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BAYRON RAFAEL CALLE RENDÓN

EFEITO DA PAISAGEM SOBRE OS MAMÍFEROS NEOTROPICAIS NA ESCALA CONTINENTAL E REGIONAL: IDENTIFICANDO ÁREAS PRIORITÁRIAS PARA SUA CONSERVAÇÃO COM ENFOQUE EM PRIMATAS

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Dedico à Angélica e ao *Orejas*, que estiveram sempre ao meu lado.

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“Eu, não sou eu, pelo menos não
sou o mesmo eu interior.”
Ché

PREFÁCIO

Em 2007, pela primeira vez, pisei na Amazônia no meu país de origem: a Colômbia. Mas foi em 2016, perto do encontro do mar com o grande rio Amazonas, que conheci o Amapá. Ali aprendi que a Amazônia não era apenas uma extensão interminável de floresta, mas também tinha ecossistemas de savana ao longo de toda a região.

As savanas do Amapá estão dentro do estado brasileiro com maior porcentagem de áreas protegidas, contudo, apenas uma pequena porção desse ecossistema está dentro de unidades de conservação. Devido ao avanço da agricultura, algumas áreas de savana estão sendo alteradas na escala de paisagem. Essas alterações não só ameaçam diferentes elementos da biodiversidade como os mamíferos, mas também os serviços que este ecossistema fornece para as populações tradicionais de Quilombolas que por anos têm habitado nessa região.

Para entender melhor a dinâmica ecológica e social das savanas do Amapá foi criado o 'Projeto Guariba AP' em 2017. Este projeto, que nasceu no Laboratório de Ecologia da Universidade Federal do Amapá, usou como espécie bandeira um primata ameaçado, o guariba-de-mãos-ruivas (*Alouatta belzebul*). Graças ao projeto foram desenvolvidas não só pesquisas relacionadas aos primatas (como esta tese), mas também atividades de educação ambiental com crianças e professores de três escolas Quilombolas nos municípios de Santana e Macapá, com o intuito de trocar ideias sobre a biodiversidade das savanas do estado (ver Anexo). Além disso, foi produzido o documentário 'Savanas do Amapá' (ver Anexo) como ferramenta de sensibilização e divulgação.

Curiosamente, o ano da minha chegada ao Amapá, foi o ano em que foi assinado o acordo de paz entre as FARC e o governo da Colômbia. Embora esse importante acontecimento nada tem a ver com minha viagem nesta região do Brasil, eu não quis deixar de lado a oportunidade de entender como esse novo período de paz poderia gerar mudanças ambientais, também na escala de paisagem, que por sua vez poderiam afetar os mamíferos.

Esta tese, que usa informações da região neotropical, do Brasil e da Colômbia, segue o formato proposto pelo Programa de Pós-Graduação em Biodiversidade Tropical (PPGBio) da Universidade Federal do Amapá, seguindo as normas da revista "Ecology" até a Introdução Geral. Depois apresenta quatro artigos que seguem as normas de cada periódico.

O artigo 1, publicado no periódico "Diversity", é uma análise continental do efeito das características da matriz sobre os primatas, usando informações já publicadas sobre comunidades de primatas em fragmentos de floresta do Neotrópico. O artigo 2, submetido no periódico "Biodiversity and Conservation", é uma avaliação do efeito dos atributos da paisagem sobre a comunidade de primatas nas savanas do Amapá. O artigo 3, que será submetido no periódico "Journal of Environmental Planning and Management", usa como estudo de caso as savanas do Amapá para propor uma rede de áreas prioritárias para a conservação dos primatas e do ecossistema de savana. Por fim, o artigo 4, publicado no periódico "Nature Conservation", apresenta como estudo de caso a Colômbia para identificar as espécies de mamíferos mais sensíveis às mudanças ambientais no pós-conflito. Este artigo contou com a participação do "Departamento de Ciencias Forestales" da "Universidad Nacional de Colombia Sede Medellín", minha *Alma Mater*.

RESUMO

Calle-Rendón, Bayron R. Efeito da paisagem sobre os mamíferos neotropicais na escala continental e regional: identificando áreas prioritárias para sua conservação com enfoque em primatas. Macapá, 2020. Tese (Doutorado em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitora de Pesquisa e Pós-Graduação – Universidade Federal do Amapá.

