Suplementario

Capítulo 2 | A global assessment of primates' responses to landscape structure

Supporting Information for:

Galán-Acedo, C., Arroyo-Rodríguez, V., Cudney-Valenzuela, S.J., Fahrig, L. A global assessment of primate responses to landscape structure.

Biological Reviews

Appendix S1: Data extracted from all published studies of primates with a landscape perspective in human-modified landscapes. Ref = references; Study designs: SL (site-landscape), PL (patch-landscape) or LS (landscape-study); Buffer (buffer type used to calculate landscape metrics): Edge (from patch edge), Centre (from the center of each patch), NI (no information available); Overlap: spatial overlap between study landscapes (Yes or Not); N scales: number of spatial scales assessed in each study; SE tested: this column indicates whether the study assesses or not the scale of effect; Scale range: the largest spatial scale divided by the smallest scale in multiscale studies; Composition (landscape composition variables): LCR (land cover richness), FC (forest cover), CL (corridor length), MC (matrix cover), AC (agroforest cover), LFC (logged forest cover), SCC (sugar cane cover), SFC (secondary forest cover), MP (matrix permeability), LQI (landscape quality indexes); Configuration (landscape configuration variables): MID (mean inter-patch distance), FR (habitat fragmentation), RA (road abundance), CA (corridor abundance), ED (edge density), MPS (mean patch size); AWF (area-weighted mean patch fractal dimension), NA (does not apply); Findings (direction of effect of each landscape predictor on each response): (-) negative response, 0 null response, (+) positive response; Control FC: studies on landscape configuration variables controlling (yes) or not the effect of forest cover.

Ref	**Realm**	**Study design**	**Buffer**	**Overlap**	**N scales**	**SE tested**	**Scale range**	**Gender**	**Species names**	**Response**	**Composition**	**Configuration**	**Findings**	**Control FC**
1	Asia	SL	Centre	Yes	1	No	0	Several	*Macaca nemestrina, Presbytis siamensis, Macaca fascicularis*	Species richness	LCR	NA	(-)	NA
2	Neotropics	PL	NI	Yes	1	No	0	*Alouatta*	*Alouatta guariba clamitans*	Abundance	NA	MID	0	NA
2	Neotropics	PL	NI	Yes	1	No	0	*Alouatta*	*Alouatta guariba clamitans*	Occurrence	NA	MID	0	NA
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Occurrence	FC	NA	0	NA
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Abundance	FC	NA	0	NA
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Occurrence	NA	FR	(+)	Yes
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Abundance	NA	FR	0	Yes
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Occurrence	NA	RA	0	Yes

3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Abundance	NA	RA	0	Yes
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Occurrence	NA	CA	0	Yes
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Abundance	NA	CA	(+)	Yes
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Occurrence	CL	NA	0	Yes
3	Neotropics	PL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta palliata*	Abundance	CL	NA	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	FC	NA	0	NA
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	MP	NA	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	NA	FR	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	NA	ED	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	NA	MID	(-)	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	FC	NA	0	NA
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	MP	NA	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	NA	FR	(+)	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	NA	ED	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Abundance	NA	MID	(+)	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Immature to female ratio	FC	NA	0	NA
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Immature to female ratio	MP	NA	(+)	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Immature to female ratio	NA	FR	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Immature to female ratio	NA	ED	0	Yes
4	Neotropics	PL	Centre	No	2	No	0.1 to 3	*Alouatta*	*Alouatta pigra*	Immature to female ratio	NA	MID	0	Yes
5	Neotropics	SL	Centre	NI	1	No	0	*Ateles*	Ateles geoffroyi	Crossing roads	FC	NA	0	NA
5	Neotropics	SL	Centre	NI	1	No	0	*Ateles*	Ateles geoffroyi	Crossing roads	SFC	NA	0	NA
6	Asia	SL	Centre	NI	1	No	0	Several	*Trachypithecus cristatus, Trachypithecus obscurus, Nycticebus coucang, Macaca fascicularis, Macaca nemestrina, Hylobates lar, Hylobates syndactylus,*	Species richness	FC	NA	(+)	NA
7	Neotropics	SL & PL	Edge	NI	1	No	0	Several	*Several: Alouatta, Aotus, Ateles, Brachyteles, Callicebus moloch, Callicebus personatus, Callithrix, Cebus albifrons, Cebus olivaceus,*	Occurrence	FC	NA	(+)	NA

									Cebus apella, Chiropotes, Lagothrix, Leontopithecus, Mico, Pitheca, Saguinus fusicollis, Saguinus niger, Saguinus oedipus, Saimiri					
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Alouatta*	*Alouatta*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Aotus*	*Aoutus*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Ateles*	*Ateles*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Brachyteles*	*Brachyteles*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Callicebus*	*Callicebus moloch*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Callicebus*	*Callicebus personatus*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Callithrix*	*Callithrix*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Cebus*	*Cebus albifrons*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Cebus*	*Cebus olivaceus*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Cebus*	*Cebus apella*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Chiropotes*	*Chiropotes*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Lagothrix*	*Lagothrix*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Leontopithecus*	*Leontopithecus*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Mico*	*Mico*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Pithecia*	*Pithecia*	Occurrence	FC	NA	0	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Saguinus*	*Saguinus*	Occurrence	FC	NA	(+)	Yes
7	Neotropics	SL & PL	Edge	NI	1	No	0	*Saimiri*	*Saimiri*	Occurrence	FC	NA	0	Yes
8	Neotropics	SL	Edge	No	3 to 12	No	3.1 to 6	Several	*Alouatta macconnelli, Ateles paniscus, Chiropotes sagulatus, Pithecia chrysocephala, Saguinus midas, Saimiri sciureus, Sapajus apella*	Community occurrence	FC	NA	0	NA
9	Neotropics	PL	Edge	No	1	No	0	Several	*Alouatta macconnelli, Ateles paniscus, Sapajus apella, Pithecia chrysocephala, Chiropotes sagulatus, Saguinus midas and Saimiri sciureus*	Species composition	FC	NA	(+)	NA
9	Neotropics	PL	Edge	No	1	No	0	Several	*Alouatta macconnelli, Ateles paniscus, Sapajus apella,*	Species richness	FC	NA	0	NA

									Pithecia chrysocephala, Chiropotes sagulatus, Saguinus midas and Saimiri sciureus					
9	Neotropics	PL	Edge	No	1	No	0	*Alouatta*	*Alouatta macconnelli*	Occurrence	FC	NA	0	NA
9	Neotropics	PL	Edge	No	1	No	0	*Ateles*	*Ateles paniscus*	Occurrence	FC	NA	(+)	NA
9	Neotropics	PL	Edge	No	1	No	0	*Sapajus*	*Sapajus apella*	Occurrence	FC	NA	0	NA
9	Neotropics	PL	Edge	No	1	No	0	*Pithecia*	*Pithecia chrysocephala*	Occurrence	FC	NA	0	NA
9	Neotropics	PL	Edge	No	1	No	0	*Saimiri*	*Saimiri sciureus*	Occurrence	FC	NA	0	NA
9	Neotropics	PL	Edge	No	1	No	0	*Alouatta*	*Alouatta macconnelli*	Occurrence	NA	FR	0	Yes
9	Neotropics	PL	Edge	No	1	No	0	*Ateles*	*Ateles paniscus*	Occurrence	NA	FR	0	Yes
9	Neotropics	PL	Edge	No	1	No	0	*Sapajus*	*Sapajus apella*	Occurrence	NA	FR	0	Yes
9	Neotropics	PL	Edge	No	1	No	0	*Pithecia*	*Pithecia chrysocephala*	Occurrence	NA	FR	0	Yes
9	Neotropics	PL	Edge	No	1	No	0	*Saimiri*	*Saimiri sciureus*	Occurrence	NA	FR	0	Yes
10	Africa	SL	Centre	No	3 to 12	Yes	0.1 to 3	*Cercopithecus*	*Cercopithecus mitis*	Abundance	FC	NA	(+)	NA
10	Africa	SL	Centre	No	3 to 12	Yes	0.1 to 3	*Cercopithecus*	*Cercopithecus ascanius*	Abundance	FC	NA	(+)	NA
10	Africa	SL	Centre	No	3 to 12	Yes	0.1 to 3	*Cercopithecus*	*Cercopithecus guereza*	Abundance	FC	NA	(+)	NA
10	Africa	SL	Centre	No	3 to 12	Yes	0.1 to 3	*Pan*	*Pan troglodytes*	Abundance	FC	NA	(+)	NA
11	Neotropics	PL	Edge	NI	1	No	0	Several	*Callithrix jacchus, Callithrix penicillata, Callithrix kuhlii, Calicebus melanochir, Callicebus barbarabrownae, Alouatta guariba, Alouatta caraya, Brachiteles hypoxanthus*	Species richness	FC	NA	0	NA
11	Neotropics	PL	Edge	NI	1	No	0	Several	*Callithrix jacchus, Callithrix penicillata, Callithrix kuhlii, Calicebus melanochir, Callicebus barbarabrownae, Alouatta guariba, Alouatta caraya, Brachiteles hypoxanthus*	Species richness	NA	MID	0	Yes
11	Neotropics	PL	Edge	NI	1	No	0	Several	*Callithrix jacchus, Callithrix penicillata, Callithrix kuhlii, Calicebus melanochir, Callicebus barbarabrownae, Alouatta guariba, Alouatta caraya, Brachiteles*	Aggregate biomass	FC	NA	0	NA

									hypoxanthus					
11	Neotropics	PL	Edge	NI	1	No	0	Several	*Callithrix jacchus, Callithrix penicillata, Callithrix kuhlii, Calicebus melanochir, Callicebus barbarabrownae, Alouatta guariba, Alouatta caraya, Brachiteles hypoxanthus*	Aggregate biomass	NA	MID	0	Yes
11	Neotropics	PL	Edge	NI	1	No	0	Several	*Callithrix jacchus, Callithrix penicillata, Callithrix kuhlii, Calicebus melanochir, Callicebus barbarabrownae, Alouatta guariba, Alouatta caraya, Brachiteles hypoxanthus*	Aggregate vulnerability	FC	NA	0	NA
11	Neotropics	PL	Edge	NI	1	No	0	Several	*Callithrix jacchus, Callithrix penicillata, Callithrix kuhlii, Calicebus melanochir, Callicebus barbarabrownae, Alouatta guariba, Alouatta caraya, Brachiteles hypoxanthus*	Aggregate vulnerability	NA	MID	0	Yes
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Callicebus*	*Callicebus ornatus*	Occurrence	FC	NA	(+)	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Callicebus*	*Callicebus ornatus*	Occurrence	NA	FR	0	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Callicebus*	*Callicebus ornatus*	Abundance	FC	NA	(-)	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Callicebus*	*Callicebus ornatus*	Abundance	NA	FR	0	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Sapajus*	*Sapajus apella fatuellus*	Occurrence	FC	NA	0	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Sapajus*	*Sapajus apella fatuellus*	Occurrence	NA	FR	0	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Sapajus*	*Sapajus apella fatuellus*	Abundance	FC	NA	0	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Sapajus*	*Sapajus apella fatuellus*	Abundance	NA	FR	(-)	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Saimiri*	*Saimiri cassiquiarensis albigena*	Occurrence	FC	NA	(+)	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Saimiri*	*Saimiri cassiquiarensis albigena*	Occurrence	NA	FR	0	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Saimiri*	*Saimiri cassiquiarensis albigena*	Abundance	FC	NA	(-)	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Saimiri*	*Saimiri cassiquiarensis albigena*	Abundance	NA	FR	0	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Alouatta*	*Alouatta seniculus*	Occurrence	FC	NA	0	NA

12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Alouatta*	*Alouatta seniculus*	Occurrence	NA	FR	(+)	No
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Alouatta*	*Alouatta seniculus*	Abundance	FC	NA	0	NA
12	Neotropics	PL	Edge	NI	3 to 12	Yes	6.1 to 9	*Alouatta*	*Alouatta seniculus*	Abundance	NA	FR	(-)	No
13	Neotropics	SL	Centre	No	3 to 12	No	9.1 to 12	*Callithrix*	*Callithrix kuhlii*	Occurrence	FC	NA	0	NA
13	Neotropics	SL	Centre	No	3 to 12	No	9.1 to 12	*Sapajus*	*Sapajus xanthosternos*	Occurrence	FC	NA	0	NA
13	Neotropics	SL	Centre	No	3 to 12	No	9.1 to 12	*Leontopithecus*	*Leontopithecus chrysomelas*	Occurrence	FC	NA	(+)	NA
14	Asia	SL	Centre	NI	3 to 12	No	6.1 to 9	*Pan*	*Pan paniscus*	Hunting	FC	NA	0	NA
14	Asia	SL	Centre	NI	4 to 12	No	6.1 to 10	*Pan*	*Pan paniscus*	Hunting	AC	NA	0	NA
14	Asia	SL	Centre	NI	5 to 12	No	6.1 to 11	*Pan*	*Pan paniscus*	Hunting	LFC	NA	0	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	Group size	FC	NA	0	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	N males	FC	NA	(+)	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	N females	FC	NA	0	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	N juveniles	FC	NA	0	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	Lambda	FC	NA	0	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	Sex ratio	FC	NA	(-)	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	Infant survival rate	FC	NA	0	NA
15	Neotropics	SL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	Dispersal events	FC	NA	(+)	NA
16	Neotropics	PL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta guariba clamitans*	Occurrence	FC	NA	0	NA
16	Neotropics	PL	Centre	Yes	1	No	0	*Sapajus*	*Sapajus nigritus*	Occurrence	FC	NA	0	NA
16	Neotropics	PL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta guariba clamitans*	Occurrence	NA	MPS	0	Yes
16	Neotropics	PL	Centre	Yes	1	No	0	*Sapajus*	*Sapajus nigritus*	Occurrence	NA	MPS	0	Yes
16	Neotropics	PL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta guariba clamitans*	Occurrence	NA	FR	0	Yes
16	Neotropics	PL	Centre	Yes	1	No	0	*Sapajus*	*Sapajus nigritus*	Occurrence	NA	FR	0	Yes
16	Neotropics	PL	Centre	Yes	1	No	0	*Alouatta*	*Alouatta guariba clamitans*	Occurrence	NA	AWF	0	Yes
16	Neotropics	PL	Centre	Yes	1	No	0	*Sapajus*	*Sapajus nigritus*	Occurrence	NA	AWF	0	Yes
17	Neotropics	SL	Centre	No	1	No	0	*Sapajus nigritus*	*Sapajus nigritus*	Abundance	NA	FR	(+)	Yes
17	Neotropics	SL	Centre	No	1	No	0	*Sapajus nigritus*	*Sapajus nigritus*	Abundance	NA	MID	0	Yes
17	Neotropics	SL	Centre	No	1	No	0	*Sapajus nigritus*	*Sapajus nigritus*	Abundance	FC	NA	0	Yes
18	Neotropics	SL	Centre	NI	1	No	0	Several	*Cebus apella, Callicebus moloch*	Species richness	LQI	NA	0	NA

18	Neotropics	SL	Centre	NI	1	No	0	Several	*Cebus apella, Callicebus moloch*	Species composition	LQI	NA	0	NA
19	Neotropics	PL	Centre	NI	2	No	3.1 to 6	Several	*Alouatta guariba, Callithrix aurita, Callithrix jacchus, Callithrix penicillata, Sapajus nigritus, Callicebus nigrifrons*	Functional diversity	FC	NA	(+)	NA
19	Neotropics	PL	Centre	NI	2	No	3.1 to 6	Several	*Alouatta guariba, Callithrix aurita, Callithrix jacchus, Callithrix penicillata, Sapajus nigritus, Callicebus nigrifrons*	Functional diversity	SCC	NA	0	NA
20	Neotropics	SL	Edge	No	1	No	0	*Ateles*	*Ateles hybridus*	Abundance	LQI	NA	0	NA
20	Neotropics	SL	Edge	No	1	No	0	*Alouatta*	*Alouatta seniculus*	Abundance	LQI	NA	0	NA
20	Neotropics	SL	Edge	No	1	No	0	*Cebus*	*Cebus albifrons*	Abundance	LQI	NA	0	NA
21	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Callicebus*	*Callicebus nigrifrons*	Occurrence	FC	NA	(+)	NA
21	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Callicebus*	*Callicebus nigrifrons*	Occurrence	NA	RA	0	Yes
21	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Callithrix*	*Callithrix aurita*	Occurrence	FC	NA	0	NA
21	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Callithrix*	*Callithrix aurita*	Occurrence	NA	RA	0	Yes
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	FC	NA	0	NA
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	FR	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	MID	(-)	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	ED	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Traveling time	FC	NA	(+)	NA
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Traveling time	NA	FR	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Traveling time	NA	MID	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Traveling time	NA	ED	(-)	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Resting time	FC	NA	(-)	NA
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Resting time	NA	FR	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Resting time	NA	MID	(-)	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Resting time	NA	ED	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	FC	NA	(+)	NA
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	FR	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	MID	(-)	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	ED	0	No

22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	FC	NA	(-)	NA
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	FR	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	MID	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	ED	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	FC	NA	0	NA
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	FR	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	MID	0	No
22	Neotropics	SL	Centre	No	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Feeding time	NA	ED	0	No
23	Neotropics	SL	Centre	NI	1	No	0	*Ateles*	*Ateles belzebuth*	Hunting	FC	NA	0	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Ateles*	*Ateles chamek*	Hunting	FC	NA	0	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Lagothrix*	*Lagothrix cana*	Hunting	FC	NA	(-)	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Lagothrix*	*Lagothrix poeppigii*	Hunting	FC	NA	(-)	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Lagothrix*	*Lagothrix lagothricha*	Hunting	FC	NA	(-)	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Pithecia*	*Pithecia irrorata*	Hunting	FC	NA	0	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Pithecia*	*Pithecia albicans*	Hunting	FC	NA	0	NA
23	Neotropics	SL	Centre	NI	1	No	0	*Cebus*	*Cebus apella*	Hunting	FC	NA	0	NA
24	Africa	SL	NI	Yes	1	No	0	*Pan*	*Pan troglodytes*	Abundance	FC	NA	(+)	NA
24	Africa	SL	NI	Yes	1	No	0	*Pan*	*Pan troglodytes*	Abundance	FC	NA	0	NA
25	Neotropics	LS	NA	No	1	No	0	Several	*Alouatta seniculus, Callicebus moloch, Mico argentata*	Species richness	FC	NA	0	NA
25	Neotropics	LS	NA	No	1	No	0	Several	*Alouatta seniculus, Callicebus moloch, Mico argentata*	Species richness	NA	FR	(-)	No
25	Neotropics	LS	NA	No	1	No	0	Several	*Alouatta seniculus, Callicebus moloch, Mico argentata*	Generalist species richness	FC	NA	0	NA
25	Neotropics	LS	NA	No	1	No	0	Several	*Alouatta seniculus, Callicebus moloch, Mico argentata*	Generalist species richness	NA	FR	0	No
26	Neotropics	PL	Edge	NI	3 to 12	No	9.1 to 12	Several	*Alouatta caraya, Aotus azarae boliviensis, Callithrix melanura, Callicebus donacophilus, Cebus libidinosus juruanus*	Species richness	FC	NA	0	NA
26	Neotropics	PL	Edge	NI	3 to 12	No	9.1 to 12	Several	*Alouatta caraya, Aotus azarae boliviensis, Callithrix melanura, Callicebus donacophilus, Cebus*	Abundance	FC	NA	(-)	NA

									libidinosus juruanus					
26	Neotropics	PL	Edge	NI	3 to 12	No	9.1 to 12	*Callithrix*	*Callithrix melanura*	Abundance	FC	NA	(-)	NA
26	Neotropics	PL	Edge	NI	3 to 12	No	9.1 to 12	*Cebus*	*Cebus libidinosus juruanus*	Abundance	FC	NA	0	NA
26	Neotropics	PL	Edge	NI	3 to 12	No	9.1 to 12	*Callicebus*	*Callicebus donacophilus*	Abundance	FC	NA	0	NA
27	Madagascar	SL	Centre	NI	1	No	0	*Propithecus*	*Propithecus tattersalli*	Diet diversity	MC	NA	(-)	NA
28	Neotropics	PL	Centre	Yes	3 to 12	Yes	9.1 to 12	Several	*Alouatta juara, Saimiri macrodon, Sapajus macrocephalus, Cacajao calvus, Ateles chamek, Pithecia cazuzai, Saimiri vanzolinii, Saimiri cassiquiarensis, Callicebus sp., Cebuella pygmaea*	Species richness	FC	NA	(+)	NA
29	Neotropics	PL	Centre	No	1	No	0	*Callicebus*	*Callicebus nigrifrons*	Occurrence	FC	NA	0	NA
29	Neotropics	PL	Centre	No	1	No	0	*Callicebus*	*Callicebus nigrifrons*	Occurrence	NA	FR	0	Yes
29	Neotropics	PL	Centre	No	1	No	0	*Callithrix*	*Callithrix penicillata*	Occurrence	FC	NA	0	NA
29	Neotropics	PL	Centre	No	1	No	0	*Callithrix*	*Callithrix penicillata*	Occurrence	NA	FR	0	Yes
30	Neotropics	SL	Centre	No	1	No	0	Several	*Alouatta discolora, Ateles marginatus, Mico argentatus, Aotus infulatus, Cebus apella, Saimiri sciureus, Chiropotes albinasus, Callicebus moloch*	Species richness	FC	NA	0	NA
31	Neotropics	PL	Edge	NI	1	No	0	*Callicebus*	*Callicebus nigrifrons*	Occurrence	MP	NA	0	NA
31	Neotropics	PL	Edge	NI	1	No	0	*Callithrix*	*Callithrix aurita*	Occurrence	MP	NA	0	NA
31	Neotropics	PL	Edge	NI	1	No	0	*Sapajus*	*Sapajus nigritus*	Occurrence	MP	NA	0	NA
32	Neotropics	PL	Edge	NI	3 to 12	Yes	3.1 to 6	*Alouatta*	*Alouatta pigra*	Occurrence	FC	NA	0	NA
32	Neotropics	PL	Edge	NI	3 to 12	Yes	3.1 to 6	*Alouatta*	*Alouatta pigra*	Occurrence	NA	FR	0	Yes
32	Neotropics	PL	Edge	NI	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Occurrence	FC	NA	(+)	NA
32	Neotropics	PL	Edge	NI	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Occurrence	NA	FR	(-)	Yes
33	Neotropics	PL	NA	NI	3 to 12	Yes	3.1 to 6	Several	*Ateles geoffroyi, Alouatta pigra*	Species richness	LQI	NA	(+)	NA

33	Neotropics	PL	NA	NI	3 to 12	Yes	3.1 to 6	*Ateles*	*Ateles geoffroyi*	Occurrence	LQI	NA	(+)	NA
33	Neotropics	PL	NA	NI	3 to 12	Yes	3.1 to 6	*Alouatta*	*Alouatta pigra*	Occurrence	LQI	NA	(+)	NA
34	Neotropics	SL	Edge	Yes	1	No	0	Several	*Alouatta pigra, Ateles geoffroyi yucatanensis*	Old-growth specialists richness	FC	NA	(+)	NA
34	Neotropics	SL	Edge	Yes	1	No	0	Several	*Alouatta pigra, Ateles geoffroyi yucatanensis*	Species diversity (Simpson)	FC	NA	0	NA
34	Neotropics	SL	Edge	Yes	1	No	0	*Alouatta*	*Alouatta pigra*	Abundance	FC	NA	0	NA
34	Neotropics	SL	Edge	Yes	1	No	0	*Ateles*	*Ateles geoffroyi yucatanensis*	Abundance	FC	NA	0	NA

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Capítulo 3 | Drivers of the spatial scale that best predict primate responses to landscape structure

Appendix 1. Landscape structure within each landscape size in each study region. Horizontal lines show the median, the dots beyond the vertical bars represent outliers, the bottom and top of each box show the 25th and 75th percentiles (or the first and third quartiles), respectively, and vertical dashed lines show 1.5 times the interquartile range of the data (approximately 2 standard deviations).

Figure A1.1 Marqués de Comillas Region

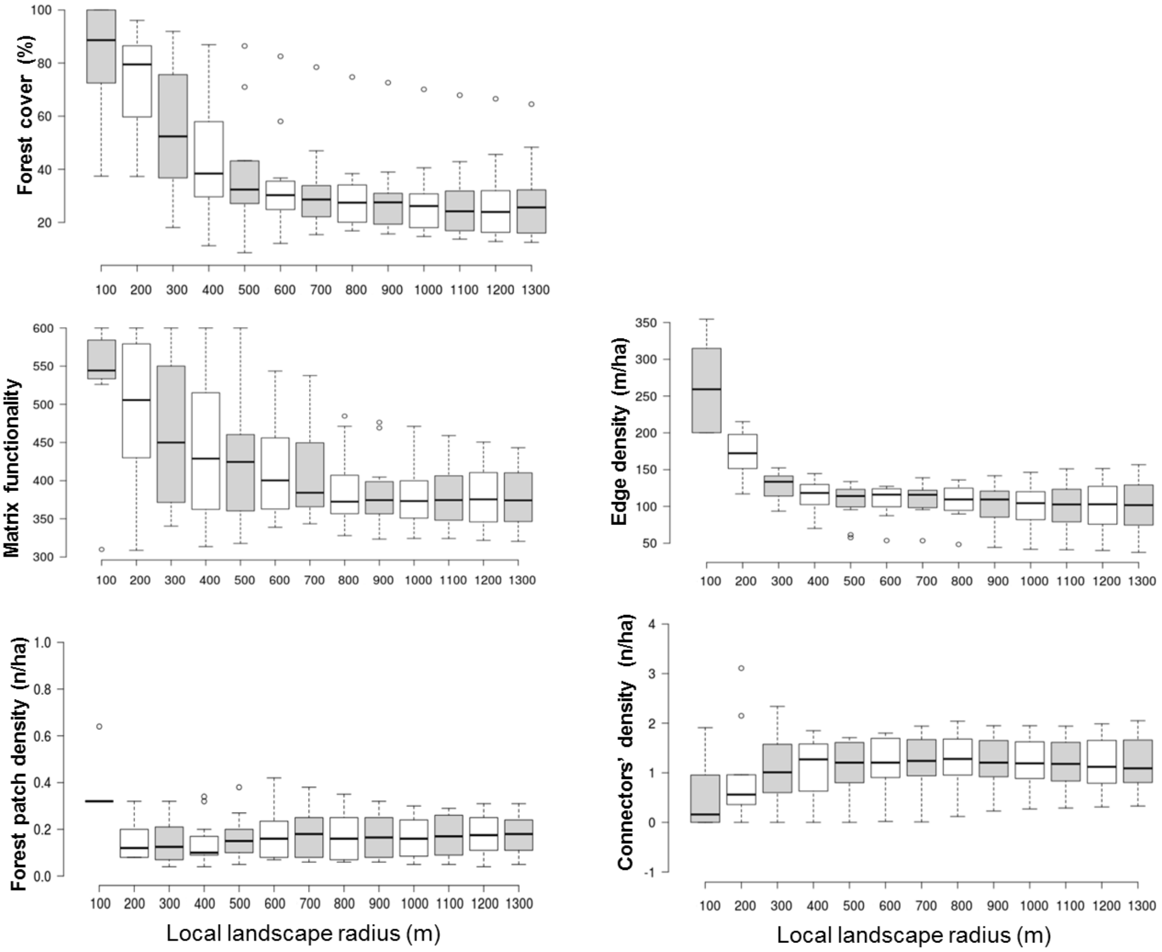


Figure A1.2 Uxpanapa Region

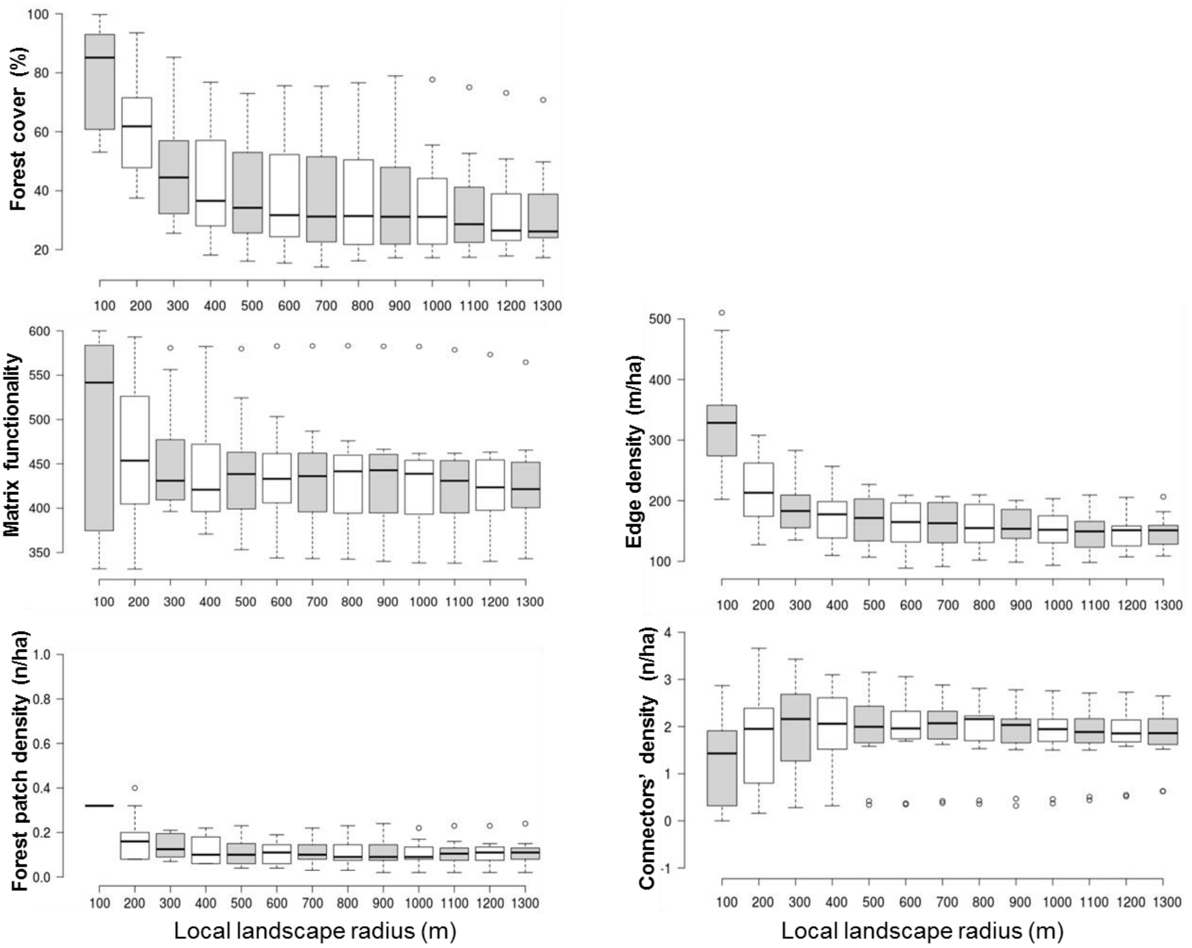


Figure A1.3 Los Tuxtlas Region

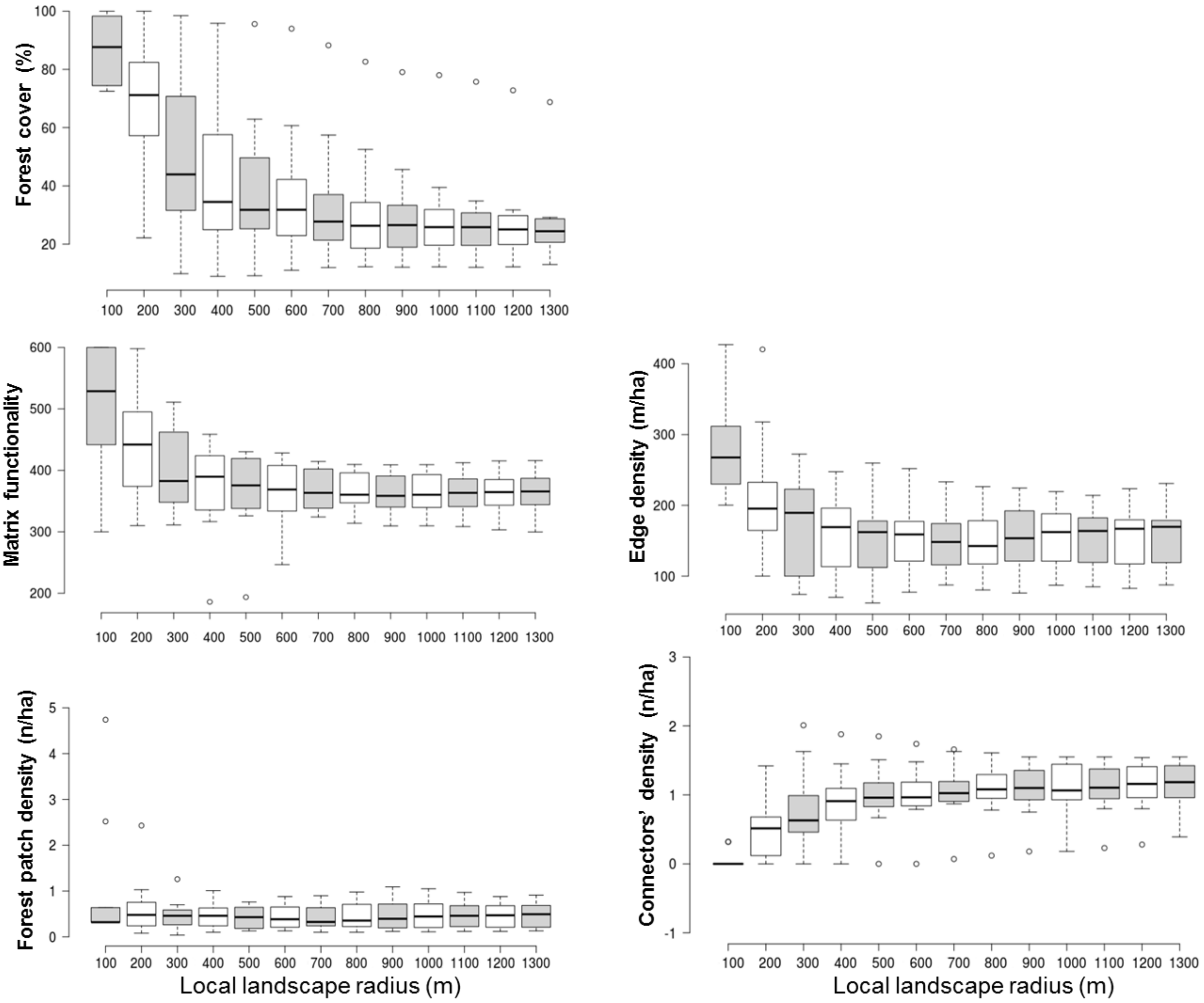
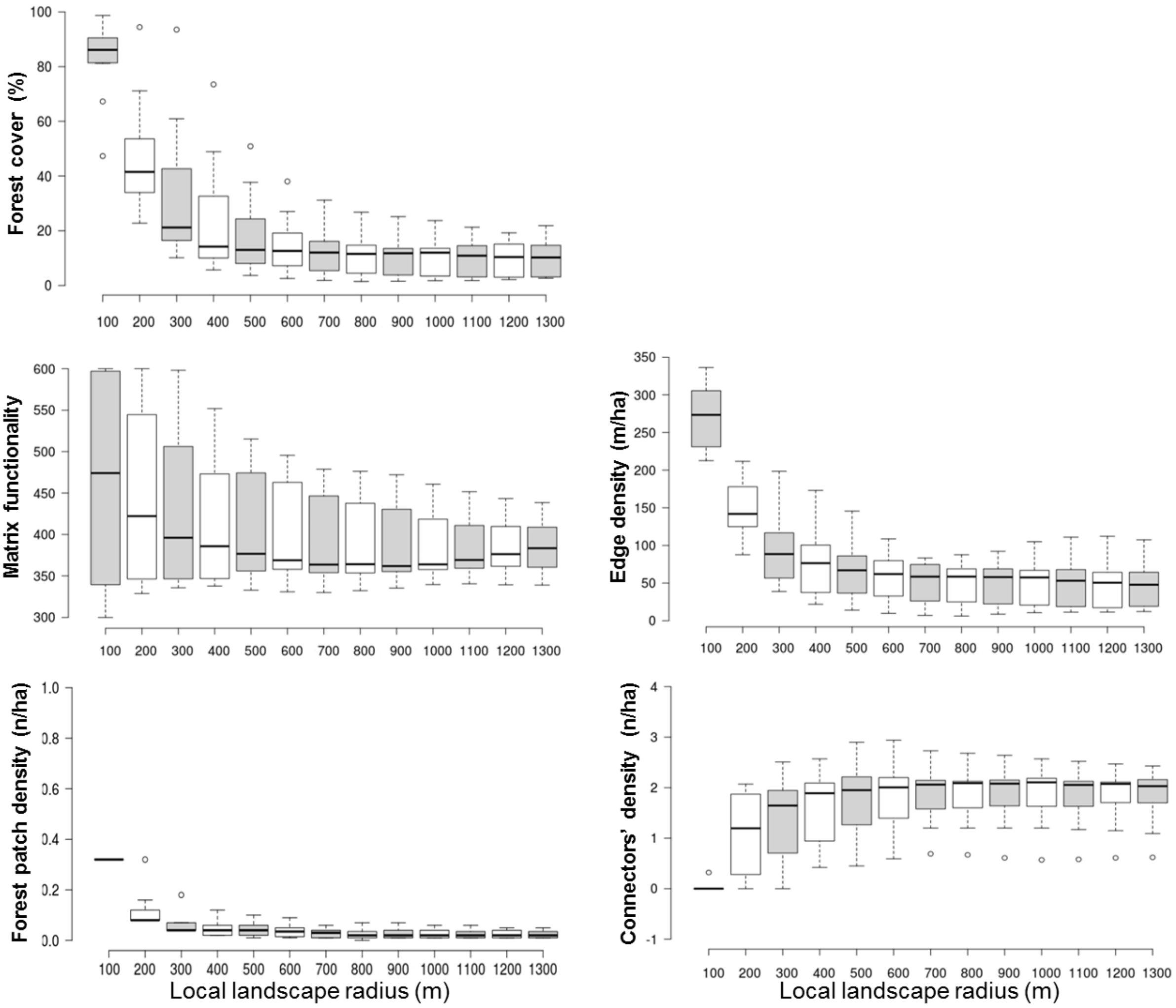


Figure A1.4 8th North Region



Capítulo 4 | Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests

Table A1. Scales of effect for each landscape attribute (i.e. forest cover, matrix functionality and patch density) and each response variable (i.e. encounter rate and immature-to-female ratio) of spider monkeys in the Marques de Comillas and Uxpanapa regions.

	Marqués de Comillas region		**Uxpanapa region**	
	Encounter rate	*Reproductive success*	*Encounter rate*	*Reproductive success*
Forest cover	500	500	400	400
Matrix functionality	400	400	1300	1300
Patch density	1000	800	1300	1300

Table A2. Results of information-theoretic-based model selection and multimodel inference for immature-to-female ratio (a proxy of reproductive success) and encounter rate (a proxy of relative abundance) of *Ateles geoffroyi* in Marqués de Comillas and Uxpanapa rainforests, Mexico. The table includes the 95% confidence set of models, i.e. those for which Akaike weights summed ($\sum w_i$) 0.95. “X” indicates variable inclusion in each individual model. The predictor variables included forest cover, matrix functionality and forest patch density.