A biodiversidade no mundo tem se debilitado rapidamente enquanto a pressão antrópica sobre os recursos aumenta. Os cenários futuros indicam que biomas como as florestas tropicais e as savanas serão alterados no presente século, principalmente pelas mudanças no uso da terra. Desta forma, as paisagens antrópicas aumentarão, reduzindo as funções ecológicas de alguns ecossistemas e alterando a distribuição de muitas espécies. Vários estudos da região Neotropical já investigaram o efeito dos atributos da paisagem sobre a riqueza e ocorrência de primatas em florestas fragmentadas, tanto na escala continental como em diferentes paisagens. Contudo, pouco se sabe sobre como as características de cada sub-região do Neotrópico afetam os primatas ao longo do continente, como a paisagem e os fatores humanos afetam os primatas em manchas de floresta quando estas ocorrem naturalmente em uma matriz de savana, como a escala do efeito (i.e. a extensão espacial na qual a relação entre um atributo da paisagem e um organismo é mais forte) afeta a relação entre primatas e a paisagem, e quão sensíveis podem ser em geral os mamíferos às mudanças no uso da terra por causa de conflitos armados. Estas informações são importantes para focar os esforços na conservação dos primatas, outros mamíferos e seus habitats. Esta tese tem como objetivos: 1) avaliar o efeito dos atributos da matriz, do fragmento e do ambiente sobre os primatas na região Neotropical (desde o México até o sul do Brasil) e nas sub-regiões Neotropicais; 2) entender a escala do efeito da composição da paisagem sobre os primatas em uma savana amazônica do Brasil no estado do Amapá, onde a paisagem está sendo transformada aceleradamente por causas antrópicas, e avaliar como os atributos da paisagem, características das manchas e fatores humanos afetam os primatas; 3) propor uma rede de áreas prioritárias para conservar tanto os primatas como o ambiente de savana através do Planejamento Sistemático para a Conservação nas Savanas do Amapá; e 4) identificar as espécies de mamíferos mais sensíveis às mudanças no uso da terra e as áreas com maior probabilidade de efeitos negativos sobre os mamíferos na Colômbia. Foi encontrado que na escala continental, a área do fragmento foi mais importante para retenção de primatas do que as características ambientais e da matriz. Ao longo do continente, fragmentos localizados dentro de áreas protegidas incidiram positivamente sobre os primatas. Entretanto, houve diferença na retenção de massa de primatas entre as sub-regiões devido à diferença na composição de espécies. Por outro lado, a avaliação nas savanas mostrou que a escala do efeito não foi diferente entre espécies de primatas, mas entre localidades com diferente composição da matriz. Além disso, os atributos da paisagem foram mais importantes para explicar a ocorrência de espécies, e os fatores humanos mais importantes para explicar a riqueza. Paisagens com matrizes menos permeáveis e com menor quantidade de hábitat proporcionaram um maior risco para manter populações da maioria das espécies. Entretanto, um maior número de pessoas na paisagem teve consequências sobre as comunidades de primatas. Foi gerada uma rede de áreas prioritárias para a conservação usando modelos de distribuição de espécies dos primatas, os tipos de vegetação da savana, e mapas de ameaça à biodiversidade e potencial agrícola. Para atingir as metas de conservação fixadas, seria necessário promover ações encaminhadas à conservação em pelo menos 3.240 km^2 ao longo das Savanas do Amapá. Por fim, foi encontrado que os primatas serão os mamíferos mais sensíveis às mudanças no uso da terra no pós-conflito na Colômbia. Hoje são mais necessários mecanismos de conservação da biodiversidade na escala da paisagem. Porém, é imperativo ir além dos aspectos biológicos e considerar aproximações sócio-ecológicas. Desta forma, tanto primatas humanos como primatas não humanos serão beneficiados pelos serviços da natureza.

Palavras-chave: Amapá; Colômbia; conservação de primatas; escala do efeito; matriz; perda de hábitat; Planejamento Sistemático para a Conservação; pós-conflito; presença humana.

ABSTRACT

Calle-Rendón, Bayron R. Landscape effect on Neotropical mammals at continental and regional scale: identifying priority areas for their conservation focusing on primates. Macapá, 2020. Thesis (Doctorate in Tropical Biodiversity) – Postgraduate Program in Tropical Biodiversity – Research and Postgraduate Dean's Office – Federal University of Amapá.

Worldwide, biodiversity is being threatened and anthropogenic pressure on natural resources is increasing. Biomes such as tropical forests and savannas will be transformed in this century, due mainly to land use changes. Anthropogenic landscapes will increase and ecological functions from many ecosystems and distribution range of several species will be altered. Several studies from the Neotropical region already investigated how landscape attributes affect primate occurrence and species richness in fragmented forests at both regional and landscape scale. However, little is known about how the attributes from each Neotropical sub-region are related to primates at continental scale, how landscape and human factors affect primates when forest fragments are within a natural matrix such as savannas, how the scale of effect (i.e. the spatial extent that maximized the strength of the relationship between landscape and species) affect the relationship between primates and landscape, and which mammal species are the most vulnerable to land use changes in zones of armed conflict. This information is crucial to improve the efforts to conserve primates, other mammal species and their habitats. The objectives of this thesis are: 1) to understand how matrix components, fragment characteristics and environmental factors affect primates in the Neotropical region (from Mexico to southern Brazil) and in the Neotropical sub-regions; 2) to understand the scale of effect of landscape composition on primates in an Amazonian savanna from northern Brazil in the state of Amapá, where anthropogenic pressure is rapidly transforming the landscape, in addition, understand how landscape attributes, patch characteristics, and human factors drive patterns of primate species richness and occurrence; 3) to suggest a network of priority areas to conserve both primates and savanna environment by using a Systematic Conservation Planning approach in the Savannas of Amapá; and 4) to identify both mammal species most sensitive and critical regions where negative effects on mammals are most likely due to land-uses change in Colombia. At continental scale, fragment size was more important for primate retention than matrix components and environmental factors. Moreover, protected fragments positively affected primates than unprotected ones. In addition, there was difference in primate mass retention between sub-regions due to differences in primate composition. In the Amazonian savannas, meanwhile, the scale of effect did not differ between primates, but did between two localities with different matrix composition. In addition, landscape attributes were the most important predictors for primate occurrence, and human factors were the most important predictors for primate richness. Landscapes with a less permeable matrix and lower habitat amount represent a risk to maintain primate populations, and a higher human population in the matrix may negatively affect the primate communities. It was created a map of potential use of the land for agriculture and another of environmental risk in those savannas, and together with species distribution models of each primate species and vegetation types, was identified the network of priority areas. Conservation targets for primates and vegetation types were met by protecting 3,240 km^2 in the savannas. Finally, primates were more vulnerable than other mammal species due to land-use changes in Colombia's post-conflict era. This thesis concludes that it is essential to create a more effective mechanism for biodiversity conservation at landscape level and as such, this must go beyond the biological aspects and needs to integrate a socio-ecological approach. Taking these aspects into consideration, both human and non-human primates will be beneficed by services nature provides.