Region/response variable	Forest cover	Matrix functionality	Patch density	AICc	ΔAICc	w_i
Marqués de Comillas rainforest						
Reproductive success						
	X			6.83	0	0.62
	X	X		8.50	1.68	0.27
	X		x	11.43	4.60	0.06
Relative abundance						
			x	26.004	0	0.53

		X	x	28.15	2.15	0.18
	X	X	x	29.38	3.38	0.1
	X			29.39	3.39	0.1
	X		x	30.59	4.58	0.05
Uxpanapa rainforest						
Reproductive success						
		X		7.51	0	0.36
	X			8.12	0.61	0.27
	X	x	x	9.03	1.52	0.17
	X	x		10.52	3.01	0.08
		x	x	11.27	3.76	0.05
	X		x	12.36	4.85	0.03
Relative abundance						
		x		16.22	0	0.7
	X	x		19.16	2.94	0.16
		x	x	19.59	3.36	0.13

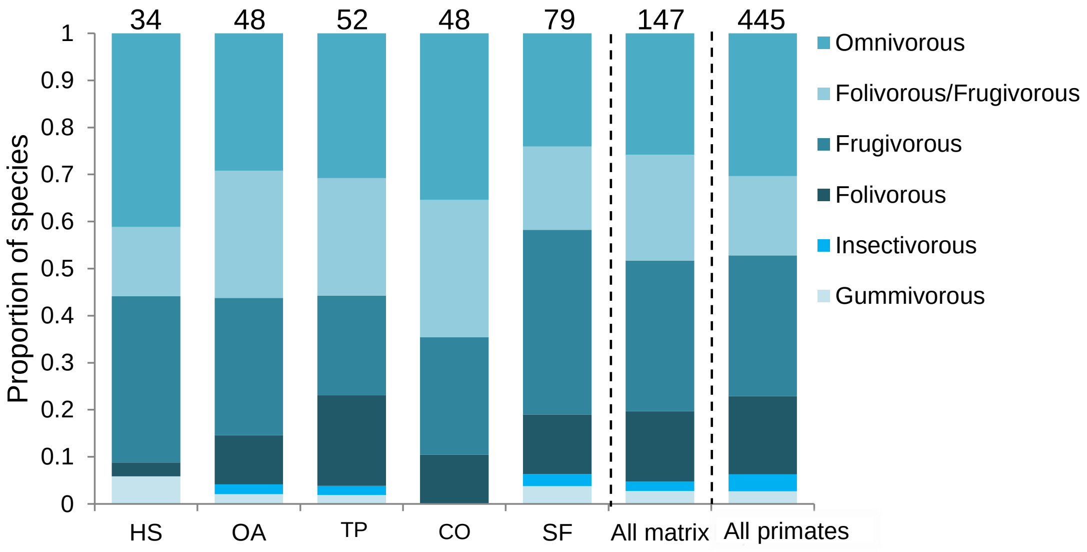
Capítulo 5 | Regional context drives howler monkeys’ responses to landscape structure

Table A1. Results of information-theoretic-based model selection and multimodel inference for abundance and immature-to-female ratio (a proxy of reproductive success) of *Alouatta palliata* and *Alouatta pigra* in Marqués de Comillas, Uxpanapa, Los Tuxltas and the 8th North regions, Mexico. The table includes the 95% confidence set of models, i.e. those for which Akaike weights summed ($\sum w_i$) 0.95. “X” indicates variable inclusion in each individual model. The predictor variables included forest cover, matrix functionality and forest patch density.

Region/response variable	Forest cover	MatriX functionality	Patch density	AICc	ΔAICc	w_i
Marqués de Comillas region (*Alouatta pigra*)						
Abundance						
	X		X	29.58	0	0.78
	X	X	X	33.31	3.74	0.12
			X	34.99	5.41	0.05
Reproductive success						
		X		30.18	0	0.42
	*	*	*	31.56	1.37	0.21
	X	X		31.99	1.80	0.17
			X	33.20	3.02	0.09
		X	X	34.90	4.71	0.04
	X			35.22	5.04	0.03
Uxpanapa región (*Alouatta palliata*)						
Abundance						
	*	*	*	14.87	0	0.51
			X	17.19	2.32	0.16
		X		17.63	2.75	0.13
	X			17.80	2.93	0.12
	X		X	20.68	5.81	0.03

		X	X	20.84	5.97	0.03
Reproductive success						
		X		15.40	0	0.37
	*	*	*	15.95	0.55	0.28
	X			17.53	2.13	0.13
			X	18.25	2.85	0.09
		X	X	19.07	3.67	0.06
	X	X		19.77	4.37	0.04
Los Tuxtlas región						
(*Alouatta palliata*)						
Abundance						
	X			11.83	0	0.46
	X	X		13.28	1.45	0.22
	X		X	14.35	2.52	0.13
	*	*	*	15.17	3.34	0.09
		X		16.83	5.00	0.04
			X	16.94	5.11	0.03
Reproductive success						
	X			-0.74	0	0.41
	*	*	*	0.05	0.78	0.28
	X	X		2.14	2.88	0.10
			X	2.68	3.41	0.07
		X		2.95	3.68	0.07
	X		X	3.83	4.57	0.04
8th North región						
(*Alouatta palliata*)						
Abundance						
	*	*	*	17.67	0	0.44
		X		19.27	1.60	0.20
			X	19.99	2.32	0.14
	X			20.26	2.59	0.12
	X	X		22.00	4.33	0.05
		X	X	22.76	5.09	0.03

Reproductive success						
	X			10.55	0	0.44
	*	*	*	12.73	2.18	0.15
			X	12.92	2.37	0.14
	X		X	13.54	3.00	0.10
		X		13.71	3.16	0.09
	X	X		15.01	4.46	0.05



Supplementary Figure 1. The proportion (and total number above bars) of primate species within different dietary categories. We tested for differences in frequencies with Chi-square tests of goodness of fit (*$P \leq 0.05$, **$P \leq 0.01$) between primates using the matrix and all the world’s primates, by separately assessing primates species that used different matrix types (HS = human settlements, OA = open areas, TP = tree plantations, CO = connectors, and SF = secondary forest). None of the tests were statistically significant. We excluded from the analyses those species for which there was no available information.

Supplementary Note 1. Despite having a similar number of species in the tree, Lepilemuridae had, as most of the other families, the greatest influence on the parameter estimate when removing it from the analyses. We expected Cercopithecidae to have a large effect on parameter estimates because it includes a larger proportion of the species analyzed. However, the distribution of matrix use within this family is not distinguishable from the order as a whole. After correcting for clade size, only Lepilemuridae had a strong influence on our estimates of D. Removing this clade from the analysis led to a significant shift in phylogenetic signal towards a truly random pattern.

Supplementary Table 1. Primate species using the matrix. The sources of studies reporting the matrix use are included in the Reference column. Matrix: CO = connectors, HS = human settlements, OA = open areas, SF = secondary forests, TP = tree plantations; Realm: M_Africa = mainland Africa; activity: TR = travel, R = resting, F = foraging, NR = not reported; conservation status (IUCN): CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concerned, DD = data deficient, NE = not evaluated; population trend (Pop_T): I = increasing, D = decreasing, S = stable, NA = no data available; diel activity (D_A): Di = diurnal, N = Nocturnal, Cath = cathemeral; locomotion: AR = arboreal locomotion, T = terrestrial locomotion; body mass (B_M): L = large (>10 kg), M = medium (2 – 10 kg), S = small (<2 kg); habitat: FS = forest specialist, N_FS = non forest specialist; trophic level (T_L), F_f = folivorous-frugivorous, Fol = folivorous, Fru = frugivorous, G = gummivorous, O = omnivorous, In = insectivorous. “N records” refers to the number of times that a given primate species was recorded using the matrix.

Matrix	**Family**[a]	***Species***	**Realm**	**Activity**	**IUCN**	**Pop_T**	**D_A**	**Locomotion**	**B_M**	**Forest specialization**	**T_L**	**N records**	**Reference**
HS	*Atelidae*	*Alouatta guariba*	Neotropics	TR	LC	D	DI	AR	M	FS	F_F	5	238
HS	*Callitrichidae*	*Callithrix jacchus*	Neotropics	F	LC	S	DI	AR	S	N_FS	G	2	243
HS	*Callitrichidae*	*Callithrix kuhlii*	Neotropics	F	NT	D	DI	AR	S	FS	O	2	210
HS	*Callitrichidae*	*Callithrix penicillata*	Neotropics	NR	LC	I	DI	AR	S	N_FS	G	7	237
HS	*Callitrichidae*	*Callithrix penicillata*	Neotropics	ALL	LC	I	DI	AR	S	N_FS	G	7	60
HS	*Callitrichidae*	*Callithrix penicillata*	Neotropics	F	LC	I	DI	AR	S	N_FS	G	7	243
HS	*Callitrichidae*	*Callithrix penicillata*	Neotropics	ALL	LC	I	DI	AR	S	N_FS	G	7	59
HS	*Callitrichidae*	*Callithrix penicillata*	Neotropics	ALL	LC	I	DI	AR	S	N_FS	G	7	61
HS	*Callitrichidae*	*Callithrix penicillata*	Neotropics	ALL	LC	I	DI	AR	S	N_FS	G	7	97
HS	*Cercopithecidae*	*Cercocebus torquatus*	M_Africa	NR	VU	D	DI	BOTH	M	FS	FRU	1	15
HS	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	94
HS	*Cercopithecidae*	*Cercopithecus erythrotis*	M_Africa	NR	VU	D	DI	AR	M	FS	FRU	1	15
HS	*Cercopithecidae*	*Cercopithecus mona*	M_Africa	NR	LC	NI	DI	AR	M	FS	FRU	2	15
HS	*Cercopithecidae*	*Cercopithecus nictitans*	M_Africa	NR	LC	D	DI	AR	M	FS	FRU	3	15
HS	*Cercopithecidae*	*Cercopithecus pogonias*	M_Africa	NR	LC	D	DI	AR	M	N_FS	FRU	3	15

HS	*Cercopithecidae*	*Cercopithecus sclateri*	M_Africa	F	VU	D	DI	AR	M	N_FS	FRU	1	12
HS	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	185
HS	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	220
HS	*Cercopithecidae*	*Chlorocebus pygerythrus*	M_Africa	NR	LC	S	DI	T	M	N_FS	O	1	154
HS	*Cercopithecidae*	*Colobus vellerosus*	M_Africa	NR	VU	NI	DI	AR	M	N_FS	FOL	1	236
HS	*Galagidae*	*Galago moholi*	M_Africa	ALL	LC	S	N	AR	S	N_FS	O	1	222
HS	*Callitrichidae*	*Leontocebus fuscicollis*	Neotropics	F	LC	D	DI	AR	S	FS	O	4	249
HS	*Cercopithecidae*	*Macaca cyclopis*	Asia	F	LC	S	DI	BOTH	M	FS	FRU	1	111
HS	*Cercopithecidae*	*Macaca fascicularis*	Asia	ALL	LC	D	DI	AR	M	FS	FRU	10	30
HS	*Cercopithecidae*	*Macaca fascicularis*	Asia	F	LC	D	DI	AR	M	FS	FRU	10	225
HS	*Cercopithecidae*	*Macaca fascicularis*	Asia	ALL	LC	D	DI	AR	M	FS	FRU	10	155
HS	*Cercopithecidae*	*Macaca fascicularis*	Asia	NR	LC	D	DI	AR	M	FS	FRU	10	82
HS	*Cercopithecidae*	*Macaca fuscata*	Asia	NR	LC	S	DI	BOTH	M	FS	F_F	6	113
HS	*Cercopithecidae*	*Macaca leonina*	Asia	ALL	VU	D	DI	AR	M	FS	FRU	1	3
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	NR	LC	NI	DI	BOTH	M	N_FS	F_F	15	175
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	17
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	114
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	124
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	F	LC	NI	DI	BOTH	M	N_FS	F_F	15	46
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	NR	LC	NI	DI	BOTH	M	N_FS	F_F	15	213
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	F	LC	NI	DI	BOTH	M	N_FS	F_F	15	45
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	NR	LC	NI	DI	BOTH	M	N_FS	F_F	15	233
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	NR	LC	NI	DI	BOTH	M	N_FS	F_F	15	231
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	85
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	147
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	232
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	195
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	125
HS	*Cercopithecidae*	*Macaca mulatta*	Asia	ALL	LC	NI	DI	BOTH	M	N_FS	F_F	15	102

HS	*Cercopithecidae*	*Macaca radiata*	Asia	ALL	LC	D	DI	BOTH	M	N_FS	FRU	11	48
HS	*Cercopithecidae*	*Macaca radiata*	Asia	ALL	LC	D	DI	BOTH	M	N_FS	FRU	11	49
HS	*Cercopithecidae*	*Macaca radiata*	Asia	ALL	LC	D	DI	BOTH	M	N_FS	FRU	11	47
HS	*Cercopithecidae*	*Macaca radiata*	Asia	ALL	LC	D	DI	BOTH	M	N_FS	FRU	11	202
HS	*Cercopithecidae*	*Macaca radiata*	Asia	ALL	LC	D	DI	BOTH	M	N_FS	FRU	11	228
HS	*Cercopithecidae*	*Macaca sinica*	Asia	TR	EN	D	DI	AR	M	FS	FRU	1	63
HS	*Cercopithecidae*	*Macaca sylvanus*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	2	141
HS	*Cercopithecidae*	*Macaca sylvanus*	M_Africa	NR	EN	D	DI	BOTH	L	N_FS	O	2	82
HS	*Cercopithecidae*	*Mandrillus leucophaeus*	M_Africa	NR	EN	NI	DI	BOTH	L	N_FS	O	1	15
HS	*Lorisidae*	*Nycticebus coucang*	Asia	R	VU	D	N	AR	S	FS	O	2	70
HS	*Hominidae*	*Pan troglodytes*	M_Africa	NR	EN	D	DI	BOTH	L	N_FS	O	17	15
HS	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	62
HS	*Cercopithecidae*	*Papio anubis*	M_Africa	F	LC	I	DI	T	L	N_FS	O	11	217
HS	*Cercopithecidae*	*Papio cynocephalus*	M_Africa	F	LC	S	DI	T	L	N_FS	O	3	4
HS	*Cercopithecidae*	*Papio ursinus*	M_Africa	ALL	LC	S	DI	T	L	N_FS	O	7	110
HS	*Cercopithecidae*	*Papio ursinus*	M_Africa	F	LC	S	DI	T	L	N_FS	O	7	75
HS	*Cercopithecidae*	*Papio ursinus*	M_Africa	F	LC	S	DI	T	L	N_FS	O	7	109
HS	*Cercopithecidae*	*Papio ursinus*	M_Africa	F	LC	S	DI	T	L	N_FS	O	7	117
HS	*Cercopithecidae*	*Papio ursinus*	M_Africa	ALL	LC	S	DI	T	L	N_FS	O	7	108
HS	*Cercopithecidae*	*Piliocolobus pennantii*	M_Africa	NR	EN	D	DI	AR	M	FS	F_F	1	15
HS	*Callitrichidae*	*Saguinus mystax*	Neotropics	F	LC	S	DI	AR	S	FS	O	4	249
HS	*Cebidae*	*Sapajus libidinosus*	Neotropics	ALL	LC	D	DI	AR	M	N_FS	O	3	89
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	NR	LC	D	DI	T	L	N_FS	F_F	8	175
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	ALL	LC	D	DI	T	L	N_FS	F_F	8	247
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	NR	LC	D	DI	T	L	N_FS	F_F	8	1
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	NR	LC	D	DI	T	L	N_FS	F_F	8	213
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	ALL	LC	D	DI	T	L	N_FS	F_F	8	180
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	ALL	LC	D	DI	T	L	N_FS	F_F	8	147
HS	*Cercopithecidae*	*Semnopithecus entellus*	Asia	ALL	LC	D	DI	T	L	N_FS	F_F	8	162

OA	*Atelidae*	*Alouatta caraya*	Neotropics	TR	LC	D	DI	AR	M	N_FS	F_F	2	22
OA	*Atelidae*	*Alouatta palliata*	Neotropics	F	LC	NI	DI	AR	M	FS	F_F	25	229
OA	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	25	95
OA	*Atelidae*	*Alouatta pigra*	Neotropics	R	EN	D	DI	AR	M	FS	F_F	12	198
OA	*Atelidae*	*Alouatta pigra*	Neotropics	F	EN	D	DI	AR	M	FS	F_F	12	196
OA	*Atelidae*	*Alouatta pigra*	Neotropics	TR	EN	D	DI	AR	M	FS	F_F	12	18
OA	*Atelidae*	*Alouatta seniculus*	Neotropics	TR	LC	NI	DI	AR	M	N_FS	F_F	7	34
OA	*Atelidae*	*Brachyteles arachnoides*	Neotropics	TR	EN	D	DI	AR	M	FS	F_F	1	132
OA	*Atelidae*	*Brachyteles hypoxanthus*	Neotropics	TR	CR	D	DI	AR	M	FS	F_F	1	57
OA	*Cebidae*	*Cebus capucinus*	Neotropics	F	LC	NI	DI	AR	M	FS	O	15	151
OA	*Cebidae*	*Cebus capucinus*	Neotropics	F	LC	NI	DI	AR	M	FS	O	15	229
OA	*Cebidae*	*Cebus capucinus*	Neotropics	TR	LC	NI	DI	AR	M	FS	O	15	72
OA	*Cebidae*	*Cebus capucinus*	Neotropics	TR	LC	NI	DI	AR	M	FS	O	15	41
OA	*Cebidae*	*Cebus capucinus*	Neotropics	F	LC	NI	DI	AR	M	FS	O	15	96
OA	*Cercopithecidae*	*Cercocebus galeritus*	M_Africa	F	EN	D	DI	BOTH	M	FS	FRU	3	164
OA	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	248
OA	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	192
OA	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	168
OA	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	83
OA	*Cercopithecidae*	*Cercopithecus campbelli*	M_Africa	F	LC	NI	DI	AR	M	N_FS	FRU	5	250
OA	*Cercopithecidae*	*Cercopithecus cephus*	M_Africa	NR	LC	NI	DI	AR	M	FS	FRU	2	146
OA	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	248
OA	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	28
OA	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	164
OA	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	178
OA	*Cercopithecidae*	*Cercopithecus mona*	M_Africa	NR	LC	NI	DI	AR	M	FS	FRU	2	146
OA	*Cercopithecidae*	*Cercopithecus nictitans*	M_Africa	NR	LC	D	DI	AR	M	FS	FRU	3	146
OA	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	248
OA	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	25

OA	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	220
OA	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	164
OA	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	120
OA	*Cercopithecidae*	*Chlorocebus djamdjamensis*	M_Africa	F	VU	D	DI	BOTH	M	FS	FOL	1	156
OA	*Cercopithecidae*	*Colobus angolensis*	M_Africa	TR	LC	NI	DI	AR	M	FS	FOL	5	6
OA	*Lemuridae*	*Lemur catta*	Madagascar	F	EN	D	DI	BOTH	M	N_FS	F_F	1	128
OA	*Cercopithecidae*	*Lophocebus ugandae*	M_Africa	F	NE	NI	DI	AR	M	FS	F_F	2	83
OA	*Cercopithecidae*	*Macaca assamensis*	Asia	F	NT	D	DI	AR	M	FS	FRU	1	207
OA	*Cercopithecidae*	*Macaca fascicularis*	Asia	F	LC	D	DI	AR	M	FS	FRU	10	143
OA	*Cercopithecidae*	*Macaca fuscata*	Asia	R	LC	S	DI	BOTH	M	FS	F_F	6	64
OA	*Cercopithecidae*	*Macaca fuscata*	Asia	F	LC	S	DI	BOTH	M	FS	F_F	6	256
OA	*Cercopithecidae*	*Macaca fuscata*	Asia	ALL	LC	S	DI	BOTH	M	FS	F_F	6	112
OA	*Cercopithecidae*	*Macaca nemestrina*	Asia	F	VU	D	DI	T	M	FS	FRU	4	143
OA	*Cercopithecidae*	*Macaca ochreata*	Asia	F	VU	D	DI	BOTH	M	FS	FRU	3	199
OA	*Cercopithecidae*	*Macaca ochreata*	Asia	F	VU	D	DI	BOTH	M	FS	FRU	3	200
OA	*Cercopithecidae*	*Macaca radiata*	Asia	F	LC	D	DI	BOTH	M	N_FS	FRU	11	226
OA	*Cercopithecidae*	*Macaca radiata*	Asia	F	LC	D	DI	BOTH	M	N_FS	FRU	11	227
OA	*Cercopithecidae*	*Macaca tonkeana*	Asia	F	VU	D	DI	BOTH	L	FS	FRU	1	208
OA	*Cercopithecidae*	*Miopithecus talapoin*	M_Africa	NR	LC	NI	DI	BOTH	S	FS	O	2	146
OA	*Lorisidae*	*Nycticebus javanicus*	Asia	NR	CR	D	N	AR	S	FS	G	2	245
OA	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	36
OA	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	107
OA	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	192
OA	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	168
OA	*Hominidae*	*Pan troglodytes*	M_Africa	ALL	EN	D	DI	BOTH	L	N_FS	O	17	241
OA	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	20
OA	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	105
OA	*Cercopithecidae*	*Papio anubis*	M_Africa	F	LC	I	DI	T	L	N_FS	O	11	131
OA	*Cercopithecidae*	*Papio anubis*	M_Africa	F	LC	I	DI	T	L	N_FS	O	11	248

OA	*Cercopithecidae*	*Papio anubis*	M_Africa	ALL	LC	I	DI	T	L	N_FS	O	11	241
OA	*Cercopithecidae*	*Papio anubis*	M_Africa	NR	LC	I	DI	T	L	N_FS	O	11	218
OA	*Cercopithecidae*	*Papio anubis*	M_Africa	F	LC	I	DI	T	L	N_FS	O	11	164
OA	*Cercopithecidae*	*Papio anubis*	M_Africa	F	LC	I	DI	T	L	N_FS	O	11	105
OA	*Cercopithecidae*	*Papio cynocephalus*	M_Africa	F	LC	S	DI	T	L	N_FS	O	3	192
OA	*Cercopithecidae*	*Papio cynocephalus*	M_Africa	F	LC	S	DI	T	L	N_FS	O	3	168
OA	*Cercopithecidae*	*Papio hamadryas*	M_Africa	F	LC	I	DI	T	L	N_FS	O	4	106
OA	*Cercopithecidae*	*Papio hamadryas*	M_Africa	TR	LC	I	DI	T	L	N_FS	O	4	187
OA	*Cercopithecidae*	*Papio ursinus*	M_Africa	ALL	LC	S	DI	T	L	N_FS	O	7	108
OA	*Cercopithecidae*	*Piliocolobus badius*	M_Africa	TR	EN	D	DI	AR	M	FS	F_F	5	93
OA	*Pitheciidae*	*Plecturocebus modestus*	Neotropics	TR	EN	D	DI	AR	S	N_FS	FRU	1	76
OA	*Pitheciidae*	*Plecturocebus moloch*	Neotropics	TR	LC	NI	DI	AR	S	FS	O	2	77
OA	*Pitheciidae*	*Plecturocebus olallae*	Neotropics	TR	EN	D	DI	AR	S	N_FS	F_F	2	76
OA	*Cercopithecidae*	*Presbytis thomasi*	Asia	F	VU	D	DI	AR	M	FS	F_F	2	143
OA	*Indriidae*	*Propithecus verreauxi*	Madagascar	F	EN	D	DI	AR	M	N_FS	F_F	4	86
OA	*Cercopithecidae*	*Rungwecebus kipunji*	M_Africa	F	CR	D	DI	AR	L	FS	O	2	28
OA	*Callitrichidae*	*Saguinus leucopus*	Neotropics	TR	EN	D	DI	AR	S	FS	FRU	7	53
OA	*Callitrichidae*	*Saguinus leucopus*	Neotropics	TR	EN	D	DI	AR	S	FS	FRU	7	127
OA	*Cebidae*	*Saimiri sciureus*	Neotropics	TR	LC	D	DI	AR	S	FS	O	3	34
OA	*Cebidae*	*Sapajus apella*	Neotropics	F	LC	D	DI	AR	M	N_FS	O	11	190
OA	*Cebidae*	*Sapajus apella*	Neotropics	TR	LC	D	DI	AR	M	N_FS	O	11	34
OA	*Cebidae*	*Sapajus libidinosus*	Neotropics	F	LC	D	DI	AR	M	N_FS	O	3	81
OA	*Tarsiidae*	*Tarsius dentatus*	Asia	TR	VU	D	N	AR	S	FS	IN	3	158
OA	*Cercopithecidae*	*Thercopithecus gelada*	M_Africa	TR	LC	D	DI	T	L	N_FS	FOL	1	121
OA	*Cercopithecidae*	*Trachypithecus germaini*	Asia	F	EN	D	DI	AR	M	FS	FOL	2	143
OA	*Cercopithecidae*	*Trachypithecus pileatus*	Asia	NR	VU	D	DI	AR	L	FS	FOL	1	219
TP	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	253
TP	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	165
TP	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	149

TP	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	68
TP	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	69
TP	*Atelidae*	*Alouatta palliata*	Neotropics	F	LC	NI	DI	AR	M	FS	F_F	25	69
TP	*Atelidae*	*Alouatta pigra*	Neotropics	F	EN	D	DI	AR	M	FS	F_F	12	258
TP	*Atelidae*	*Alouatta pigra*	Neotropics	ALL	EN	D	DI	AR	M	FS	F_F	12	198
TP	*Atelidae*	*Alouatta pigra*	Neotropics	ALL	EN	D	DI	AR	M	FS	F_F	12	197
TP	*Atelidae*	*Alouatta pigra*	Neotropics	NR	EN	D	DI	AR	M	FS	F_F	12	69
TP	*Aotidae*	*Aotus lemurinus*	Neotropics	F	VU	D	N	AR	S	FS	O	2	100
TP	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	68
TP	*Atelidae*	*Ateles geoffroyi*	Neotropics	ALL	EN	D	DI	AR	M	FS	FRU	19	69
TP	*Indriidae*	*Avahi laniger*	Madagascar	F	VU	D	N	AR	S	FS	FOL	2	86
TP	*Callitrichidae*	*Callithrix kuhlii*	Neotropics	ALL	NT	D	DI	AR	S	FS	O	2	240
TP	*Cebidae*	*Cebus capucinus*	Neotropics	F	LC	NI	DI	AR	M	FS	O	15	151
TP	*Cebidae*	*Cebus capucinus*	Neotropics	NR	LC	NI	DI	AR	M	FS	O	15	69
TP	*Cercopithecidae*	*Cercocebus galeritus*	M_Africa	F	EN	D	DI	BOTH	M	FS	FRU	3	164
TP	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	13
TP	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	83
TP	*Cercopithecidae*	*Cercopithecus campbelli*	M_Africa	F	LC	NI	DI	AR	M	N_FS	FRU	5	250
TP	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	164
TP	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	178
TP	*Cheirogaleidae*	*Cheirogaleus major*	Madagascar	ALL	DD	D	N	AR	S	FS	F_F	2	86
TP	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	25
TP	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	220
TP	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	164
TP	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	F	LC	S	DI	T	M	N_FS	O	12	120
TP	*Cercopithecidae*	*Colobus angolensis*	M_Africa	ALL	LC	NI	DI	AR	M	FS	FOL	5	6
TP	*Cercopithecidae*	*Colobus angolensis*	M_Africa	F	LC	NI	DI	AR	M	FS	FOL	5	7
TP	*Lemuridae*	*Eulemur fulvus*	Madagascar	ALL	NT	D	CATH	AR	M	FS	F_F	2	86
TP	*Lemuridae*	*Hapalemur griseus*	Madagascar	F	VU	D	DI	AR	S	FS	FOL	2	86

TP	*Hylobatidae*	*Hylobates lar*	Asia	NR	EN	D	DI	AR	M	FS	FRU	2	11
TP	*Indriidae*	*Indri indri*	Madagascar	TR	CR	D	DI	AR	M	FS	FOL	1	86
TP	*Callitrichidae*	*Leontopithecus chrysomelas*	Neotropics	ALL	EN	D	DI	AR	S	FS	O	4	176
TP	*Callitrichidae*	*Leontopithecus chrysomelas*	Neotropics	ALL	EN	D	DI	AR	S	FS	O	4	177
TP	*Callitrichidae*	*Leontopithecus chrysomelas*	Neotropics	ALL	EN	D	DI	AR	S	FS	O	4	240
TP	*Lepilemuridae*	*Lepilemur mustelinus*	Madagascar	ALL	NT	D	N	AR	S	FS	FOL	1	86
TP	*Cercopithecidae*	*Lophocebus ugandae*	M_Africa	F	NE	NI	DI	AR	M	FS	F_F	2	83
TP	*Cercopithecidae*	*Macaca fascicularis*	Asia	NR	LC	D	DI	AR	M	FS	FRU	10	167
TP	*Cercopithecidae*	*Macaca fascicularis*	Asia	NR	LC	D	DI	AR	M	FS	FRU	10	11
TP	*Cercopithecidae*	*Macaca fascicularis*	Asia	F	LC	D	DI	AR	M	FS	FRU	10	143
TP	*Cercopithecidae*	*Macaca fuscata*	Asia	F	LC	S	DI	BOTH	M	FS	F_F	6	256
TP	*Cercopithecidae*	*Macaca fuscata*	Asia	F	LC	S	DI	BOTH	M	FS	F_F	6	221
TP	*Cercopithecidae*	*Macaca nemestrina*	Asia	NR	VU	D	DI	T	M	FS	FRU	4	11
TP	*Cercopithecidae*	*Macaca nemestrina*	Asia	F	VU	D	DI	T	M	FS	FRU	4	143
TP	*Cercopithecidae*	*Macaca ochreata*	Asia	F	VU	D	DI	BOTH	M	FS	FRU	3	200
TP	*Cercopithecidae*	*Macaca radiata*	Asia	NR	LC	D	DI	BOTH	M	N_FS	FRU	11	119
TP	*Cercopithecidae*	*Macaca radiata*	Asia	F	LC	D	DI	BOTH	M	N_FS	FRU	11	226
TP	*Cercopithecidae*	*Macaca radiata*	Asia	F	LC	D	DI	BOTH	M	N_FS	FRU	11	227
TP	*Cercopithecidae*	*Macaca radiata*	Asia	F	LC	D	DI	BOTH	M	N_FS	FRU	11	21
TP	*Cheirogaleidae*	*Microcebus murinus*	Madagascar	NR	LC	D	N	AR	S	N_FS	O	3	8
TP	*Cheirogaleidae*	*Microcebus rufus*	Madagascar	R	VU	D	N	AR	S	FS	O	1	86
TP	*Cercopithecidae*	*Nasalis larvatus*	Asia	TR	EN	D	DI	AR	L	FS	F_F	1	23
TP	*Lorisidae*	*Nycticebus coucang*	Asia	NR	VU	D	N	AR	S	FS	O	2	11
TP	*Lorisidae*	*Nycticebus javanicus*	Asia	NR	CR	D	N	AR	S	FS	G	2	245
TP	*Hominidae*	*Pan troglodytes*	M_Africa	ALL	EN	D	DI	BOTH	L	N_FS	O	17	241
TP	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	20
TP	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	37
TP	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	101
TP	*Cercopithecidae*	*Papio anubis*	M_Africa	ALL	LC	I	DI	T	L	N_FS	O	11	241

TP	*Cercopithecidae*	*Papio anubis*	M_Africa	F	LC	I	DI	T	L	N_FS	O	11	164
TP	*Cercopithecidae*	*Papio hamadryas*	M_Africa	F	LC	I	DI	T	L	N_FS	O	4	104
TP	*Cercopithecidae*	*Papio ursinus*	M_Africa	ALL	LC	S	DI	T	L	N_FS	O	7	108
TP	*Cercopithecidae*	*Piliocolobus gordonorum*	M_Africa	ALL	EN	D	DI	AR	M	FS	F_F	1	173
TP	*Cercopithecidae*	*Piliocolobus rufomitratus*	M_Africa	F	EN	D	DI	AR	M	FS	FOL	1	164
TP	*Hominidae*	*Pongo abelii*	Asia	ALL	CR	D	DI	AR	L	FS	FRU	2	31
TP	*Hominidae*	*Pongo abelii*	Asia	F	CR	D	DI	AR	L	FS	FRU	2	143
TP	*Hominidae*	*Pongo pygmaeus*	Asia	F	EN	D	DI	AR	L	FS	FRU	2	206
TP	*Cercopithecidae*	*Presbytis thomasi*	Asia	F	VU	D	DI	AR	M	FS	F_F	2	143
TP	*Indriidae*	*Propithecus verreauxi*	Madagascar	ALL	EN	D	DI	AR	M	N_FS	F_F	4	86
TP	*Indriidae*	*Propithecus verreauxi*	Madagascar	F	EN	D	DI	AR	M	N_FS	F_F	4	86
TP	*Cebidae*	*Saimiri oerstedii*	Neotropics	NR	VU	D	DI	AR	S	FS	O	3	69
TP	*Cebidae*	*Sapajus nigritus*	Neotropics	F	NT	D	DI	AR	M	FS	O	4	136
TP	*Cebidae*	*Sapajus nigritus*	Neotropics	F	NT	D	DI	AR	M	FS	O	4	160
TP	*Cebidae*	*Sapajus nigritus*	Neotropics	F	NT	D	DI	AR	M	FS	O	4	161
TP	*Cebidae*	*Sapajus xanthosternos*	Neotropics	F	CR	D	DI	AR	M	FS	O	4	32
TP	*Cercopithecidae*	*Semnopithecus entellus*	Asia	NR	LC	D	DI	T	L	N_FS	F_F	8	119
TP	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	F	EN	D	DI	AR	M	FS	F_F	10	182
TP	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	NR	EN	D	DI	AR	M	FS	F_F	10	211
TP	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	F	EN	D	DI	AR	M	FS	F_F	10	55
TP	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	F	EN	D	DI	AR	M	FS	F_F	10	56
TP	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	F	EN	D	DI	AR	M	FS	F_F	10	215
TP	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	F	EN	D	DI	AR	M	FS	F_F	10	67
TP	*Hylobatidae*	*Symphalangus syndactylus*	Asia	NR	EN	D	DI	AR	L	FS	F_F	1	11
TP	*Tarsiidae*	*Tarsius dentatus*	Asia	TR	VU	D	N	AR	S	FS	IN	3	158
TP	*Tarsiidae*	*Tarsius dentatus*	Asia	R	VU	D	N	AR	S	FS	IN	3	159
TP	*Cercopithecidae*	*Trachypithecus auratus*	Asia	TR	VU	D	DI	AR	M	FS	FOL	2	170
TP	*Cercopithecidae*	*Trachypithecus cristatus*	Asia	NR	NT	D	DI	AR	M	FS	FOL	1	11
TP	*Cercopithecidae*	*Trachypithecus germaini*	Asia	F	EN	D	DI	AR	M	FS	FOL	2	143

TP	*Cercopithecidae*	*Trachypithecus obscurus*	Asia	NR	NT	D	DI	AR	M	FS	FOL	2	11
CO	*Atelidae*	*Alouatta caraya*	Neotropics	ALL	LC	D	DI	AR	M	N_FS	F_F	2	2
CO	*Atelidae*	*Alouatta guariba*	Neotropics	TR	LC	D	DI	AR	M	FS	F_F	5	238
CO	*Atelidae*	*Alouatta guariba*	Neotropics	TR	LC	D	DI	AR	M	FS	F_F	5	138
CO	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	10
CO	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	150
CO	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	69
CO	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	69
CO	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	21	152
CO	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	234
CO	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	25	73
CO	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	25	58
CO	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	25	137
CO	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	25	166
CO	*Atelidae*	*Alouatta palliata*	Neotropics	ALL	LC	NI	DI	AR	M	FS	F_F	25	139
CO	*Atelidae*	*Alouatta pigra*	Neotropics	ALL	EN	D	DI	AR	M	FS	F_F	12	197
CO	*Atelidae*	*Alouatta pigra*	Neotropics	ALL	EN	D	DI	AR	M	FS	F_F	12	198
CO	*Atelidae*	*Alouatta pigra*	Neotropics	NR	EN	D	DI	AR	M	FS	F_F	12	69
CO	*Atelidae*	*Alouatta pigra*	Neotropics	F	EN	D	DI	AR	M	FS	F_F	12	9
CO	*Atelidae*	*Alouatta seniculus*	Neotropics	F	LC	NI	DI	AR	M	N_FS	F_F	7	194
CO	*Atelidae*	*Alouatta seniculus*	Neotropics	F	LC	NI	DI	AR	M	N_FS	F_F	7	34
CO	*Atelidae*	*Alouatta seniculus*	Neotropics	ALL	LC	NI	DI	AR	M	N_FS	F_F	7	169
CO	*Atelidae*	*Alouatta seniculus*	Neotropics	TR	LC	NI	DI	AR	M	N_FS	F_F	7	29
CO	*Aotidae*	*Aotus lemurinus*	Neotropics	F	VU	D	N	AR	S	FS	O	2	38
CO	*Atelidae*	*Ateles belzebuth*	Neotropics	TR	EN	D	DI	AR	M	FS	FRU	2	98
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	157
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	69
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	F	EN	D	DI	AR	M	FS	FRU	19	191
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	F	EN	D	DI	AR	M	FS	FRU	19	191

CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	F	EN	D	DI	AR	M	FS	FRU	19	191
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	254
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	TR	EN	D	DI	AR	M	FS	FRU	19	58
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	TR	EN	D	DI	AR	M	FS	FRU	19	166
CO	*Atelidae*	*Ateles geoffroyi*	Neotropics	TR	EN	D	DI	AR	M	FS	FRU	19	139
CO	*Indriidae*	*Avahi laniger*	Madagascar	TR	VU	D	N	AR	S	FS	FOL	2	145
CO	*Cebidae*	*Cebus capucinus*	Neotropics	NR	LC	NI	DI	AR	M	FS	O	15	69
CO	*Cebidae*	*Cebus capucinus*	Neotropics	F	LC	NI	DI	AR	M	FS	O	15	252
CO	*Cebidae*	*Cebus capucinus*	Neotropics	TR	LC	NI	DI	AR	M	FS	O	15	142
CO	*Atelidae*	*Cebus capucinus*	Neotropics	TR	LC	NI	DI	AR	M	FS	O	15	139
CO	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	TR	LC	NI	DI	AR	M	FS	FRU	12	44
CO	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	TR	LC	NI	DI	AR	M	FS	FRU	12	179
CO	*Cercopithecidae*	*Cercopithecus campbelli*	M_Africa	F	LC	NI	DI	AR	M	N_FS	FRU	5	92
CO	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	186
CO	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	TR	LC	D	DI	AR	M	FS	O	10	28
CO	*Cheirogaleidae*	*Cheirogaleus major*	Madagascar	TR	DD	D	N	AR	S	FS	F_F	2	145
CO	*Pitheciidae*	*Chiropotes chiropotes*	Neotropics	TR	LC	S	DI	AR	M	FS	FRU	2	27
CO	*Pitheciidae*	*Chiropotes satanas*	Neotropics	TR	CR	D	DI	AR	M	FS	FRU	2	26
CO	*Cercopithecidae*	*Chlorocebus aethiops*	M_Africa	R	LC	S	DI	T	M	N_FS	O	12	235
CO	*Cercopithecidae*	*Colobus angolensis*	M_Africa	TR	LC	NI	DI	AR	M	FS	FOL	5	6
CO	*Lemuridae*	*Eulemur fulvus*	Madagascar	TR	NT	D	CATH	AR	M	FS	F_F	2	145
CO	*Lemuridae*	*Eulemur rubriventer*	Madagascar	TR	VU	D	CATH	AR	S	FS	F_F	1	145
CO	*Lemuridae*	*Hapalemur griseus*	Madagascar	TR	VU	D	DI	AR	S	FS	FOL	2	145
CO	*Lemuridae*	*Hapalemur meridionalis*	Madagascar	ALL	VU	D	CATH	AR	S	FS	FOL	1	65
CO	*Hylobatidae*	*Hoolock hoolock*	Asia	TR	EN	D	DI	AR	M	FS	FRU	1	52
CO	*Hylobatidae*	*Hylobates agilis*	Asia	F	EN	D	DI	AR	M	FS	FRU	1	167
CO	*Callitrichidae*	*Leontopithecus chrysomelas*	Neotropics	ALL	EN	D	DI	AR	S	FS	O	4	201
CO	*Callitrichidae*	*Leontopithecus chrysopygus*	Neotropics	TR	EN	D	DI	AR	S	FS	FRU	1	244
CO	*Cercopithecidae*	*Macaca fascicularis*	Asia	F	LC	D	DI	AR	M	FS	FRU	10	167

CO	*Cheirogaleidae*	*Microcebus murinus*	Madagascar	TR	LC	D	N	AR	S	N_FS	O	3	8
CO	*Hylobatidae*	*Nomascus concolor*	Asia	F	CR	D	DI	AR	M	FS	F_F	2	189
CO	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	153
CO	*Cercopithecidae*	*Papio anubis*	M_Africa	ALL	LC	I	DI	T	L	N_FS	O	11	214
CO	*Cercopithecidae*	*Papio hamadryas*	M_Africa	TR	LC	I	DI	T	L	N_FS	O	4	188
CO	*Cercopithecidae*	*Piliocolobus badius*	M_Africa	R	EN	D	DI	AR	M	FS	F_F	5	84
CO	*Pitheciidae*	*Plecturocebus cupreus*	Neotropics	TR	LC	NI	DI	AR	S	FS	FRU	2	194
CO	*Pitheciidae*	*Plecturocebus moloch*	Neotropics	NR	LC	NI	DI	AR	S	FS	O	2	130
CO	*Pitheciidae*	*Plecturocebus oenanthe*	Neotropics	F	CR	D	DI	AR	S	N_FS	O	1	66
CO	*Pitheciidae*	*Plecturocebus olallae*	Neotropics	NR	EN	D	DI	AR	S	N_FS	F_F	2	76
CO	*Cercopithecidae*	*Presbytis melalophos*	Asia	F	NT	D	DI	AR	M	N_FS	F_F	2	167
CO	*Indriidae*	*Propithecus diadema*	Madagascar	TR	CR	D	DI	AR	M	FS	F_F	1	145
CO	*Cercopithecidae*	*Rhinopithecus bieti*	Asia	TR	EN	D	DI	BOTH	L	FS	FOL	2	134
CO	*Cercopithecidae*	*Rungwecebus kipunji*	M_Africa	TR	CR	D	DI	AR	L	FS	O	2	28
CO	*Callitrichidae*	*Saguinus leucopus*	Neotropics	TR	EN	D	DI	AR	S	FS	FRU	7	209
CO	*Callitrichidae*	*Saguinus leucopus*	Neotropics	F	EN	D	DI	AR	S	FS	FRU	7	53
CO	*Callitrichidae*	*Saguinus leucopus*	Neotropics	TR	EN	D	DI	AR	S	FS	FRU	7	127
CO	*Cebidae*	*Saimiri cassiquiarensis*	Neotropics	NR	LC	NI	DI	AR	S	N_FS	O	1	35
CO	*Cebidae*	*Saimiri oerstedii*	Neotropics	NR	VU	D	DI	AR	S	FS	O	3	69
CO	*Cebidae*	*Saimiri sciureus*	Neotropics	F	LC	D	DI	AR	S	FS	O	3	194
CO	*Cebidae*	*Sapajus apella*	Neotropics	F	LC	D	DI	AR	M	N_FS	O	11	194
CO	*Cebidae*	*Sapajus apella*	Neotropics	NR	LC	D	DI	AR	M	N_FS	O	11	130
CO	*Cebidae*	*Sapajus apella*	Neotropics	TR	LC	D	DI	AR	M	N_FS	O	11	244
CO	*Cebidae*	*Sapajus libidinosus*	Neotropics	ALL	LC	D	DI	AR	M	N_FS	O	3	2
CO	*Cebidae*	*Sapajus nigritus*	Neotropics	ALL	NT	D	DI	AR	M	FS	O	4	2
CO	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	TR	EN	D	DI	AR	M	FS	F_F	10	211
CO	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	TR	EN	D	DI	AR	M	FS	F_F	10	163
CO	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	TR	EN	D	DI	AR	M	FS	F_F	10	182
CO	*Cercopithecidae*	*Semnopithecus vetulus*	Asia	F	EN	D	DI	AR	M	FS	F_F	10	56