Key words: Amapá; Colombia; habitat loss; human presence; matrix; post-conflict; primate conservation; scale of effect; Systematic Conservation Planning.

RESUMEN

Calle-Rendón, Bayron R. Efecto del paisaje en los mamíferos Neotropicales a escala continental y regional: identificando áreas prioritarias para su conservación con enfoque en primates. Macapá, 2020. Tesis (Doctorado en Biodiversidad Tropical) – Programa de Postgrado en Biodiversidad Tropical – Decanatura de Investigación y Postgrado – Universidad Federal de Amapá.

En todo el mundo la biodiversidad está siendo amenazada y al mismo tiempo la presión antrópica sobre los recursos aumenta. Los escenarios futuros indican que biomas como los bosques tropicales y las sabanas serán alterados en el presente siglo, debido principalmente a los cambios en el uso del suelo. Como consecuencia, los paisajes antrópicos aumentarán, reduciendo las funciones ecológicas de muchos ecosistemas y alterando el rango de distribución de muchas especies. Diversos estudios realizados en el Neotrópico investigaron el efecto de los atributos del paisaje sobre la riqueza y ocurrencia de primates en bosques fragmentados, tanto a escala continental como en diferentes paisajes. No obstante, se conoce poco sobre cómo las características de cada subregión del Neotrópico afectan a los primates a lo largo de todo el continente, cómo el paisaje y los factores humanos afectan a los primates en manchas de bosque cuando estas ocurren naturalmente en una matriz de sabana, cómo la escala del efecto (i.e. la extensión espacial en la cual la relación entre un atributo del paisaje y un organismo es más fuerte) actúa sobre la relación entre los primates y el paisaje, y cuan sensibles son en general los mamíferos a los cambios en el uso del suelo debido a los conflictos armados. Entender estas relaciones permitiría enfocar los esfuerzos para la conservación de los primates, otros mamíferos, y sus hábitats. Los objetivos de esta tesis son: 1) evaluar cómo los atributos de la matriz, del fragmento y del ambiente afectan a los primates en la región Neotropical (desde México hasta el sur del Brasil) y en las subregiones; 2) entender cómo actúa la escala del efecto de la composición del paisaje sobre los primates en una sabana amazónica del norte del Brasil (estado de Amapá), donde el paisaje está siendo transformado de manera acelerada por causas antrópicas; adicionalmente, evaluar cómo los atributos del paisaje, las características del fragmento y los factores humanos afectan a los primates; 3) proponer una red de áreas prioritarias para la conservación de los primates y el ambiente de sabana, a través del uso de la Planificación Sistemática para la Conservación en las Sabanas de Amapá; y 4) identificar las especies de mamíferos más sensibles a los cambios en el uso del suelo y las áreas con mayor probabilidad de efectos negativos sobre los mamíferos en Colombia. Se encontró que a escala continental, el área del fragmento fue más importante para la retención de primates, mientras que las características ambientales y de la matriz fueron menos importantes. A lo largo de todo el continente, los fragmentos al interior de áreas protegidas incidieron positivamente sobre los primates. También, hubo diferencia de la retención de masa de primates entre subregiones debido a la diferencia en la composición de especies. Por otra parte, la evaluación en las sabanas dio como resultado que no hubo diferencia de la escala del efecto entre las especies de primates, pero sí la hubo entre localidades con diferente composición de la matriz. Adicionalmente, los atributos del paisaje fueron más importantes para explicar la ocurrencia de especies, mientras que los factores humanos lo fueron para la riqueza de *especies. Paisajes con matrices menos permeables y con menor cantidad de hábitat ofrecieron mayor riesgo para las poblaciones de primates, mientras que paisajes con matrices más pobladas representaron mayor riesgo para las comunidades de primates. Fue generada una red de áreas prioritarias usando modelos de distribución de especies de los primates de la sabana, los tipos de vegetación, y mapas sobre amenazas a la biodiversidad y el potencial de uso agrícola. Para cumplir las metas de conservación establecidas, sería necesario promover acciones encaminadas a la conservación de por lo menos 3.240 km*^{2} *en las Sabanas de Amapá. Finalmente, se encontró que los primates serán más vulnerables que otros mamíferos a los cambios en el uso del suelo en la era del post-conflicto colombiano. Hoy son más necesarios mecanismo de conservación de la biodiversidad a escala de paisaje; no obstante, es importante ir más allá de los aspectos biológicos y considerar aproximaciones socio ecológicas. De esta manera, primates humanos y primates no humanos serán beneficiados por los servicios de la naturaleza.*

Palabras clave: Amapá; Colombia; conservación de primates; escala del efecto; matriz; pérdida de hábitat; Planificación Sistemática para la Conservación; post-conflicto; presencia humana.

SUMÁRIO

1. INTRODUÇÃO

O planeta enfrenta a sexta extinção em massa e mecanismos de conservação efetivos são necessários para a conservação da biodiversidade (Barnosky et al. 2011). Alguns indicadores mostram que a biodiversidade no mundo tem se debilitado em uma escala temporal de poucas décadas, enquanto a pressão antrópica sobre os recursos aumenta (Butchart et al. 2010, Dirzo et al. 2014, Anderson and Mammides 2020). Essa pressão, além de afetar os organismos e seus hábitats, reduz as funções ecológicas dos ecossistemas (Chapin III et al. 2000) e, consequentemente, os bens e serviços para a humanidade (Cardinale et al. 2012). Os cenários futuros são críticos e é esperado que biomas como as florestas tropicais e as savanas sejam alterados no presente século, principalmente pelas mudanças no uso da terra (Chapin III et al. 2000, Sala et al. 2000), gerando paisagens antrópicas onde será necessária a coexistência entre as pessoas e a natureza (Melo et al. 2013). Contudo, políticas que apoiam a delimitação de áreas para proteção da biodiversidade e seu uso sustentável surgem como resposta a tais ameaças (Butchart et al. 2010). Dessa forma, é esperado que das paisagens seja ainda possível obter bens e serviços e, inclusive, incorporar um tipo de manejo que abranja tanto aspectos ecológicos como características sociais (Palomo et al. 2014)