SF	*Cercopithecidae*	*Allochrocebus lhoesti*	M_Africa	NR	VU	D	DI	T	M	N_FS	O	2	140
SF	*Cercopithecidae*	*Allochrocebus lhoesti*	M_Africa	ALL	VU	D	DI	T	M	N_FS	O	2	118
SF	*Atelidae*	*Alouatta belzebul*	Neotropics	NR	VU	D	DI	AR	M	FS	F_F	1	246
SF	*Atelidae*	*Alouatta guariba*	Neotropics	NR	LC	D	DI	AR	M	FS	F_F	5	193
SF	*Atelidae*	*Alouatta guariba*	Neotropics	ALL	LC	D	DI	AR	M	FS	F_F	5	116
SF	*Atelidae*	*Alouatta macconnelli*	Neotropics	NR	LC	NI	DI	AR	M	N_FS	F_F	3	133
SF	*Atelidae*	*Alouatta macconnelli*	Neotropics	NR	LC	NI	DI	AR	M	N_FS	F_F	3	184
SF	*Atelidae*	*Alouatta macconnelli*	Neotropics	NR	LC	NI	DI	AR	M	N_FS	F_F	3	183
SF	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	181
SF	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	230
SF	*Atelidae*	*Alouatta palliata*	Neotropics	TR	LC	NI	DI	AR	M	FS	F_F	25	74
SF	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	54
SF	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	40
SF	*Atelidae*	*Alouatta palliata*	Neotropics	NR	LC	NI	DI	AR	M	FS	F_F	25	41
SF	*Atelidae*	*Alouatta pigra*	Neotropics	NR	EN	D	DI	AR	M	FS	F_F	12	242
SF	*Atelidae*	*Alouatta seniculus*	Neotropics	ALL	LC	NI	DI	AR	M	N_FS	F_F	7	98
SF	*Atelidae*	*Alouatta seniculus*	Neotropics	NR	LC	NI	DI	AR	M	N_FS	F_F	7	19
SF	*Lorisidae*	*Arctocebus calabarensis*	M_Africa	NR	LC	NI	N	AR	S	FS	IN	1	88
SF	*Atelidae*	*Ateles belzebuth*	Neotropics	ALL	EN	D	DI	AR	M	FS	FRU	2	98
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	230
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	54
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	F	EN	D	DI	AR	M	FS	FRU	19	203
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	42
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	242
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	TR	EN	D	DI	AR	M	FS	FRU	19	204
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	F	EN	D	DI	AR	M	FS	FRU	19	205
SF	*Atelidae*	*Ateles geoffroyi*	Neotropics	NR	EN	D	DI	AR	M	FS	FRU	19	41
SF	*Atelidae*	*Ateles paniscus*	Neotropics	NR	VU	D	DI	AR	M	FS	FRU	2	133
SF	*Atelidae*	*Ateles paniscus*	Neotropics	NR	VU	D	DI	AR	M	FS	FRU	2	184

SF	*Pitheciidae*	*Callicebus coimbrai*	Neotropics	NR	EN	D	DI	AR	S	N_FS	FRU	1	39
SF	*Pitheciidae*	*Callicebus melanochir*	Neotropics	NR	VU	D	DI	AR	S	FS	FRU	1	80
SF	*Pitheciidae*	*Callicebus personatus*	Neotropics	NR	VU	D	DI	AR	S	FS	FRU	2	193
SF	*Pitheciidae*	*Callicebus personatus*	Neotropics	ALL	VU	D	DI	AR	S	FS	FRU	2	103
SF	*Callitrichidae*	*Callithrix jacchus*	Neotropics	NR	LC	S	DI	AR	S	N_FS	G	2	39
SF	*Callitrichidae*	*Callithrix penicillata*	Neotropics	NR	LC	I	DI	AR	S	N_FS	G	7	80
SF	*Cebidae*	*Cebus albifrons*	Neotropics	ALL	LC	D	DI	BOTH	M	FS	O	2	98
SF	*Cebidae*	*Cebus albifrons*	Neotropics	NR	LC	D	DI	BOTH	M	FS	O	2	19
SF	*Cebidae*	*Cebus capucinus*	Neotropics	NR	LC	NI	DI	AR	M	FS	O	15	230
SF	*Cebidae*	*Cebus capucinus*	Neotropics	NR	LC	NI	DI	AR	M	FS	O	15	54
SF	*Cebidae*	*Cebus capucinus*	Neotropics	ALL	LC	NI	DI	AR	M	FS	O	15	43
SF	*Cebidae*	*Cebus capucinus*	Neotropics	NR	LC	NI	DI	AR	M	FS	O	15	41
SF	*Cercopithecidae*	*Cercocebus atys*	M_Africa	NR	NT	D	DI	T	M	N_FS	FRU	2	79
SF	*Cercopithecidae*	*Cercocebus atys*	M_Africa	NR	NT	D	DI	T	M	N_FS	FRU	2	78
SF	*Cercopithecidae*	*Cercocebus galeritus*	M_Africa	F	EN	D	DI	BOTH	M	FS	FRU	3	251
SF	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	NR	LC	NI	DI	AR	M	FS	FRU	12	239
SF	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	F	LC	NI	DI	AR	M	FS	FRU	12	223
SF	*Cercopithecidae*	*Cercopithecus ascanius*	M_Africa	NR	LC	NI	DI	AR	M	FS	FRU	12	140
SF	*Cercopithecidae*	*Cercopithecus campbelli*	M_Africa	NR	LC	NI	DI	AR	M	N_FS	FRU	5	79
SF	*Cercopithecidae*	*Cercopithecus campbelli*	M_Africa	NR	LC	NI	DI	AR	M	N_FS	FRU	5	78
SF	*Cercopithecidae*	*Cercopithecus cephus*	M_Africa	NR	LC	NI	DI	AR	M	FS	FRU	2	88
SF	*Cercopithecidae*	*Cercopithecus diana*	M_Africa	NR	VU	D	DI	AR	M	FS	FRU	2	79
SF	*Cercopithecidae*	*Cercopithecus diana*	M_Africa	NR	VU	D	DI	AR	M	FS	FRU	2	78
SF	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	NR	LC	D	DI	AR	M	FS	O	10	239
SF	*Cercopithecidae*	*Cercopithecus mitis*	M_Africa	F	LC	D	DI	AR	M	FS	O	10	118
SF	*Cercopithecidae*	*Cercopithecus nictitans*	M_Africa	NR	LC	D	DI	AR	M	FS	FRU	3	88
SF	*Cercopithecidae*	*Cercopithecus petaurista*	M_Africa	NR	LC	NI	DI	AR	M	N_FS	O	2	79
SF	*Cercopithecidae*	*Cercopithecus petaurista*	M_Africa	NR	LC	NI	DI	AR	M	N_FS	O	2	78
SF	*Cercopithecidae*	*Cercopithecus pogonias*	M_Africa	NR	LC	D	DI	AR	M	N_FS	FRU	3	88

SF	*Cercopithecidae*	*Cercopithecus pogonias*	M_Africa	NR	LC	D	DI	AR	M	N_FS	FRU	3	239
SF	*Pitheciidae*	*Chiropotes chiropotes*	Neotropics	NR	LC	S	DI	AR	M	FS	FRU	2	133
SF	*Pitheciidae*	*Chiropotes satanas*	Neotropics	TR	CR	D	DI	AR	M	FS	FRU	2	90
SF	*Cercopithecidae*	*Colobus angolensis*	M_Africa	NR	LC	NI	DI	AR	M	FS	FOL	5	239
SF	*Cercopithecidae*	*Colobus guereza*	M_Africa	NR	LC	NI	DI	AR	M	FS	F_F	3	239
SF	*Cercopithecidae*	*Colobus guereza*	M_Africa	NR	LC	NI	DI	AR	M	FS	F_F	3	140
SF	*Cercopithecidae*	*Colobus guereza*	M_Africa	F	LC	NI	DI	AR	M	FS	F_F	3	71
SF	*Cercopithecidae*	*Colobus polykomos*	M_Africa	NR	VU	NI	DI	AR	M	FS	FOL	2	79
SF	*Cercopithecidae*	*Colobus polykomos*	M_Africa	NR	VU	NI	DI	AR	M	FS	FOL	2	78
SF	*Daubentoniidae*	*Daubentonia madagascariensis*	Madagascar	ALL	EN	D	N	AR	M	N_FS	IN	1	5
SF	*Lemuridae*	*Eulemur flavifrons*	Madagascar	ALL	CR	D	CATH	AR	S	FS	F_F	1	224
SF	*Lemuridae*	*Eulemur macaco*	Madagascar	ALL	VU	D	CATH	AR	M	FS	FRU	1	16
SF	*Galagidae*	*Galago elegantulus*	M_Africa	NR	LC	S	N	AR	S	FS	G	1	88
SF	*Galagidae*	*Galagoides demidovii*	M_Africa	NR	LC	S	N	AR	S	FS	O	1	88
SF	*Hominidae*	*Gorilla beringei*	M_Africa	F	EN	D	DI	BOTH	L	FS	F_F	1	257
SF	*Hominidae*	*Gorilla gorilla*	M_Africa	R	CR	D	DI	BOTH	L	FS	F_F	2	88
SF	*Hominidae*	*Gorilla gorilla*	M_Africa	R	CR	D	DI	BOTH	L	FS	F_F	2	148
SF	*Hylobatidae*	*Hylobates lar*	Asia	NR	EN	D	DI	AR	M	FS	FRU	2	115
SF	*Hylobatidae*	*Hylobates muelleri*	Asia	NR	EN	D	DI	AR	M	FS	FRU	1	91
SF	*Callitrichidae*	*Leontocebus fuscicollis*	Neotropics	F	LC	D	DI	AR	S	FS	O	4	50
SF	*Callitrichidae*	*Leontocebus fuscicollis*	Neotropics	F	LC	D	DI	AR	S	FS	O	4	51
SF	*Callitrichidae*	*Leontocebus fuscicollis*	Neotropics	R	LC	D	DI	AR	S	FS	O	4	129
SF	*Callitrichidae*	*Leontocebus nigrifrons*	Neotropics	F	LC	D	DI	AR	S	FS	O	1	126
SF	*Cercopithecidae*	*Lophocebus albigena*	M_Africa	NR	LC	D	DI	AR	M	FS	FRU	2	239
SF	*Cercopithecidae*	*Lophocebus albigena*	M_Africa	NR	LC	D	DI	AR	M	FS	FRU	2	140
SF	*Cercopithecidae*	*Macaca fascicularis*	Asia	NR	LC	D	DI	AR	M	FS	FRU	10	115
SF	*Cercopithecidae*	*Macaca nemestrina*	Asia	NR	VU	D	DI	T	M	FS	FRU	4	115
SF	*Cercopithecidae*	*Macaca nigra*	Asia	F	CR	D	DI	T	M	FS	FRU	1	212
SF	*Cercopithecidae*	*Mandrillus sphinx*	M_Africa	ALL	VU	NI	DI	T	L	FS	O	1	88

SF	*Cheirogaleidae*	*Microcebus murinus*	Madagascar	NR	LC	D	N	AR	S	N_FS	O	3	87
SF	*Cercopithecidae*	*Miopithecus talapoin*	M_Africa	NR	LC	NI	DI	BOTH	S	FS	O	2	88
SF	*Hylobatidae*	*Nomascus concolor*	Asia	ALL	CR	D	DI	AR	M	FS	F_F	2	189
SF	*Hominidae*	*Pan troglodytes*	M_Africa	F	EN	D	DI	BOTH	L	N_FS	O	17	14
SF	*Hominidae*	*Pan troglodytes*	M_Africa	R	EN	D	DI	BOTH	L	N_FS	O	17	88
SF	*Hominidae*	*Pan troglodytes*	M_Africa	NR	EN	D	DI	BOTH	L	N_FS	O	17	140
SF	*Cercopithecidae*	*Papio anubis*	M_Africa	NR	LC	I	DI	T	L	N_FS	O	11	140
SF	*Lorisidae*	*Perodicticus potto*	M_Africa	NR	LC	S	N	AR	S	FS	FRU	1	88
SF	*Cercopithecidae*	*Piliocolobus badius*	M_Africa	NR	EN	D	DI	AR	M	FS	F_F	5	239
SF	*Cercopithecidae*	*Piliocolobus badius*	M_Africa	NR	EN	D	DI	AR	M	FS	F_F	5	79
SF	*Cercopithecidae*	*Piliocolobus badius*	M_Africa	NR	EN	D	DI	AR	M	FS	F_F	5	78
SF	*Cercopithecidae*	*Piliocolobus tephrosceles*	M_Africa	NR	EN	D	DI	AR	M	FS	FOL	1	140
SF	*Pitheciidae*	*Pithecia irrorata*	Neotropics	NR	LC	NI	DI	AR	M	FS	FRU	1	246
SF	*Pitheciidae*	*Pithecia pithecia*	Neotropics	NR	LC	NI	DI	AR	S	FS	FRU	2	133
SF	*Pitheciidae*	*Pithecia pithecia*	Neotropics	NR	LC	NI	DI	AR	S	FS	FRU	2	183
SF	*Pitheciidae*	*Plecturocebus cupreus*	Neotropics	ALL	LC	NI	DI	AR	S	FS	FRU	2	123
SF	*Hominidae*	*Pongo pygmaeus*	Asia	ALL	EN	D	DI	AR	L	FS	FRU	2	216
SF	*Cercopithecidae*	*Presbytis hosei*	Asia	NR	DD	D	DI	AR	M	FS	FOL	1	171
SF	*Cercopithecidae*	*Presbytis melalophos*	Asia	NR	NT	D	DI	AR	M	N_FS	F_F	2	115
SF	*Cercopithecidae*	*Procolobus verus*	M_Africa	NR	NT	NI	DI	AR	M	FS	FOL	2	79
SF	*Cercopithecidae*	*Procolobus verus*	M_Africa	ALL	NT	NI	DI	AR	M	FS	FOL	2	174
SF	*Indriidae*	*Propithecus verreauxi*	Madagascar	ALL	EN	D	DI	AR	M	N_FS	F_F	4	172
SF	*Cercopithecidae*	*Rhinopithecus bieti*	Asia	F	EN	D	DI	BOTH	L	FS	FOL	2	255
SF	*Cercopithecidae*	*Rhinopithecus roxellana*	Asia	NR	EN	D	DI	BOTH	L	FS	FOL	1	135
SF	*Callitrichidae*	*Saguinus leucopus*	Neotropics	ALL	EN	D	DI	AR	S	FS	FRU	7	98
SF	*Callitrichidae*	*Saguinus leucopus*	Neotropics	ALL	EN	D	DI	AR	S	FS	FRU	7	19
SF	*Callitrichidae*	*Saguinus midas*	Neotropics	NR	LC	S	DI	AR	S	N_FS	O	2	133
SF	*Callitrichidae*	*Saguinus midas*	Neotropics	NR	LC	S	DI	AR	S	N_FS	O	2	183
SF	*Callitrichidae*	*Saguinus mystax*	Neotropics	F	LC	S	DI	AR	S	FS	O	4	50

SF	*Callitrichidae*	*Saguinus mystax*	Neotropics	F	LC	S	DI	AR	S	FS	O	4	51
SF	*Callitrichidae*	*Saguinus mystax*	Neotropics	R	LC	S	DI	AR	S	FS	O	4	129
SF	*Cebidae*	*Saimiri oerstedii*	Neotropics	ALL	VU	D	DI	AR	S	FS	O	3	24
SF	*Cebidae*	*Saimiri sciureus*	Neotropics	NR	LC	D	DI	AR	S	FS	O	3	183
SF	*Cebidae*	*Sapajus apella*	Neotropics	NR	LC	D	DI	AR	M	N_FS	O	11	133
SF	*Cebidae*	*Sapajus apella*	Neotropics	NR	LC	D	DI	AR	M	N_FS	O	11	184
SF	*Cebidae*	*Sapajus apella*	Neotropics	NR	LC	D	DI	AR	M	N_FS	O	11	193
SF	*Cebidae*	*Sapajus apella*	Neotropics	NR	LC	D	DI	AR	M	N_FS	O	11	183
SF	*Cebidae*	*Sapajus apella*	Neotropics	TR	LC	D	DI	AR	M	N_FS	O	11	90
SF	*Cebidae*	*Sapajus apella*	Neotropics	NR	LC	D	DI	AR	M	N_FS	O	11	246
SF	*Cebidae*	*Sapajus xanthosternos*	Neotropics	NR	CR	D	DI	AR	M	FS	O	4	80
SF	*Cebidae*	*Sapajus xanthosternos*	Neotropics	NR	CR	D	DI	AR	M	FS	O	4	39
SF	*Cebidae*	*Sapajus xanthosternos*	Neotropics	F	CR	D	DI	AR	M	FS	O	4	33
SF	*Galagidae*	*Sciurocheirus alleni*	M_Africa	NR	EN	NI	N	AR	S	FS	FRU	1	88
SF	*Cercopithecidae*	*Trachypithecus auratus*	Asia	ALL	VU	D	DI	AR	M	FS	FOL	2	122
SF	*Cercopithecidae*	*Trachypithecus obscurus*	Asia	NR	NT	D	DI	AR	M	FS	FOL	2	115
SF	*Cercopithecidae*	*Trachypithecus phayrei*	Asia	ALL	EN	D	DI	AR	M	N_FS	FOL	1	99
SF	*Lemuridae*	*Varecia rubra*	Madagascar	F	CR	D	DI	AR	M	FS	FRU	1	144

[a] For taxonomy, we followed: Estrada, A. *et al.* Impending extinction crisis of the world's primates: why primates matter. *Sci. Adv.* **3,** e1600946 (2017).

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Table 2. Ecological traits of all the world's primates. The sources of ecological traits (diel activity, locomotion, body mass, habitat and trophic level) are included in the right column besides each trait (Ref). Realm: M_Africa = mainland Africa; activity: TR = travel, R = resting, F = foraging, NR = not reported; conservation status (IUCN): CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concerned, DD = data deficient, NE = not evaluated; population trend (Pop_T): I = increasing, D = decreasing, S = stable, NA = no data available; diel activity (D_A): Di = diurnal, N = Nocturnal, Cath = cathemeral; locomotion: AR = arboreal locomotion, T = terrestrial locomotion; body mass (B_M): L = large (>10 kg), M = medium (2 – 10 kg), S = small (<2 kg); habitat: FS = forest specialist, N_FS = non forest specialist; trophic level (T_L), F_f = folivorous-frugivorous, Fol = folivorous, Fru = frugivorous, G = gummivorous, O = omnivorous, In = insectivorous. N records refers to the number of times that a primate specie has been registered using the matrix.