1.1. Conceitos chave sobre a escala no nível de região, paisagem e fragmento

A distribuição global da biodiversidade segue padrões dependentes de fatores bióticos e abióticos, os quais apresentam uma variação regional ou de grande escala (Kreft and Jetz 2007, Kissling et al. 2009, Gouveia et al. 2014). Por exemplo, há uma relação positiva entre riqueza de plantas vasculares e precipitação (Kreft and Jetz 2007), portanto, é esperado um maior número de espécies de plantas em regiões mais úmidas (ver exemplo na Fig. 1a). Porém, devido à pressão exercida pelos humanos sobre os recursos naturais em muitas regiões do mundo (Anderson and Mammides 2020), é provável que o padrão de distribuição de muitas espécies dependa de mecanismos que são exercidos em escalas menores.

Devido a causas antrópicas, como o desmatamento e o desenvolvimento de alguns empreendimentos, muitas florestas contínuas estão perdendo extensas áreas ou estão se tornando grandes territórios de floresta fragmentada (Riitters et al. 2000, Curtis et al. 2018). Nesses territórios, os fragmentos de floresta estão localizados em uma matriz composta de elementos diferentes, como campos agrícolas e pecuários, rodovias, povoados e corpos artificiais de água (Anderson et al. 2007, Laurance et al. 2009, Benchimol and Venticinque 2014, Tee et al. 2018). Entender os padrões de distribuição das espécies nesses territórios antrópicos na escala da paisagem é vital para propor mecanismos com o intuito de manejar, tanto o território como as espécies que ali habitam (Fahrig and Merriam 1994, Arroyo-Rodríguez and Fahrig 2014).

Pensar em uma escala de paisagem é pensar em uma área de grande tamanho (ou paisagem) espacialmente heterogênea dentro de uma região determinada, e com distintos tipos de coberturas ou elementos em proporções diferentes (i.e. composição da paisagem) (Arroyo-Rodríguez et al. 2019). Por sua vez, as coberturas estão organizadas de certa forma que confere características especiais a essas áreas (i.e. configuração da paisagem) (Fig. 1b) (Arroyo-Rodríguez et al. 2019). Para o primeiro caso, uma paisagem poderia ser composta essencialmente por fragmentos de floresta (i.e. hábitat) de diferentes tamanhos, rodeados por uma matriz (i.e. o que não é hábitat) de pastagens para a criação de gado, na qual há também presença de árvores isoladas que podem atuar como *stepping stones* (Fig. 1b). Para o segundo caso, tanto a quantidade de fragmentos nesta paisagem como a relação entre a quantidade de fragmentos e o tamanho da paisagem denotam um aspecto sobre a configuração dessa paisagem (Fig. 1b) (Arroyo-Rodríguez et al. 2019).

Em estudos de ecologia da paisagem, a escala de estudo depende principalmente do organismo a ser analisado (Brennan et al 2002). Duas espécies podem habitar uma mesma paisagem, mas uma delas pode ser de grande porte (e por sua vez ter uma área de vida grande) e portanto precisará de uma área maior que uma espécie de menor tamanho (Fig. 1b). Embora as escalas de estudo sejam diferentes para ambas as espécies, é necessário definir em qual tamanho de escala de estudo será mais forte o efeito de algum atributo da paisagem sobre a espécie, o que é conhecido como escala do efeito (Arroyo-Rodriguez and Fahrig 2014). Esta escala do efeito significa que há escalas nas quais os elementos que compõem a paisagem podem afetar de forma mais forte as espécies de estudo.