Family[a]	Species	Realm	IUCN	Pop_T	D_A	Ref	Locomotion	Ref	B_M	Ref	Forest specialization	Ref	T_L	Ref	N records
Cercopithecidae	*Allenopithecus nigroviridis*	M_Africa	LC	NI	DI	75	BOTH	75	M	25	FS	49	FRU	75	0
Cheirogaleidae	*Allocebus trichotis*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	O	75	0
Cercopithecidae	*Allochrocebus lhoesti*	M_Africa	VU	D	DI	75	T	75	M	25	N_FS	75, 41	O	75	2
Cercopithecidae	*Allochrocebus preussi*	M_Africa	EN	D	DI	75	T	75	M	57, 117	FS	75	O	75	0
Cercopithecidae	*Allochrocebus solatus*	M_Africa	VU	NI	DI	75	BOTH	75	M	25	FS	75	O	57	0
Atelidae	*Alouatta arctoidea*	Neotropics	LC	NI	DI	75	AR	75	M	75	N_FS	49	FOL	75	0
Atelidae	*Alouatta belzebul*	Neotropics	VU	D	DI	75	AR	75	M	25	FS	49	F_F	75	1
Atelidae	*Alouatta caraya*	Neotropics	LC	D	DI	75	AR	75	M	25	N_FS	49	F_F	75	2
Atelidae	*Alouatta discolor*	Neotropics	VU	D	DI	75	AR	75	M	NI	FS	49	F_F	75	0
Atelidae	*Alouatta guariba*	Neotropics	LC	D	DI	75	AR	75	M	25	FS	49	F_F	75	5
Atelidae	*Alouatta macconnelli*	Neotropics	LC	NI	DI	75	AR	75	M	25	N_FS	49	F_F	75	3
Atelidae	*Alouatta nigérrima*	Neotropics	LC	NI	DI	75	AR	75	M	75	N_FS	49	F_F	9	0
Atelidae	*Alouatta palliata*	Neotropics	LC	NI	DI	75	AR	75	M	25	FS	49	F_F	75	25
Atelidae	*Alouatta pigra*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	F_F	75	12
Atelidae	*Alouatta sara*	Neotropics	LC	D	DI	75	AR	75	M	75	N_FS	49	F_F	108	0
Atelidae	*Alouatta seniculus*	Neotropics	LC	NI	DI	75	AR	75	M	5, 104	N_FS	49	F_F	75	7

Atelidae	*Alouatta ululata*	Neotropics	EN	D	DI	75	AR	75	M	123	FS	49	F_F	95	0
Aotidae	*Aotus azarae*	Neotropics	LC	D	CAT H	75	AR	75	S	25	N_FS	49	O	75	0
Aotidae	*Aotus brumbacki*	Neotropics	VU	D	N	75	AR	75	S	25	N_FS	49	O	75	0
Aotidae	*Aotus griseimembra*	Neotropics	VU	D	N	75	AR	75	S	25	FS	49	O	NI	0
Aotidae	*Aotus jorgehernandezi*	Neotropics	DD	NI	N	75	AR	75	NI	NI	FS	49	NI	NI	0
Aotidae	*Aotus lemurinus*	Neotropics	VU	D	N	75	AR	75	S	25	FS	49	O	75	2
Aotidae	*Aotus miconax*	Neotropics	VU	D	N	75	AR	75	S	53	FS	49	O	75	0
Aotidae	*Aotus nancymaae*	Neotropics	LC	NI	N	75	AR	75	S	25	FS	49	FRU	23, 43, 77	0
Aotidae	*Aotus nigriceps*	Neotropics	LC	NI	N	75	AR	75	S	25	FS	49	FRU	75	0
Aotidae	*Aotus trivirgatus*	Neotropics	LC	NI	N	75	AR	75	S	25	FS	49	O	127	0
Aotidae	*Aotus vociferans*	Neotropics	LC	D	N	75	AR	75	S	25	FS	49	FRU	75	0
Aotidae	*Aotus zonalis*	Neotropics	DD	NI	N	75	AR	75	S	25	FS	49	FRU	75	0
Lorisidae	*Arctocebus aureus*	M_Africa	LC	NI	N	75	AR	75	S	25	FS	49	IN	75	0
Lorisidae	*Arctocebus calabarensis*	M_Africa	LC	NI	N	75	AR	75	S	25	FS	49	IN	75	1
Atelidae	*Ateles belzebuth*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	2
Atelidae	*Ateles chamek*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Atelidae	*Ateles fusciceps*	Neotropics	CR	D	DI	75	AR	75	M	25	FS	49	FRU	76	0
Atelidae	*Ateles geoffroyi*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	19
Atelidae	*Ateles hybridus*	Neotropics	CR	D	DI	75	AR	75	M	25	FS	49	FRU	19	0
Atelidae	*Ateles marginatus*	Neotropics	EN	D	DI	75	AR	75	M	28, 75	FS	49	FRU	75	0
Atelidae	*Ateles paniscus*	Neotropics	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	2
Indriidae	*Avahi betsileo*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Indriidae	*Avahi cleesei*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Indriidae	*Avahi laniger*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	FOL	75	2
Indriidae	*Avahi meridionalis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Indriidae	*Avahi mooreorum*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	109	0
Indriidae	*Avahi occidentalis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Indriidae	*Avahi peyrierasi*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	FOL	75	0

Indriidae	*Avahi ramanantsoavanai*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	FOL	NI	0
Indriidae	*Avahi unicolor*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	40	0
Atelidae	*Brachyteles arachnoides*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	F_F	75	1
Atelidae	*Brachyteles hypoxanthus*	Neotropics	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	1
Pitheciidae	*Cacajao calvus*	Neotropics	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Pitheciidae	*Cacajao melanocephalus*	Neotropics	LC	S	DI	75	AR	75	M	25	FS	49	FRU	75	0
Pitheciidae	*Cacajao ouakary*	Neotropics	VU	D	DI	75	AR	75	M	25	N_FS	75	FRU	75	0
Callitrichidae	*Callibella humilis*	Neotropics	VU	S	DI	75	AR	75	S	96	FS	49	O	75	0
Pitheciidae	*Callicebus barbarabrownae*	Neotropics	CR	D	DI	75	AR	75	S	75	N_FS	49	FRU	NI	0
Pitheciidae	*Callicebus coimbrai*	Neotropics	EN	D	DI	75	AR	75	S	60	N_FS	49	FRU	75	1
Pitheciidae	*Callicebus melanochir*	Neotropics	VU	D	DI	75	AR	75	S	47	FS	49	FRU	75	1
Pitheciidae	*Callicebus nigrifrons*	Neotropics	NT	D	DI	75	AR	75	NI	NI	FS	49	FRU	75	0
Pitheciidae	*Callicebus personatus*	Neotropics	VU	D	DI	75	AR	75	S	25	FS	49	FRU	75	2
Callitrichidae	*Callimico goeldii*	Neotropics	VU	D	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Callithrix aurita*	Neotropics	VU	D	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Callithrix flaviceps*	Neotropics	EN	D	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Callithrix geoffroyi*	Neotropics	LC	S	DI	75	AR	75	S	25	N_FS	49	G	75	0
Callitrichidae	*Callithrix jacchus*	Neotropics	LC	S	DI	75	AR	75	S	25	N_FS	49	G	75	2
Callitrichidae	*Callithrix kuhlii*	Neotropics	NT	D	DI	75	AR	75	S	25	FS	49	O	75	2
Callitrichidae	*Callithrix penicillata*	Neotropics	LC	I	DI	75	AR	75	S	25	N_FS	49	G	75	7
Tarsiidae	*Carlito syrichta*	Asia	NT	D	N	75	AR	75	S	25	FS	75	IN	75	0
Callitrichidae	*Cebuella pygmaea*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	49	O	75	0
Cebidae	*Cebus aequatorialis*	Neotropics	CR	D	DI	75	AR	75	M	25	N_FS	75	O	75	0
Cebidae	*Cebus albifrons*	Neotropics	LC	D	DI	75	BOTH	75	M	25	FS	75	O	75	2
Cebidae	*Cebus brunneus*	Neotropics	LC	NI	DI	75	AR	75	M	NI	FS	75	O	NI	0
Cebidae	*Cebus capucinus*	Neotropics	LC	NI	DI	75	AR	75	M	25	FS	75	O	75	15
Cebidae	*Cebus cesarae*	Neotropics	DD	D	DI	75	AR	75	M	NI	FS	75	O	NI	0
Cebidae	*Cebus cuscinus*	Neotropics	NT	D	DI	75	AR	75	M	75	FS	75	O	75	0
Cebidae	*Cebus imitator*	Neotropics	LC	D	DI	75	AR	75	M	75	FS	75	O	75	0

Cebidae	*Cebus kaapori*	Neotropics	CR	D	DI	75	AR	75	M	65	FS	49	O	20	0
Cebidae	*Cebus leucocephalus*	Neotropics	NE	NI	DI	75	AR	75	M	NI	FS	75	O	NI	0
Cebidae	*Cebus malitiosus*	Neotropics	EN	D	DI	75	AR	75	M	NI	FS	75	O	NI	0
Cebidae	*Cebus olivaceus*	Neotropics	LC	NI	DI	75	AR	75	M	25	FS	75	O	75	0
Cebidae	*Cebus unicolor*	Neotropics	LC	NI	DI	75	AR	75	M	NI	FS	75	O	NI	0
Cebidae	*Cebus versicolor*	Neotropics	EN	D	DI	75	AR	75	M	NI	FS	75	O	NI	0
Cebidae	*Cebus yuracus*	Neotropics	NE	NI	DI	75	AR	75	M	25	FS	75	O	75	0
Tarsiidae	*Cephalopachus bancanus*	Asia	VU	D	N	75	AR	75	S	25	FS	75	IN	75	0
Cercopithecidae	*Cercocebus agilis*	M_Africa	LC	S	DI	75	BOTH	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Cercocebus atys*	M_Africa	NT	D	DI	75	T	75	M	25	N_FS	49	FRU	75	2
Cercopithecidae	*Cercocebus chrysogaster*	M_Africa	DD	D	DI	75	T	75	M	57	FS	49	FRU	75	0
Cercopithecidae	*Cercocebus galeritus*	M_Africa	EN	D	DI	75	BOTH	75	M	25	FS	49	FRU	75	3
Cercopithecidae	*Cercocebus lunulatus*	M_Africa	EN	D	DI	75	T	75	M	25	FS	75	FRU	75	0
Cercopithecidae	*Cercocebus sanjei*	M_Africa	EN	D	DI	75	BOTH	75	M	57	FS	49	FRU	75	0
Cercopithecidae	*Cercocebus torquatus*	M_Africa	VU	D	DI	75	BOTH	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Cercopithecus albogularis*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Cercopithecus ascanius*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	49	FRU	75	12
Cercopithecidae	*Cercopithecus campbelli*	M_Africa	LC	NI	DI	75	AR	75	M	25	N_FS	49	FRU	75	5
Cercopithecidae	*Cercopithecus cephus*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	49	FRU	75	2
Cercopithecidae	*Cercopithecus denti*	M_Africa	LC	D	DI	75	AR	75	M	25	FS	75	O	75	0
Cercopithecidae	*Cercopithecus diana*	M_Africa	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	2
Cercopithecidae	*Cercopithecus doggetti*	M_Africa	LC	D	DI	75	AR	75	M	NI	FS	75	O	75	0
Cercopithecidae	*Cercopithecus dryas*	M_Africa	CR	NI	DI	75	BOTH	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Cercopithecus erythrogaster*	M_Africa	VU	D	DI	75	AR	75	M	25	FS	49	NI	NI	0
Cercopithecidae	*Cercopithecus erythrotis*	M_Africa	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Cercopithecus hamlyni*	M_Africa	VU	D	DI	75	BOTH	75	M	25	FS	49	O	75	0
Cercopithecidae	*Cercopithecus kandti*	M_Africa	EN	D	DI	75	AR	75	M	25	FS	75	FOL	75	0
Cercopithecidae	*Cercopithecus lomamiensis*	M_Africa	NE	NI	DI	75	BOTH	75	M	25	FS	75	F_F	75	0
Cercopithecidae	*Cercopithecus lowei*	M_Africa	LC	NI	DI	75	AR	75	M	25	N_FS	75	FRU	75	0

Cercopithecidae	*Cercopithecus mitis*	M_Africa	LC	D	DI	75	AR	75	M	25	FS	49	O	75, 12, 55	10
Cercopithecidae	*Cercopithecus mona*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	49	FRU	75	2
Cercopithecidae	*Cercopithecus neglectus*	M_Africa	LC	NI	DI	75	BOTH	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Cercopithecus nictitans*	M_Africa	LC	D	DI	75	AR	75	M	25	FS	75, 37, 42	FRU	75	3
Cercopithecidae	*Cercopithecus petaurista*	M_Africa	LC	NI	DI	75	AR	75	M	25	N_FS	49	O	75	2
Cercopithecidae	*Cercopithecus pogonias*	M_Africa	LC	D	DI	16	AR	75	M	25	N_FS	75	FRU	75	3
Cercopithecidae	*Cercopithecus roloway*	M_Africa	EN	D	DI	75	AR	75	M	25	FS	75	O	75	0
Cercopithecidae	*Cercopithecus sclateri*	M_Africa	VU	D	DI	75	AR	75	M	25	N_FS	49	FRU	75	1
Cercopithecidae	*Cercopithecus wolfi*	M_Africa	LC	D	DI	75	AR	75	M	25	N_FS	75	O	75	0
Cheirogaleidae	*Cheirogaleus andysabini*	Madagascar	NE	NI	N	75	NI	NI	NI	NI	NI	NI	NI	NI	0
Cheirogaleidae	*Cheirogaleus crossleyi*	Madagascar	DD	D	N	75	AR	75	S	25	FS	49	O	40	0
Cheirogaleidae	*Cheirogaleus lavasoensis*	Madagascar	NE	NI	N	75	NI	NI	NI	NI	NI	NI	NI	NI	0
Cheirogaleidae	*Cheirogaleus major*	Madagascar	DD	D	N	75	AR	75	S	25	FS	49	F_F	75	2
Cheirogaleidae	*Cheirogaleus medius*	Madagascar	LC	D	N	75	AR	75	S	25	FS	49	F_F	75	0
Cheirogaleidae	*Cheirogaleus minusculus*	Madagascar	DD	D	N	75	AR	75	S	119, 7	FS	49	NI	NI	0
Cheirogaleidae	*Cheirogaleus sibreei*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Cheirogaleus thomasi*	Madagascar	NE	NI	N	75	NI	NI	NI	NI	NI	NI	NI	NI	0
Pitheciidae	*Cheracebus lucifer*	Neotropics	LC	NI	DI	75	AR	75	S	75	FS	75	FRU	75	0
Pitheciidae	*Cheracebus lugens*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	FRU	75	0
Pitheciidae	*Cheracebus medemi*	Neotropics	VU	D	DI	75	AR	75	S	25	FS	75	FRU	NI	0
Pitheciidae	*Cheracebus purinus*	Neotropics	LC	NI	DI	75	AR	75	S	52	FS	75	NI	NI	0
Pitheciidae	*Cheracebus regulus*	Neotropics	LC	NI	DI	75	AR	75	S	75	FS	75	NI	NI	0
Pitheciidae	*Cheracebus torquatus*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	FRU	90, 59	0
Pitheciidae	*Chiropotes albinasus*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Pitheciidae	*Chiropotes chiropotes*	Neotropics	LC	S	DI	75	AR	75	M	25	FS	49	FRU	75	2
Pitheciidae	*Chiropotes sagulatus*	Neotropics	NE	NI	DI	75	AR	75	M	25	N_FS	75	FRU	75	0
Pitheciidae	*Chiropotes satanas*	Neotropics	CR	D	DI	75	AR	75	M	46	FS	49	FRU	75	2
Pitheciidae	*Chiropotes utahickae*	Neotropics	EN	D	DI	75	AR	75	M	75	FS	49	FRU	75	0

Cercopithecidae	*Chlorocebus aethiops*	M_Africa	LC	S	DI	75	T	75	M	25	N_FS	49	O	75	12
Cercopithecidae	*Chlorocebus cynosuros*	M_Africa	LC	S	DI	75	T	75	M	75	N_FS	49	O	75	0
Cercopithecidae	*Chlorocebus djamdjamensis*	M_Africa	VU	D	DI	75	BOTH	75	M	25	FS	49	FOL	75	1
Cercopithecidae	*Chlorocebus pygerythrus*	M_Africa	LC	S	DI	75	T	75	M	57	N_FS	49	O	75	1
Cercopithecidae	*Chlorocebus sabaeus*	M_Africa	LC	S	DI	75	T	75	M	57	N_FS	49	O	75	0
Cercopithecidae	*Chlorocebus tantalus*	M_Africa	LC	S	DI	75	T	75	M	57	N_FS	49	O	75	0
Cercopithecidae	*Colobus angolensis*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	49	FOL	75	5
Cercopithecidae	*Colobus guereza*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	49	F_F	75	3
Cercopithecidae	*Colobus polykomos*	M_Africa	VU	NI	DI	75	AR	75	M	25	FS	49	FOL	75	2
Cercopithecidae	*Colobus satanas*	M_Africa	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Colobus vellerosus*	M_Africa	VU	NI	DI	75	AR	75	M	25	N_FS	49	FOL	75	1
Daubentoniidae	*Daubentonia madagascariensis*	Madagascar	EN	D	N	75	AR	75	M	25	N_FS	49	IN	75	1
Cercopithecidae	*Erythrocebus patas*	M_Africa	LC	D	DI	75	T	75	M	25	N_FS	49	O	75	0
Lemuridae	*Eulemur albifrons*	Madagascar	EN	D	CATH	75	AR	75	M	25	FS	49	FRU	75	0
Lemuridae	*Eulemur cinereiceps*	Madagascar	CR	D	CATH	75	AR	75	M	25	FS	49	FRU	75	0
Lemuridae	*Eulemur collaris*	Madagascar	EN	D	CATH	75	AR	75	M	25	FS	49	FRU	75	0
Lemuridae	*Eulemur coronatus*	Madagascar	EN	D	CATH	75	AR	75	S	25	FS	49	FRU	75	0
Lemuridae	*Eulemur flavifrons*	Madagascar	CR	D	CATH	75	AR	75	S	25	FS	49	F_F	75	1
Lemuridae	*Eulemur fulvus*	Madagascar	NT	D	CATH	75	AR	75	M	25	FS	49	F_F	75	2
Lemuridae	*Eulemur macaco*	Madagascar	VU	D	CATH	75	AR	75	M	25	FS	49	FRU	75, 6, 116	1
Lemuridae	*Eulemur mongoz*	Madagascar	CR	D	CATH	75	AR	75	S	25	FS	49	F_F	75	0
Lemuridae	*Eulemur rubriventer*	Madagascar	VU	D	CATH	75	AR	75	S	25	FS	49	F_F	75	1
Lemuridae	*Eulemur rufifrons*	Madagascar	NT	D	CATH	75	AR	75	M	25	FS	49	F_F	75	0
Lemuridae	*Eulemur rufus*	Madagascar	VU	D	CATH	75	AR	75	M	25	FS	49	FRU	89	0

Lemuridae	*Eulemur sanfordi*	Madagascar	EN	D	CATH	75	AR	75	S	25	FS	49	FRU	75	0
Galagidae	*Euoticus elegantulus*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	G	75	1
Galagidae	*Euoticus pallidus*	M_Africa	LC	NI	N	75	AR	75	S	25	FS	49	G	75	0
Galagidae	*Galago gallarum*	M_Africa	LC	S	N	75	AR	75	S	25	N_FS	49	O	75	0
Galagidae	*Galago matschiei*	M_Africa	LC	D	N	75	AR	75	S	25	FS	49	O	75	0
Galagidae	*Galago moholi*	M_Africa	LC	S	N	75	AR	75	S	25	N_FS	49	O	75	1
Galagidae	*Galago senegalensis*	M_Africa	LC	S	N	75	AR	75	S	25	N_FS	49	O	75	0
Galagidae	*Galagoides cocos*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	O	75	0
Galagidae	*Galagoides demidovii*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	O	75	1
Galagidae	*Galagoides granti*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	O	75	0
Galagidae	*Galagoides orinus*	M_Africa	NT	D	N	75	AR	75	S	93, 94	FS	49	O	75	0
Galagidae	*Galagoides rondoensis*	M_Africa	CR	D	N	75	AR	75	S	25	FS	49	O	75	0
Galagidae	*Galagoides thomasi*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	O	75	0
Galagidae	*Galagoides zanzibaricus*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	O	75	0
Hominidae	*Gorilla beringei*	M_Africa	EN	D	DI	75	BOTH	75	L	25	FS	49	F_F	75	1
Hominidae	*Gorilla gorilla*	M_Africa	CR	D	DI	75	BOTH	75	L	25	FS	49	F_F	75	2
Lemuridae	*Hapalemur alaotrensis*	Madagascar	CR	D	CATH	75	AR	75	S	25	N_FS	49	FOL	75	0
Lemuridae	*Hapalemur aureus*	Madagascar	CR	D	DI	75	AR	75	S	25	FS	49	FOL	75	0
Lemuridae	*Hapalemur griseus*	Madagascar	VU	D	DI	75	AR	75	S	25	FS	49	FOL	75	2
Lemuridae	*Hapalemur meridionalis*	Madagascar	VU	D	CATH	24	AR	75	S	25	FS	49	FOL	75	1
Lemuridae	*Hapalemur occidentalis*	Madagascar	VU	D	CATH	75	AR	75	S	25	FS	49	F_F	75	0
Hylobatidae	*Hoolock hoolock*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Hylobatidae	*Hoolock leuconedys*	Asia	VU	D	DI	75	AR	75	M	75	FS	49	FRU	10, 2	0
Hylobatidae	*Hylobates abbotti*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	FRU	NI	0
Hylobatidae	*Hylobates agilis*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Hylobatidae	*Hylobates albibarbis*	Asia	EN	D	DI	75	AR	75	M	75	FS	49	FRU	75	0
Hylobatidae	*Hylobates funereus*	Asia	EN	D	DI	75	AR	75	M	75	FS	75	FRU	75	0

Hylobatidae	*Hylobates klossii*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Hylobatidae	*Hylobates lar*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	2
Hylobatidae	*Hylobates Moloch*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Hylobatidae	*Hylobates muelleri*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Hylobatidae	*Hylobates pileatus*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Indriidae	*Indri indri*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	FOL	75	1
Atelidae	*Lagothrix cana*	Neotropics	EN	D	DI	75	AR	75	M	25	N_FS	49	FRU	75	0
Atelidae	*Lagothrix flavicauda*	Neotropics	CR	D	DI	75	AR	75	M	92	FS	49	FRU	75	0
Atelidae	*Lagothrix lagothricha*	Neotropics	VU	D	DI	75	AR	75	M	25	N_FS	49	FRU	75	0
Atelidae	*Lagotrix lugens*	Neotropics	VU	D	DI	75	AR	75	M	25	NI	NI	FRU	NI	0
Atelidae	*Lagothrix poeppigii*	Neotropics	CR	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Lemuridae	*Lemur catta*	Madagascar	EN	D	DI	75	BOTH	75	M	25	N_FS	49	F_F	75	1
Callitrichidae	*Leontocebus cruzlimai*	Neotropics	LC	NI	DI	75	AR	75	S	NI	NI	NI	O	NI	0
Callitrichidae	*Leontocebus fuscicollis*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75	4
Callitrichidae	*Leontocebus fuscus*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75	0
Callitrichidae	*Leontocebus illigeri*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75	0
Callitrichidae	*Leontocebus lagonotus*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75	0
Callitrichidae	*Leontocebus leucogenys*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75	0
Callitrichidae	*Leontocebus nigricollis*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75, 50	0
Callitrichidae	*Leontocebus nigrifrons*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	75	1
Callitrichidae	*Leontocebus tripartitus*	Neotropics	NT	D	DI	75	AR	75	S	75	FS	75	O	75	0
Callitrichidae	*Leontocebus weddelli*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	112, 36	0
Callitrichidae	*Leontopithecus caissara*	Neotropics	CR	D	DI	75	AR	75	S	25	FS	49	FRU	75	0
Callitrichidae	*Leontopithecus chrysomelas*	Neotropics	EN	D	DI	75	AR	75	S	25	FS	49	O	86, 44	4
Callitrichidae	*Leontopithecus chrysopygus*	Neotropics	EN	D	DI	75	AR	75	S	25	FS	49	FRU	75	1
Callitrichidae	*Leontopithecus rosalia*	Neotropics	EN	S	DI	75	AR	75	S	25	FS	49	FRU	75	0
Lepilemuridae	*Lepilemur aeeclis*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur ahmansonorum*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur ankaranensis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	F_F	75	0

Lepilemuridae	*Lepilemur betsileo*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur dorsalis*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Lepilemuridae	*Lepilemur edwardsi*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Lepilemuridae	*Lepilemur fleuretae*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur grewcockorum*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur hollandorum*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur hubbardi*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur jamesorum*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur leucopus*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Lepilemuridae	*Lepilemur microdon*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	F_F	75	0
Lepilemuridae	*Lepilemur milanoii*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur mittermeieri*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	126	0
Lepilemuridae	*Lepilemur mustelinus*	Madagascar	NT	D	N	75	AR	75	S	25	FS	49	FOL	110, 66	1
Lepilemuridae	*Lepilemur otto*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur petteri*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur randrianasoloi*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Lepilemuridae	*Lepilemur ruficaudatus*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Lepilemuridae	*Lepilemur sahamalazensis*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	FOL	75	0
Lepilemuridae	*Lepilemur scottorum*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	FOL	109	0
Lepilemuridae	*Lepilemur seali*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	FOL	78	0
Lepilemuridae	*Lepilemur septentrionalis*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	FOL	110	0
Lepilemuridae	*Lepilemur tymerlachsoni*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	F_F	75	0
Lepilemuridae	*Lepilemur wrightae*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cercopithecidae	*Lophocebus albigena*	M_Africa	LC	D	DI	75	AR	75	M	25	FS	49	FRU	75	2
Cercopithecidae	*Lophocebus aterrimus*	M_Africa	NT	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Lophocebus johnstoni*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	75	FRU	NI	0
Cercopithecidae	*Lophocebus opdenboschi*	M_Africa	DD	D	DI	75	AR	75	M	25	FS	75	FRU	NI	0
Cercopithecidae	*Lophocebus osmani*	M_Africa	LC	NI	DI	75	AR	75	M	25	FS	75	FRU	NI	0
Cercopithecidae	*Lophocebus ugandae*	M_Africa	NE	NI	DI	75	AR	75	M	25	FS	75	F_F	75	2

Lorisidae	*Loris lydekkerianus*	Asia	LC	D	N	75	AR	75	S	56	FS	49	IN	75	0
Lorisidae	*Loris tardigradus*	Asia	EN	D	N	75	AR	75	S	25	FS	49	IN	75	0
Cercopithecidae	*Macaca arctoides*	Asia	VU	D	DI	75	T	75	L	25	FS	49	F_F	75	0
Cercopithecidae	*Macaca assamensis*	Asia	NT	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Macaca cyclopis*	Asia	LC	S	DI	75	BOTH	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Macaca fascicularis*	Asia	LC	D	DI	75	AR	75	M	25	FS	49	FRU	75	10
Cercopithecidae	*Macaca fuscata*	Asia	LC	S	DI	75	BOTH	75	M	25	FS	49	F_F	75	6
Cercopithecidae	*Macaca hecki*	Asia	VU	D	DI	75	AR	75	M	25	FS	49	O	75	0
Cercopithecidae	*Macaca leonina*	Asia	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Macaca leucogenys*	Asia	NE	NI	DI	75	NI	NI	NI	NI	NI	NI	NI	NI	0
Cercopithecidae	*Macaca maura*	Asia	EN	D	DI	75	BOTH	75	M	25	N_FS	49	FRU	75	0
Cercopithecidae	*Macaca mulatta*	Asia	LC	NI	DI	75	BOTH	75	M	25	N_FS	49	F_F	75	15
Cercopithecidae	*Macaca munzala*	Asia	EN	D	DI	75	T	75	L	74	FS	49	F_F	73, 7	0
Cercopithecidae	*Macaca nemestrina*	Asia	VU	D	DI	75	T	75	M	25	FS	49	FRU	75	4
Cercopithecidae	*Macaca nigra*	Asia	CR	D	DI	75	T	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Macaca nigrescens*	Asia	VU	D	DI	75	AR	75	M	124, 62	FS	49	FRU	75	0
Cercopithecidae	*Macaca ochreata*	Asia	VU	D	DI	75	BOTH	75	M	25	FS	49	FRU	75	3
Cercopithecidae	*Macaca pagensis*	Asia	CR	D	DI	75	BOTH	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Macaca radiata*	Asia	LC	D	DI	75	BOTH	75	M	25	N_FS	49	FRU	75	11
Cercopithecidae	*Macaca siberu*	Asia	VU	D	DI	75	T	75	M	125	FS	49	FRU	75	0
Cercopithecidae	*Macaca silenus*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Cercopithecidae	*Macaca sínica*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Cercopithecidae	*Macaca sylvanus*	M_Africa	EN	D	DI	75	BOTH	75	L	25	N_FS	49	O	75	2
Cercopithecidae	*Macaca tibetana*	Asia	NT	D	DI	75	T	75	L	25	FS	49	FRU	75	0
Cercopithecidae	*Macaca tonkeana*	Asia	VU	D	DI	75	BOTH	75	L	25	FS	49	FRU	75	1
Cercopithecidae	*Mandrillus leucophaeus*	M_Africa	EN	NI	DI	75	BOTH	75	L	57	N_FS	49	O	75	1
Cercopithecidae	*Mandrillus sphinx*	M_Africa	VU	NI	DI	75	T	75	L	25	FS	49	O	75	1
Callitrichidae	*Mico acariensis*	Neotropics	DD	NI	DI	75	AR	29	S	106, 1	FS	49	O	75	0
Callitrichidae	*Mico argentatus*	Neotropics	LC	D	DI	75	AR	75	S	25	N_FS	49	O	75	0

Callitrichidae	*Mico chrysoleucos*	Neotropics	DD	NI	DI	75	AR	29	S	75	FS	49	O	75	0
Callitrichidae	*Mico emiliae*	Neotropics	DD	NI	DI	75	AR	75	S	25	N_FS	49	O	75	0
Callitrichidae	*Mico humeralifer*	Neotropics	DD	NI	DI	75	AR	29	S	25	FS	49	O	75	0
Callitrichidae	*Mico intermedius*	Neotropics	LC	D	DI	75	AR	75	S	107	FS	49	O	75	0
Callitrichidae	*Mico leucippe*	Neotropics	VU	D	DI	75	AR	75	S	75	FS	49	O	75	0
Callitrichidae	*Mico marcai*	Neotropics	DD	NI	DI	75	AR	29	S	75	FS	49	NI	NI	0
Callitrichidae	*Mico mauesi*	Neotropics	LC	S	DI	75	AR	29	S	25	FS	49	O	75	0
Callitrichidae	*Mico melanurus*	Neotropics	LC	NI	DI	75	AR	75	S	25	N_FS	49	O	75	0
Callitrichidae	*Mico nigriceps*	Neotropics	DD	NI	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Mico rondoni*	Neotropics	VU	D	DI	75	AR	75	S	75	FS	49	O	75	0
Callitrichidae	*Mico saterei*	Neotropics	LC	NI	DI	75	AR	29	S	115	FS	49	O	75	0
Cheirogaleidae	*Microcebus arnholdi*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus berthae*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	40	0
Cheirogaleidae	*Microcebus bongolavensis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus danfossi*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus gerpi*	Madagascar	CR	D	N	75	AR	75	S	98	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus griseorufus*	Madagascar	LC	D	N	75	AR	75	S	25	N_FS	49	O	40	0
Cheirogaleidae	*Microcebus jollyae*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus lehilahytsara*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	O	75	0
Cheirogaleidae	*Microcebus macarthurii*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	78	0
Cheirogaleidae	*Microcebus mamiratra*	Madagascar	CR	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus margotmarshae*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus marohita*	Madagascar	CR	D	N	75	NI	NI	S	99	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus mittermeieri*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	78	0
Cheirogaleidae	*Microcebus murinus*	Madagascar	LC	D	N	75	AR	75	S	25	N_FS	49	O	75	3
Cheirogaleidae	*Microcebus myoxinus*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	O	40	0
Cheirogaleidae	*Microcebus ravelobensis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	75	0
Cheirogaleidae	*Microcebus rufus*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	O	75	1
Cheirogaleidae	*Microcebus sambiranensis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	40	0

Cheirogaleidae	*Microcebus simmonsi*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	NI	NI	0
Cheirogaleidae	*Microcebus tanosi*	Madagascar	NE	NI	N	75	NI	NI	S	100	NI	NI	NI	NI	0
Cheirogaleidae	*Microcebus tavaratra*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	O	40	0
Cercopithecidae	*Miopithecus ogouensis*	M_Africa	LC	S	DI	75	BOTH	75	S	25	FS	49	FRU	75	0
Cercopithecidae	*Miopithecus talapoin*	M_Africa	LC	NI	DI	75	BOTH	75	S	25	FS	49	O	75	2
Cheirogaleidae	*Mirza coquereli*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	75	0
Cheirogaleidae	*Mirza zaza*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	O	75	0
Cercopithecidae	*Nasalis larvatus*	Asia	EN	D	DI	75	AR	75	L	25	FS	49	F_F	75	1
Hylobatidae	*Nomascus annamensis*	Asia	NE	NI	DI	75	AR	75	M	25	FS	75	FRU	75	0
Hylobatidae	*Nomascus concolor*	Asia	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	2
Hylobatidae	*Nomascus gabriellae*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Hylobatidae	*Nomascus hainanus*	Asia	CR	S	DI	75	AR	75	M	38	FS	49	FRU	11, 39	0
Hylobatidae	*Nomascus leucogenys*	Asia	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Hylobatidae	*Nomascus nasutus*	Asia	CR	D	DI	75	AR	75	M	NI	FS	49	FRU	75	0
Hylobatidae	*Nomascus siki*	Asia	EN	D	DI	75	AR	75	M	102	FS	49	FRU	120, 67, 13	0
Lorisidae	*Nycticebus bancanus*	Asia	NE	NI	N	75	AR	75	S	NI	FS	49	O	NI	0
Lorisidae	*Nycticebus bengalensis*	Asia	VU	D	N	75	AR	75	S	25	FS	49	G	75	0
Lorisidae	*Nycticebus borneanus*	Asia	NE	NI	N	75	AR	75	S	85	FS	49	O	NI	0
Lorisidae	*Nycticebus coucang*	Asia	VU	D	N	75	AR	75	S	25	FS	49	O	75	2
Lorisidae	*Nycticebus javanicus*	Asia	CR	D	N	75	AR	75	S	56, 85	FS	49	G	15	2
Lorisidae	*Nycticebus kayan*	Asia	NE	NI	N	75	AR	75	S	85	NI	NI	NI	NI	0
Lorisidae	*Nycticebus menagensis*	Asia	VU	D	N	75	AR	75	S	25	FS	49	O	101	0
Lorisidae	*Nycticebus pygmaeus*	Asia	VU	D	N	75	AR	75	S	25	FS	49	G	84	0
Galagidae	*Otolemur crassicaudatus*	M_Africa	LC	S	N	75	AR	75	S	25	N_FS	49	O	75	0
Galagidae	*Otolemur garnettii*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	O	75	0
Hominidae	*Pan paniscus*	M_Africa	EN	D	DI	75	BOTH	75	L	25	FS	49	O	75	0
Hominidae	*Pan troglodytes*	M_Africa	EN	D	DI	75	BOTH	75	L	25	N_FS	49	O	75	17
Cercopithecidae	*Papio anubis*	M_Africa	LC	I	DI	75	T	75	L	25	N_FS	49	O	75	11
Cercopithecidae	*Papio cynocephalus*	M_Africa	LC	S	DI	75	T	75	L	25	N_FS	49	O	75	3

Cercopithecidae	*Papio hamadryas*	M_Africa	LC	I	DI	75	T	75	L	25	N_FS	49	O	75	4
Cercopithecidae	*Papio kindae*	M_Africa	LC	S	DI	75	T	75	L	25	N_FS	75, 55	O	NI	0
Cercopithecidae	*Papio papio*	M_Africa	NT	NI	DI	75	T	75	L	25	N_FS	49	O	75	0
Cercopithecidae	*Papio ursinus*	M_Africa	LC	S	DI	75	T	75	L	25	N_FS	49	O	75	7
Lorisidae	*Perodicticus edwardsi*	M_Africa	LC	S	N	75	AR	75	S	25	FS	75	FRU	75	0
Lorisidae	*Perodicticus ibeanus*	M_Africa	LC	S	N	75	AR	75	S	25	FS	75	FRU	NI	0
Lorisidae	*Perodicticus potto*	M_Africa	LC	S	N	75	AR	75	S	25	FS	49	FRU	84, 14	1
Cheirogaleidae	*Phaner electromontis*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	G	75	0
Cheirogaleidae	*Phaner furcifer*	Madagascar	VU	D	N	75	AR	75	S	25	FS	49	G	75, 109	0
Cheirogaleidae	*Phaner pallescens*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	G	75	0
Cheirogaleidae	*Phaner parienti*	Madagascar	EN	D	N	75	AR	75	S	25	FS	49	G	NI	0
Cercopithecidae	*Piliocolobus badius*	M_Africa	EN	D	DI	75	AR	75	M	25	FS	75	F_F	75	5
Cercopithecidae	*Piliocolobus bouvieri*	M_Africa	CR	NI	DI	75	AR	75	M	NI	FS	75	F_F	75	0
Cercopithecidae	*Piliocolobus epieni*	M_Africa	CR	D	DI	75	AR	75	M	NI	FS	75	FOL	75	0
Cercopithecidae	*Piliocolobus foai*	M_Africa	NE	NI	DI	75	AR	75	M	25	FS	75	F_F	75	0
Cercopithecidae	*Piliocolobus gordonorum*	M_Africa	EN	D	DI	75	AR	75	M	54	FS	75	F_F	75	1
Cercopithecidae	*Piliocolobus kirkii*	M_Africa	EN	D	DI	75	AR	75	M	25	N_FS	75, 113, 114	F_F	75	0
Cercopithecidae	*Piliocolobus langi*	M_Africa	NE	NI	DI	75	AR	75	M	25	FS	75	F_F	75	0
Cercopithecidae	*Piliocolobus oustaleti*	M_Africa	LC	D	DI	75	AR	75	M	25	N_FS	75	FOL	57	0
Cercopithecidae	*Piliocolobus parmentieri*	M_Africa	NE	NI	DI	75	AR	75	M	25	FS	75	FOL	75	0
Cercopithecidae	*Piliocolobus pennantii*	M_Africa	EN	D	DI	75	AR	75	M	25	FS	75	F_F	75	1
Cercopithecidae	*Piliocolobus preussi*	M_Africa	CR	D	DI	75	AR	75	M	25	FS	75	FOL	75	0
Cercopithecidae	*Piliocolobus rufomitratus*	M_Africa	EN	D	DI	75	AR	75	M	25	FS	49	FOL	75	1
Cercopithecidae	*Piliocolobus semlikiensis*	M_Africa	NE	NI	DI	75	AR	75	M	NI	FS	75	FOL	NI	0
Cercopithecidae	*Piliocolobus temminckii*	M_Africa	EN	D	DI	75	AR	75	M	63	N_FS	75, 34, 118, 35	FOL	75	0
Cercopithecidae	*Piliocolobus tephrosceles*	M_Africa	EN	D	DI	75	AR	75	M	25	FS	75	FOL	75	1