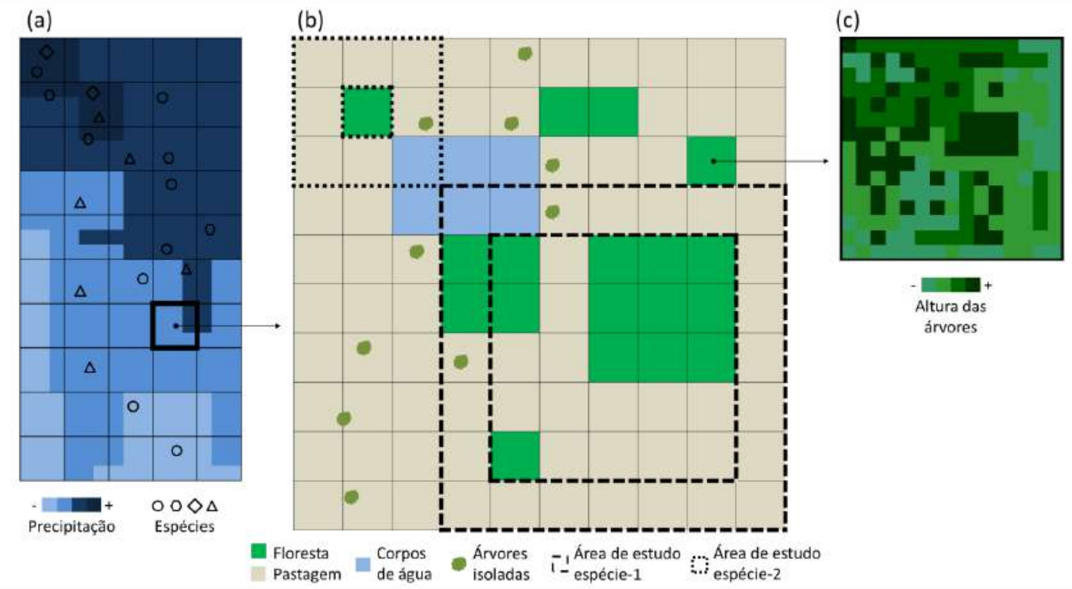

Figura 1 – Escala em diferentes níveis. (a) Região constituída por várias paisagens (quadros) com um padrão de maior riqueza de espécies em áreas de maior precipitação. (b) Paisagem de fragmentos de floresta em uma matriz de pastagem. Cada quadro na paisagem é de área um, indicando que a paisagem toda tem uma área de 100. À respeito da composição da paisagem, a quantidade de floresta é 18, de corpos de água 6, de pastagem 76, e há 10 árvores isoladas. À respeito da configuração da paisagem, o número de fragmentos na paisagem é 6, e a densidade de fragmentos é 6/100 (i.e. #fragmentos/área da paisagem). Note que a escala para avaliar a relação entre a paisagem e a espécie-1 (espécie com maior área de vida) é maior do que a escala usada para o estudo da espécie-2 (espécie com menor área de vida). Porém, a relação entre tais espécies e algum atributo da paisagem dependerá de como a espécie usa a paisagem. Para ambas as espécies, conforme sua área de estudo (linhas tracejadas) é maior, aparecem na paisagem elementos que não estão presentes na paisagem menor (e.g. árvores isoladas e corpos de água). Inclusive, para a espécie-1 a quantidade de habitat aumenta de 12 para 14 conforme aumenta a escala de estudo. (c) Características da escala de fragmento com variação na altura das árvores.

Por outro lado, pensar em uma escala de fragmento significa pensar nas características que são próprias de cada fragmento (Fahrig 2005). Por exemplo, o tamanho de cada fragmento pode ser diferente, a quantidade de borda pode variar conforme varia a área do fragmento, e atributos próprios da estrutura da floresta, como altura das árvores também pode variar (Fig. 1c).

1.2. Biodiversidade: entre a perda e a fragmentação do hábitat

As florestas são reconhecidas por serem uns dos ecossistemas com maior biodiversidade e por estarem associadas a serviços ecossistêmicos relevantes, como regulação hidro climática e sequestro de carbono (Balvanera 2012). Atualmente, as florestas abrangem uma área de 3.999 milhões de hectares no mundo (FAO 2015). Contudo, a superfície florestal está diminuindo a taxas aceleradas (Hansen et al. 2013), provocando não só a desaparecimento de espécies, mas também a redução das funções ecossistêmicas que elas desenvolvem (Haddad et al. 2015).

Durante os dois últimos séculos, a humanidade transformou áreas de floresta em terras agrícolas como parte dos processos de desenvolvimento dos países por meio da perda e da fragmentação do hábitat (FAO 2016). Ambos os processos têm implícita a redução na quantidade de hábitat, contudo, a fragmentação provoca a divisão da área original em diferentes núcleos menores (Fig. 2). Neste último processo, além da diminuição da quantidade de hábitat, o número de blocos de hábitat torna-se maior, podendo variar em tamanho, incrementando o isolamento entre os fragmentos, e aumentando a quantidade de bordas (Fahrig 2003). Nesse sentido, devido ao maior limiar de hábitat no processo de fragmentação, tem sido sugerido que os efeitos negativos da perda de hábitat sobre a biodiversidade são maiores do que os efeitos da fragmentação (Fahrig 2017, Galán-Acedo et al. 2019a). Dessa forma, mesmo como fragmentos de floresta rodeados por matrizes, as florestas continuam sendo elementos essenciais para a manutenção da biodiversidade em muitas paisagens antrópicas (Galán-Acedo et al. 2019b).

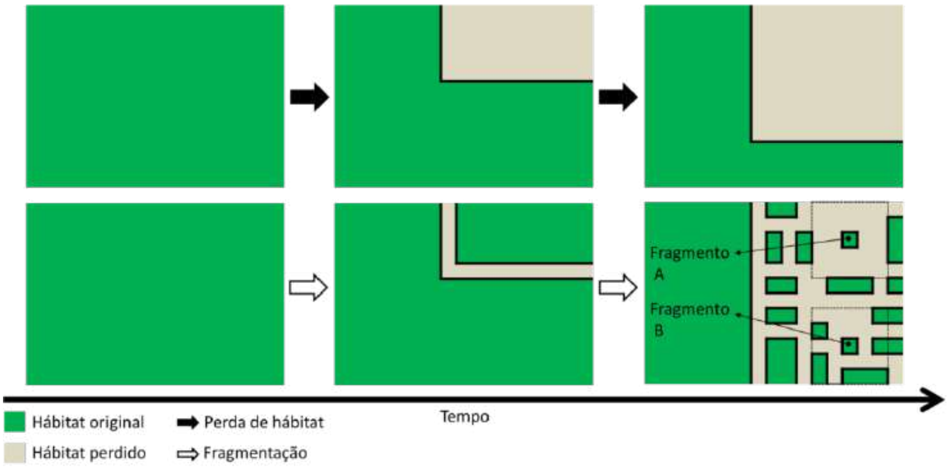

Figura 2 – Processos de perda e de fragmentação do hábitat através do tempo. A fragmentação aumenta as bordas (linhas contínuas em cada fragmento), o número de fragmentos, e o isolamento. Note que no processo final de fragmentação, a quantidade de hábitat diminui até deixar uns fragmentos mais isolados (fragmento A) do que outros (fragmento B), o que pode ser evidenciado pela quantidade de hábitat nos *buffers* (linhas tracejadas) de cada fragmento.

Vários trabalhos evidenciam que a área do fragmento influencia a presença, abundância e riqueza de espécies (Michalski and Peres 2005, Benedick et al. 2006, Arroyo-Rodriguez et al. 2008, Boyle and Smith 2010a, Benchimol and Venticinque 2014, Bregman et al. 2014, da Silva et al. 2015, Almeida-Gomes et al. 2016, Puig-Lagunes et al. 2016, Carretero-Pinzón et al. 2017, Carretero-Pinzón 2018). À respeito desta última variável, a teoria da biogeografia de ilhas (MacArthur and Wilson 1967) diz que o número de espécies que ocorre em uma ilha é o resultado do balanço entre imigração e extinção, parâmetros que vão depender do tamanho da ilha (fragmento) e da distância ao continente (hábitat contínuo). Porém, existe outro mecanismo que explica que a riqueza de espécies não depende em si da área do fragmento, mas da quantidade de hábitat na paisagem, o qual é conhecido como hipótese da quantidade de hábitat (Fahrig 2013). O conceito anterior significa que um fragmento de pouca área poderia ter um número alto de espécies, sempre que o fragmento tiver outras áreas florestais por perto, e que a matriz seja suficientemente permeável para que as espécies consigam trocar de um fragmento para outro. Este processo de troca entre fragmentos ocorre porque muitas espécies não desenvolvem as suas atividades estritamente dentro dos fragmentos de floresta, mas também usam ou complementam as suas atividades se deslocando pela matriz e aproveitando alguns recursos disponíveis (Galán-Acedo et al. 2019b), processo que é conhecido como suplementação da paisagem (Arroyo-Rodriguez et al. 2019). Desta forma, e como consequência da perda de hábitat, a persistência de algumas espécies na paisagem pode depender da sua habilidade para se adaptar a uma nova paisagem.

Espécies de hábitos mais especialistas poderiam ser mais afetadas do que as espécies de hábitos mais generalistas, o que dependerá dos traços de cada espécie. Por exemplo, a sensibilidade das aves à perda de hábitat varia globalmente segundo o grupo funcional ao que pertencem, resultando que uma maior proporção de espécies frugívoras e insetívoras podem desaparecer dos fragmentos conforme sua área é menor (Bregman et al. 2014). Concomitante com a seleção de espécies por causa dos traços, algumas espécies, mesmo que persistam nos fragmentos, podem alterar suas atividades. Por exemplo, o orçamento de tempo que algumas espécies de primatas gastam para desenvolver suas atividades varia segundo a área do fragmento de floresta (Chapman et al. 2007, Cristóbal-Azkarate and Arroyo-Rodríguez 2007, Boyle and Smith 2010b). Além disso, algumas espécies podem mudar seus padrões espaciais e apresentar maior abundância nas bordas do que no interior dos fragmentos (Pardini 2004, Lenz et al. 2014), ocasionando um processo interativo entre os dois ambientes (habitat e matriz) através do efeito de borda, com alterações na dinâmica dos organismos que habitam essas paisagens (Fahrig and Merriam 1994, Murcia 1995).

No processo de fragmentação do hábitat, os fragmentos resultantes não são uniformes em tamanho e quantidade de borda, como consequência, esses fragmentos podem apresentar formas variadas. A relação entre a área e a borda do fragmento pode ser modelada usando equações simples (e.g. Laurance 1991) que dão como resultado valores chamados de índice de forma. Como padrão geral, esses índices tentam saber quão circular ou irregular é um fragmento. Dessa forma, fragmentos mais irregulares podem apresentar um maior efeito de borda que fragmentos menos irregulares ou arredondados (Arroyo-Rodríguez et al. 2008).

O efeito de borda gerado pela transição abrupta entre os elementos diferentes da paisagem pode ter efeitos de três tipos: 1) abióticos, os quais correspondem a mudanças nas características ambientais; 2) biológicos diretos, os quais correspondem a mudanças na composição de espécies em resposta às mudanças abióticas; e 3) biológicos indiretos, os quais correspondem a mudanças por causa da alteração nas interações interespecíficas (Murcia 1995). Estes efeitos podem ser observados facilmente na transição floresta-pastagem ou floresta-rodovia, com algumas consequências negativas ou positivas sobre as interações entre os organismos e o padrão de distribuição das populações (Jules 1998, Bruna 2002, Chalfoun et al. 2002). Nessas bordas, existem marcadas diferenças entre velocidade do vento, temperatura e radiação solar, sendo todas maiores na área aberta (Murcia 1995, Harper 2005, Delgado et al. 2007). Devido à maior radiação, é possível a ocupação de plantas mais demandantes de energia solar, que podem atrair insetos herbívoros que, por sua vez, podem atrair aves insetívoras, fazendo que aumente a quantidade de predadores de ninhos (Murcia 1995, Chalfoun et al. 2002). Dessa forma, as bordas e o tamanho dos fragmentos alteram os padrões de recrutamento de algumas plantas, incidindo diretamente nos padrões demográficos (Jules 1998) e possivelmente nas interações planta-animal (Bruna 2002).