Cercopithecidae	*Piliocolobus tholloni*	M_Africa	NT	D	DI	75	AR	75	NI	NI	FS	75	FOL	75	0
Cercopithecidae	*Piliocolobus waldronae*	M_Africa	CR	D	DI	75	AR	75	M	25	FS	75	FOL	75	0
Pitheciidae	*Pithecia aequatorialis*	Neotropics	LC	D	DI	75	AR	75	M	25	FS	49	NI	NI	0
Pitheciidae	*Pithecia albicans*	Neotropics	VU	D	DI	75	AR	75	M	25	FS	49	FRU	75	0
Pitheciidae	*Pithecia cazuzai*	Neotropics	NE	NI	DI	75	AR	75	NI	NI	NI	NI	NI	NI	0
Pitheciidae	*Pithecia chrysocephala*	Neotropics	LC	NI	DI	75	AR	75	S	25	NI	NI	FRU	NI	0
Pitheciidae	*Pithecia hirsuta*	Neotropics	NE	NI	DI	75	AR	75	M	NI	NI	NI	FRU	45	0
Pitheciidae	*Pithecia inusta*	Neotropics	NE	NI	DI	75	AR	75	M	NI	NI	NI	FRU	NI	0
Pitheciidae	*Pithecia irrorata*	Neotropics	LC	NI	DI	75	AR	75	M	25	FS	75	FRU	75	1
Pitheciidae	*Pithecia Isabela*	Neotropics	NE	NI	DI	75	AR	75	NI	NI	NI	NI	NI	NI	0
Pitheciidae	*Pithecia milleri*	Neotropics	DD	NI	DI	75	AR	75	M	NI	NI	NI	FRU	NI	0
Pitheciidae	*Pithecia mittermeieri*	Neotropics	NE	NI	DI	75	AR	75	NI	NI	NI	NI	NI	NI	0
Pitheciidae	*Pithecia monachus*	Neotropics	LC	NI	DI	75	AR	75	M	25	FS	75	FRU	NI	0
Pitheciidae	*Pithecia napensis*	Neotropics	NE	NI	DI	75	AR	75	NI	NI	NI	NI	NI	NI	0
Pitheciidae	*Pithecia pissinattii*	Neotropics	NE	NI	DI	75	AR	75	NI	NI	NI	NI	NI	NI	0
Pitheciidae	*Pithecia pithecia*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	FRU	75	2
Pitheciidae	*Pithecia rylandsi*	Neotropics	NE	NI	DI	75	AR	75	NI	25	NI	NI	NI	NI	0
Pitheciidae	*Pithecia vanzolinii*	Neotropics	DD	NI	DI	75	AR	75	M	NI	NI	NI	FRU	NI	0
Pitheciidae	*Plecturocebus aureipalatii*	Neotropics	LC	S	DI	75	AR	75	S	75	FS	75	FRU	75	0
Pitheciidae	*Plecturocebus baptista*	Neotropics	LC	NI	DI	75	AR	75	S	75	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus bernhardi*	Neotropics	LC	NI	DI	75	AR	75	S	75	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus brunneus*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	FRU	75	0
Pitheciidae	*Plecturocebus caligatus*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus caquetensis*	Neotropics	CR	D	DI	75	AR	75	NI	25	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus cinerascens*	Neotropics	LC	NI	DI	75	AR	75	S	75	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus cupreus*	Neotropics	LC	NI	DI	75	AR	58	S	25	FS	75	FRU	75	2
Pitheciidae	*Plecturocebus discolor*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75, 128, 27	FRU	75	0
Pitheciidae	*Plecturocebus donacophilus*	Neotropics	LC	D	DI	75	AR	75	S	25	N_FS	75, 68	FRU	127	0

Pitheciidae	*Plecturocebus hoffmannsi*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus miltoni*	Neotropics	NE	NI	DI	75	AR	75	S	25	NI	NI	NI	NI	0
Pitheciidae	*Plecturocebus modestus*	Neotropics	EN	D	DI	75	AR	26	S	75	N_FS	75, 68	FRU	69, 4	1
Pitheciidae	*Plecturocebus Moloch*	Neotropics	LC	NI	DI	75	AR	75	S	25	FS	75	O	103, 72, 18	2
Pitheciidae	*Plecturocebus oenanthe*	Neotropics	CR	D	DI	75	AR	75	S	75	N_FS	75, 22	O	75, 21	1
Pitheciidae	*Plecturocebus olallae*	Neotropics	EN	D	DI	75	AR	75	S	75	N_FS	75, 68	F_F	73, 64	2
Pitheciidae	*Plecturocebus ornatus*	Neotropics	VU	D	DI	75	AR	75	S	25	FS	75	FRU	75	0
Pitheciidae	*Plecturocebus pallescens*	Neotropics	LC	S	DI	75	AR	75	S	47	N_FS	75	NI	NI	0
Pitheciidae	*Plecturocebus stephennashi*	Neotropics	DD	NI	DI	75	AR	75	S	105, 70	FS	75	NI	NI	0
Pitheciidae	*Plecturocebus toppini*	Neotropics	NE	NI	DI	75	AR	75	NI	25	NI	NI	NI	NI	0
Pitheciidae	*Plecturocebus urubambensis*	Neotropics	NE	NI	DI	75	AR	75	NI	25	NI	NI	NI	NI	0
Pitheciidae	*Plecturocebus vieirai*	Neotropics	NE	NI	DI	75	AR	75	S	25	FS	75	NI	NI	0
Hominidae	*Pongo abelii*	Asia	CR	D	DI	75	AR	75	L	25	FS	49	FRU	75	2
Hominidae	*Pongo pygmaeus*	Asia	EN	D	DI	75	AR	75	L	25	FS	49	FRU	75	2
Cercopithecidae	*Presbytis bicolor*	Asia	DD	D	DI	75	AR	75	M	25	FS	75	F_F	75	0
Cercopithecidae	*Presbytis canicrus*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	FOL	75	0
Cercopithecidae	*Presbytis chrysomelas*	Asia	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Cercopithecidae	*Presbytis comata*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FOL	75	0
Cercopithecidae	*Presbytis femoralis*	Asia	NT	D	DI	75	AR	75	M	25	N_FS	49	F_F	75	0
Cercopithecidae	*Presbytis frontata*	Asia	VU	D	DI	75	AR	75	M	25	FS	49	FOL	75	0
Cercopithecidae	*Presbytis hosei*	Asia	DD	D	DI	75	AR	75	M	25	FS	49	FOL	75	1
Cercopithecidae	*Presbytis melalophos*	Asia	NT	D	DI	75	AR	75	M	25	N_FS	49	F_F	75	2
Cercopithecidae	*Presbytis mitrata*	Asia	EN	D	DI	75	AR	75	M	25	N_FS	75	F_F	75	0
Cercopithecidae	*Presbytis natunae*	Asia	VU	D	DI	75	AR	75	M	25	FS	49	NI	NI	0
Cercopithecidae	*Presbytis potenziani*	Asia	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Cercopithecidae	*Presbytis rubicunda*	Asia	LC	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Cercopithecidae	*Presbytis sabana*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	F_F	75	0
Cercopithecidae	*Presbytis siamensis*	Asia	NT	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Cercopithecidae	*Presbytis siberu*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	F_F	75	0

Cercopithecidae	*Presbytis sumatrana*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	F_F	75	0
Cercopithecidae	*Presbytis thomasi*	Asia	VU	D	DI	75	AR	75	M	25	FS	49	F_F	75	2
Cercopithecidae	*Procolobus verus*	M_Africa	NT	NI	DI	75	AR	75	M	25	FS	49	FOL	75	2
Lemuridae	*Prolemur simus*	Madagascar	CR	D	CATH	75	AR	75	S	25	FS	49	FOL	75	0
Indriidae	*Propithecus candidus*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Indriidae	*Propithecus coquereli*	Madagascar	EN	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Indriidae	*Propithecus coronatus*	Madagascar	EN	D	DI	75	AR	75	M	25	FS	49	FOL	75	0
Indriidae	*Propithecus deckenii*	Madagascar	EN	D	DI	75	AR	75	M	25	FS	49	F_F	NI	0
Indriidae	*Propithecus diadema*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	1
Indriidae	*Propithecus edwardsi*	Madagascar	EN	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Indriidae	*Propithecus perrieri*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Indriidae	*Propithecus tattersalli*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Indriidae	*Propithecus verreauxi*	Madagascar	EN	D	DI	75	AR	75	M	25	N_FS	49	F_F	75	4
Cercopithecidae	*Pygathrix cinérea*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	FOL	75	0
Cercopithecidae	*Pygathrix nemaeus*	Madagascar	EN	D	DI	75	AR	75	M	25	FS	49	FOL	75	0
Cercopithecidae	*Pygathrix nigripes*	Madagascar	EN	D	DI	75	AR	75	M	25	FS	49	F_F	75	0
Cercopithecidae	*Rhinopithecus avunculus*	Asia	CR	D	DI	75	AR	75	L	25	FS	49	F_F	75	0
Cercopithecidae	*Rhinopithecus bieti*	Asia	EN	D	DI	75	BOTH	75	L	25	FS	49	FOL	75	2
Cercopithecidae	*Rhinopithecus brelichi*	Asia	EN	D	DI	75	BOTH	75	L	25	FS	49	FOL	75	0
Cercopithecidae	*Rhinopithecus roxellana*	Asia	EN	D	DI	75	BOTH	75	L	51	FS	49	FOL	75	1
Cercopithecidae	*Rhinopithecus strykeri*	Asia	CR	D	DI	75	BOTH	75	L	75	FS	49	FOL	75	0
Cercopithecidae	*Rungwecebus kipunji*	M_Africa	CR	D	DI	75	AR	75	L	25	FS	49	O	75	2
Callitrichidae	*Saguinus bicolor*	Neotropics	EN	D	DI	75	AR	75	S	25	FS	49	FRU	75	0
Callitrichidae	*Saguinus geoffroyi*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Saguinus imperator*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Saguinus inustus*	Neotropics	LC	S	DI	75	AR	75	S	25	FS	49	NI	NI	0
Callitrichidae	*Saguinus labiatus*	Neotropics	LC	S	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Saguinus leucopus*	Neotropics	EN	D	DI	75	AR	75	S	25	FS	49	FRU	75	7
Callitrichidae	*Saguinus martinsi*	Neotropics	LC	NI	DI	75	AR	75	S	75	FS	49	FRU	3	0

Callitrichidae	*Saguinus midas*	Neotropics	LC	S	DI	75	AR	75	S	25	N_FS	49	O	75	2
Callitrichidae	*Saguinus mystax*	Neotropics	LC	S	DI	75	AR	75	S	25	FS	49	O	75	4
Callitrichidae	*Saguinus niger*	Neotropics	VU	D	DI	75	AR	75	S	87, 97	FS	49	O	75	0
Callitrichidae	*Saguinus oedipus*	Neotropics	CR	D	DI	75	AR	75	S	25	FS	49	O	75	0
Callitrichidae	*Saguinus ursulus*	Neotropics	NE	NI	DI	75	AR	75	S	NI	NI	NI	O	NI	0
Cebidae	*Saimiri boliviensis*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	49	O	75	0
Cebidae	*Saimiri cassiquiarensis*	Neotropics	LC	NI	DI	75	AR	75	S	25	N_FS	75	O	75	1
Cebidae	*Saimiri macrodon*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	75	O	NI	0
Cebidae	*Saimiri oerstedii*	Neotropics	VU	D	DI	75	AR	75	S	25	FS	49	O	75	3
Cebidae	*Saimiri sciureus*	Neotropics	LC	D	DI	75	AR	75	S	25	FS	49	O	75	3
Cebidae	*Saimiri ustus*	Neotropics	NT	D	DI	75	AR	75	S	25	FS	49	O	3	0
Cebidae	*Saimiri vanzolinii*	Neotropics	VU	NI	DI	75	AR	75	S	5	FS	49	O	75	0
Cebidae	*Sapajus apella*	Neotropics	LC	D	DI	75	AR	75	M	25	N_FS	49	O	75	11
Cebidae	*Sapajus cay*	Neotropics	LC	D	DI	75	AR	75	M	75	N_FS	49	O	30	0
Cebidae	*Sapajus flavius*	Neotropics	CR	D	DI	75	AR	32	M	75, 88, 31	FS	49	O	83, 17	0
Cebidae	*Sapajus libidinosus*	Neotropics	LC	D	DI	75	AR	75	M	25	N_FS	49	O	75	3
Cebidae	*Sapajus macrocephalus*	Neotropics	LC	D	DI	75	AR	122	M	75	FS	49	O	75	0
Cebidae	*Sapajus nigritus*	Neotropics	NT	D	DI	75	AR	75	M	25	FS	49	O	75	4
Cebidae	*Sapajus robustus*	Neotropics	EN	D	DI	75	AR	75	M	25	FS	49	FRU	71	0
Cebidae	*Sapajus xanthosternos*	Neotropics	CR	D	DI	75	AR	75	M	25	FS	49	O	75	4
Galagidae	*Sciurocheirus alleni*	M_Africa	EN	NI	N	75	AR	75	S	25	FS	49	FRU	75	1
Galagidae	*Sciurocheirus cameronensis*	M_Africa	LC	NI	N	75	AR	75	S	75	FS	75	FRU	75	0
Galagidae	*Sciurocheirus gabonensis*	M_Africa	LC	NI	N	75	AR	75	S	25	FS	49	FRU	75	0
Galagidae	*Sciurocheirus makandensis*	M_Africa	NE	NI	DI	75	AR	75	NI	NI	NI	NI	NI	NI	0
Cercopithecidae	*Semnopithecus Ajax*	Asia	EN	D	DI	75	T	75	L	25	FS	49	F_F	75	0
Cercopithecidae	*Semnopithecus entellus*	Asia	LC	D	DI	75	T	75	L	25	N_FS	49	F_F	75	8
Cercopithecidae	*Semnopithecus hector*	Asia	NT	D	DI	75	BOTH	75	L	25	FS	49	FOL	75	0
Cercopithecidae	*Semnopithecus hypoleucos*	Asia	VU	D	DI	75	T	75	L	75	FS	49	FOL	75	0
Cercopithecidae	*Semnopithecus johnii*	Asia	VU	D	DI	75	AR	75	L	25	FS	49	F_F	75, 91	0

Cercopithecidae	*Semnopithecus priam*	Asia	NT	D	DI	75	T	75	L	25	N_FS	49	F_F	75	0
Cercopithecidae	*Semnopithecus schistaceus*	Asia	LC	D	DI	75	BOTH	75	L	25	N_FS	49	F_F	75	0
Cercopithecidae	*Semnopithecus vetulus*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	F_F	75	10
Cercopithecidae	*Simias concolor*	Asia	CR	D	DI	75	BOTH	75	M	25	FS	49	FOL	75	0
Hylobatidae	*Symphalangus syndactylus*	Asia	EN	D	DI	75	AR	75	L	25	FS	49	F_F	75	1
Tarsiidae	*Tarsius dentatus*	Asia	VU	D	N	75	AR	75	S	25	FS	49	IN	75	3
Tarsiidae	*Tarsius fuscus*	Asia	NE	NI	N	75	AR	75	S	25	FS	49	IN	NI	0
Tarsiidae	*Tarsius lariang*	Asia	DD	D	N	75	AR	75	S	25	FS	49	IN	75	0
Tarsiidae	*Tarsius pelengensis*	Asia	EN	D	N	75	AR	75	S	33	FS	49	IN	75	0
Tarsiidae	*Tarsius pumilus*	Asia	DD	D	N	75	AR	75	S	25	FS	49	IN	75	0
Tarsiidae	*Tarsius sangirensis*	Asia	EN	D	N	75	AR	75	S	25	FS	49	IN	75	0
Tarsiidae	*Tarsius tarsier*	Asia	VU	D	N	75	AR	75	S	25	FS	49	IN	111	0
Tarsiidae	*Tarsius tumpara*	Asia	CR	D	N	75	AR	75	S	112	FS	49	IN	75	0
Tarsiidae	*Tarsius wallacei*	Asia	DD	D	N	75	AR	75	S	25	FS	49	IN	75	0
Cercopithecidae	*Theropithecus gelada*	M_Africa	LC	D	DI	75	T	75	L	25	N_FS	49	FOL	75	1
Cercopithecidae	*Trachypithecus auratus*	Asia	VU	D	DI	75	AR	75	M	25	FS	49	FOL	75	2
Cercopithecidae	*Trachypithecus barbei*	Asia	DD	D	DI	75	NI	NI	M	25	FS	49	NI	NI	0
Cercopithecidae	*Trachypithecus crepusculus*	Asia	EN	D	DI	75	AR	75	M	25	FS	75	F_F	61, 1	0
Cercopithecidae	*Trachypithecus cristatus*	Asia	NT	D	DI	75	AR	75	M	25	FS	49	FOL	75	1
Cercopithecidae	*Trachypithecus delacouri*	Asia	CR	D	DI	75	BOTH	75	M	82, 81	FS	49	FOL	75	0
Cercopithecidae	*Trachypithecus ebenus*	Asia	EN	D	DI	75	BOTH	75	L	25	FS	49	FOL	NI	0
Cercopithecidae	*Trachypithecus francoisi*	Asia	EN	D	DI	75	BOTH	75	M	25	FS	49	FOL	75	0
Cercopithecidae	*Trachypithecus geei*	Asia	EN	D	DI	75	AR	75	L	25	FS	49	FOL	75	0
Cercopithecidae	*Trachypithecus germaini*	Asia	EN	D	DI	75	AR	75	M	25	FS	49	FOL	75	2
Cercopithecidae	*Trachypithecus hatinhensis*	Asia	EN	D	DI	75	BOTH	75	M	82	FS	49	FOL	75	0
Cercopithecidae	*Trachypithecus laotum*	Asia	VU	D	DI	75	BOTH	75	M	75	FS	49	FOL	121	0
Cercopithecidae	*Trachypithecus leucocephalus*	Asia	CR	D	DI	75	BOTH	75	M	25	N_FS	75, 129	FOL	75	0
Cercopithecidae	*Trachypithecus margarita*	Asia	EN	D	DI	75	AR	41	NI	NI	FS	49	FOL	62	0
Cercopithecidae	*Trachypithecus mauritius*	Asia	VU	D	DI	75	AR	75	M	75	FS	75	FOL	NI	0

Cercopithecidae	*Trachypithecus obscurus*	Asia	NT	D	DI	75	AR	75	M	25	FS	49	FOL	75	2
Cercopithecidae	*Trachypithecus phayrei*	Asia	EN	D	DI	75	AR	75	M	25	N_FS	49	FOL	75	1
Cercopithecidae	*Trachypithecus pileatus*	Asia	VU	D	DI	75	AR	75	L	25	FS	49	FOL	75	1
Cercopithecidae	*Trachypithecus piliocephalus*	Asia	CR	D	DI	75	BOTH	75	M	25	N_FS	75, 80, 79	FOL	75	0
Cercopithecidae	*Trachypithecus selangorensis*	Asia	NE	NI	DI	75	AR	75	M	NI	FS	75	FOL	75	0
Cercopithecidae	*Trachypithecus shortridgei*	Asia	EN	D	DI	75	AR	75	L	NI	FS	49	FOL	48	0
Lemuridae	*Varecia rubra*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	FRU	75	1
Lemuridae	*Varecia variegata*	Madagascar	CR	D	DI	75	AR	75	M	25	FS	49	FRU	75	0

[a] For taxonomy, we followed: Estrada, A. et al. Impending extinction crisis of the world's primates: why primates matter. Sci. Adv. 3, e1600946 (2017).

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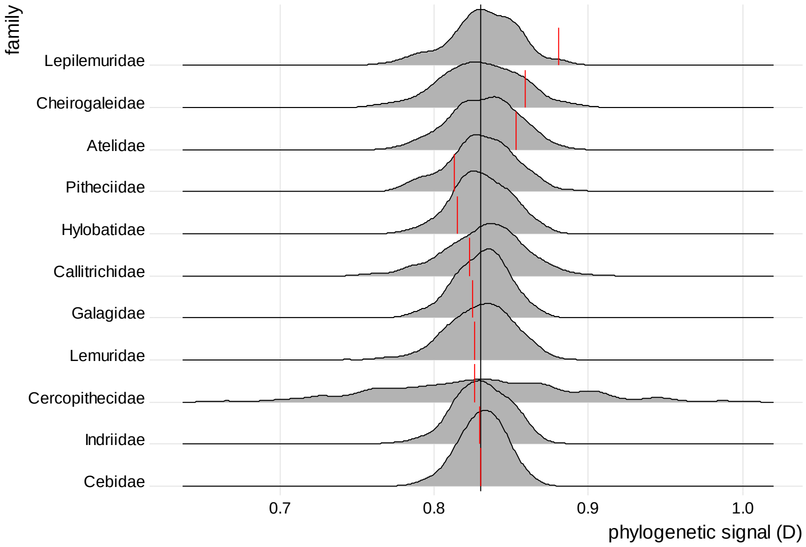
Supplementary Table 3. Sensitivity analysis for phylogenetic signal in matrix use. Each row shows the focal family with its number of species (N), the estimate of D obtained after removing it, the % change from the value for the whole order, and the results from the randomization test. m.null.estimate is the mean value of the null distribution of estimates after 500 randomizations. Pval.randomization is the result of testing if the change in parameter estimate is significantly different from the null distribution.

Clade removed	N	D	Percent change	m.null.estimate	Pval.randomization
Lepilemuridae	24	0.881	5.7	0.832	0.025
Cheirogaleidae	28	0.859	3.1	0.830	0.135
Atelidae	22	0.853	2.5	0.832	0.165
Pitheciidae	18	0.813	2.4	0.831	0.190
Hylobatidae	18	0.815	2.1	0.831	0.170
Callitrichidae	29	0.823	1.2	0.833	0.328
Galagidae	14	0.825	0.9	0.831	0.350
Cercopithecidae	120	0.827	0.8	0.827	0.495
Lemuridae	21	0.826	0.8	0.830	0.415
Indriidae	15	0.830	0.4	0.831	0.455
Cebidae	12	0.830	0.3	0.831	0.463



Supplementary Figure 2. Sensitivity analysis results for phylogenetic signal tests. Black line shows the estimate of D for the whole order. Red lines are the estimates after removing each family, and gray density plots show the distribution of D values obtained by randomly removing the number of species in the family 500 times.