Além das mudanças provocadas pelo efeito de borda, características inerentes da paisagem como o tipo de elementos da matriz e sua localização no espaço podem influenciar a abundância dos organismos (Martensen et al. 2012, Villard and Metzger 2014). As espécies podem se beneficiar de elementos como a cobertura de floresta e *stepping stones*, os quais têm relação com o isolamento e a conectividade (Fahrig 2003). Contudo, seu uso depende em grande medida das adaptações dos organismos para usá-los, pois esses elementos podem oferecer conectividade estrutural e/ou funcional (Tischendorf and Fahrig 2000). Por exemplo, em uma paisagem urbana da Austrália a presença de um marsupial (*Isoodon macrourus*) de hábito generalista foi explicada pela conectividade funcional ao comparar com outros elementos da matriz (FitzGibbon et al. 2007). Embora a espécie seja habilitada para usar atributos estruturalmente diferentes na matriz (i.e. conectividade funcional), estes componentes representam risco de mortalidade, fazem a espécie expressar um padrão de deslocamento diferente ao habitual, e a obrigam atravessar uma borda (Tischendorf and Fahrig 2000). Por outro lado, a quantidade de hábitat contornando o fragmento poderia oferecer conectividade estrutural para o organismo, pois independente da espécie, estas áreas representam condições similares às do fragmento. Porém, em muitas ocasiões a possibilidade de chegar até outro fragmento dependerá do tipo de alteração na matriz e a sua permeabilidade, pois as paisagens têm componentes variados, como corpos de água (principalmente devido à construção de usinas hidrelétricas), campos agrícolas, pastagens, plantações florestais, savanas e rodovias (Brockerhoff et al. 2008, Laurance et al. 2009, Benchimol and Venticinque 2014, da Silva et al. 2015, Borges-Matos et al. 2016) e nesse caso, cada componente da matriz oferece um risco diferente.

Os efeitos das rodovias estão entre os mais destacados por suas consequências negativas sobre a biodiversidade no mundo (Laurance et al. 2009, Laurance et al. 2014, Vilela et al. 2020). Além do efeito de borda, elas podem provocar atropelamentos da fauna (Taylor and Goldingay 2004, do Prado et al. 2006, Baskaran and Boominathan 2010) e incentivar a colonização humana que, por sua vez, incentiva a exploração descontrolada de recursos (Laurance et al. 2009). Adicionalmente, as rodovias constituem junto à construção de povoados humanos, barreiras ao deslocamento de fauna (Develey and Stouffer 2001, Goosem

2001, Blake et al. 2008, Hamilton et al. 2016), fontes que induzem processos de invasão de espécies exóticas (Parendes and Jones 2000, Gavier-Pizarro et al. 2010) e diminuem a diversidade, abundância e riqueza de espécies dentro das paisagens (Friesen 1998, Watkins et al. 2003). No entanto, o tipo e quantidade destes elementos na matriz podem depender da região. Na América do Sul, por exemplo, a região amazônica difere substancialmente de áreas como a Mata Atlântica na densidade de rodovias (Laurance et al. 2014), o que poderia apoiar a ideia de que as mudanças na matriz podem também ter relação com as características da região.

No Neotrópico, regiões como o Chocó Biogeográfico na Colômbia e algumas áreas na Amazônia ainda são consideradas zonas com poucas intervenções humanas, enquanto regiões como a Mata Atlântica e o sul do México, as quais têm processos antigos de ocupação humana, estão mais alteradas (da Fonseca et al. 2004, Rodríguez-Mahecha et al. 2004, Mittermeier et al. 2004, Perz et al. 2005, Haddad et al. 2015). Nesse caso, não só o tempo que leva ocupada uma área, mas também o número de pessoas nessas áreas pode ter um efeito variado sobre a biodiversidade, o que leva a considerar que fatores humanos também podem intervir na forma como as espécies são distribuídas em uma paisagem.

1.3. Efeito de alguns fatores humanos na biodiversidade

A correlação entre densidade de pessoas e riqueza de espécies é dependente da escala (Urquiza-Haas et al. 2009). Quando avaliada em uma escala grande, há uma correlação positiva, porém, quando avaliada em uma escala menor a correlação é negativa (Thompson and Jones 1999, Luck 2007ab, Urquiza-Haas et al. 2009). No primeiro caso, as pessoas tendem a se localizar em áreas de maior quantidade de recursos e produtividade, o que significa se localizar em áreas onde há maior número de espécies (Luck 2007a). Para o segundo caso, quanto maior o número de pessoas, algumas atividades como desmatamento surgem, provocando impactos diretos sobre a biodiversidade (Laurance et al. 2002).

Além de densidade humana, outros determinantes são usados para avaliar o efeito de fatores humanos sobre a perda de biodiversidade na escala de paisagem. Por exemplo, em paisagens da Amazônia e do México foi usada a distância até cidades como proxy de pressão humana (Michalski and Peres 2005, Arroyo-Rodríguez et al. 2008, Silvestre et al. 2020). Nestes casos, quando os fragmentos de floresta estão localizados mais perto de cidades, tanto a ocorrência de primatas como a riqueza de carnívoros e primatas é menor (Michalski and Peres 2005, Arroyo-Rodríguez et al. 2008), e quando localidades rurais estão mais perto das cidades, as pessoas aumentam a frequência de caça (Silvestre et al. 2020). De fato, a caça é um dos principais determinantes da diminuição da abundância de muitas espécies de mamíferos (Naranjo and Bodmer 2007, Urquiza-Haas et al. 2009, Zapata-Ríos et al. 2009), contudo, este processo pode afetar de forma diferencial às espécies, sendo os primatas um dos grupos mais afetados (Gonzalez-Kirchner and Maza 1998, Zapata-Ríos et al. 2009, Parathian and Maldonado 2010, Mesquita and Barreto 2015).

1.4. Primatas em paisagens fragmentadas

Hoje são reconhecidas 504 espécies de primatas no mundo, das quais 33,9% estão no Neotrópico (171 espécies), 22% na África (111 espécies), 20,4% em Madagascar (103 espécies), e 23,6% na Ásia (119 espécies). Em cada um dos continentes as espécies estão distribuídas com um padrão comum, sendo maior a riqueza perto da Linha do Equador. Adicionalmente, 55% das espécies de primatas no mundo estão ameaçadas de extinção e 75% têm populações em declínio (Fig. 3) (Estrada et al. 2017).

Os primatas representam entre 25 e 40% da biomassa dos frugívoros nas florestas tropicais (Chapman 1995). Eles desenvolvem diferentes funções ecológicas, como dispersão de sementes, polinização, e transporte de nutrientes (Wrangham et al. 1994, Dew and Wright 1998, Andresen 1999, Stevenson 2000, Poulsen et al. 2001, Andresen 2002, McConkey et al. 2002, Knogge and Heymann 2003, Wehncke et al. 2004, Link and Di Fiore 2006, Stevenson and Guzmán-Caro 2010, Heymann 2011, Barnett et al. 2012, Bufalo et al. 2016). Além disso, estão associados à manutenção da riqueza de espécies de plantas com sementes grandes nas florestas (Barrera et al. 2008, Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Stevenson 2011, Effiom et al. 2013, Calle-Rendón et al. 2016) sendo que sua ausência pode induzir à formação de florestas menos diversas e diminuir os estoques de carbono (Peres et al. 2016, Gardner et al. 2019).

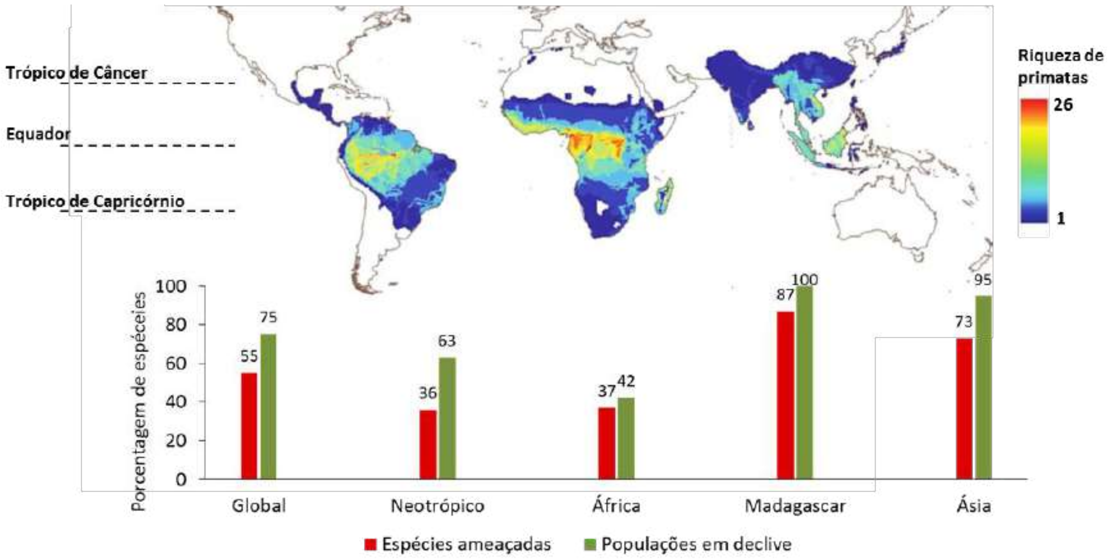

Figura 3 – Distribuição global da riqueza de primatas e porcentagem de espécies ameaçadas e de populações em declínio. Adaptado de Estrada et al. (2017).

Os primatas têm importância variada para as populações humanas (Mittermeir 1987). Algumas espécies têm valor devido a aspectos culturais, ao uso como medicina e animais de estimação, e por aspectos relacionados a mitos, folclore e religião (Cormier 2006, Parathian and Maldonado 2010, Fuentes 2012). Por outro lado, muitas espécies, especialmente as de grande porte, são importantes devido ao consumo de carne em diferentes regiões (Peres 1990, Gonzalez-Kirchner and Maza 1998, Fa et al. 2000, de Thoisy et al. 2005). Esta última razão constitui uma ameaça para muitas populações de primatas, tendo como resultado a diminuição do tamanho populacional de algumas espécies e chegando a representar ameaça de extinção da espécie como um todo.

Além da caça para o consumo, outras ameaças vêm se acentuando rapidamente, como as mudanças climáticas (Graham et al. 2016), conflitos armados (Kanyamibwa 1998, Glew and Hudson 2007), e a perda de hábitat (Galán-Acedo et al. 2019a). Previsões indicam que no presente século a expansão agrícola terá sobreposição com 68% das áreas habitadas por primatas no mundo e 75% das espécies serão afetadas, sendo os maiores conflitos em regiões como a Mata Atlântica no Brasil, os Andes centrais na América do Sul, o Caribe na Colômbia, a África Subsaariana, e o sudeste Asiático (Fig. 4) (Estrada et al. 2017).

Algumas avaliações continentais mostram certos padrões da distribuição de primatas que dependem tanto de variáveis ambientais como das características do hábitat. Globalmente, a riqueza de primatas está correlacionada com a altura da floresta (Gouveia et al. 2014), mas ao nível continental esse padrão é mantido apenas para o Neotrópico, África e Madagascar, pois na Ásia é a precipitação que tem a maior influencia na distribuição das espécies (Gouveia et al. 2014). Similarmente, a riqueza global de primatas incrementa quando a área dos fragmentos é maior (Harcourt and Doherty 2005), da mesma forma incrementa a riqueza em fragmentos do Neotrópico e Madagascar (Harcourt and Doherty 2005, Benchimol and Peres 2013), mas não em fragmentos da África (Harcourt and Doherty 2005). Os padrões globais e continentais mostram também que algumas características específicas das espécies tem relação com o tamanho mínimo do fragmento onde os primatas habitam (Gibbons and Harcourt 2009). Por exemplo, os primatas têm maior probabilidade de ocorrer em fragmentos pequenos quanto mais tipos de habitat a espécie use, e quanto maior seja a quantidade de itens na dieta (Gibbons and Harcourt 2009).

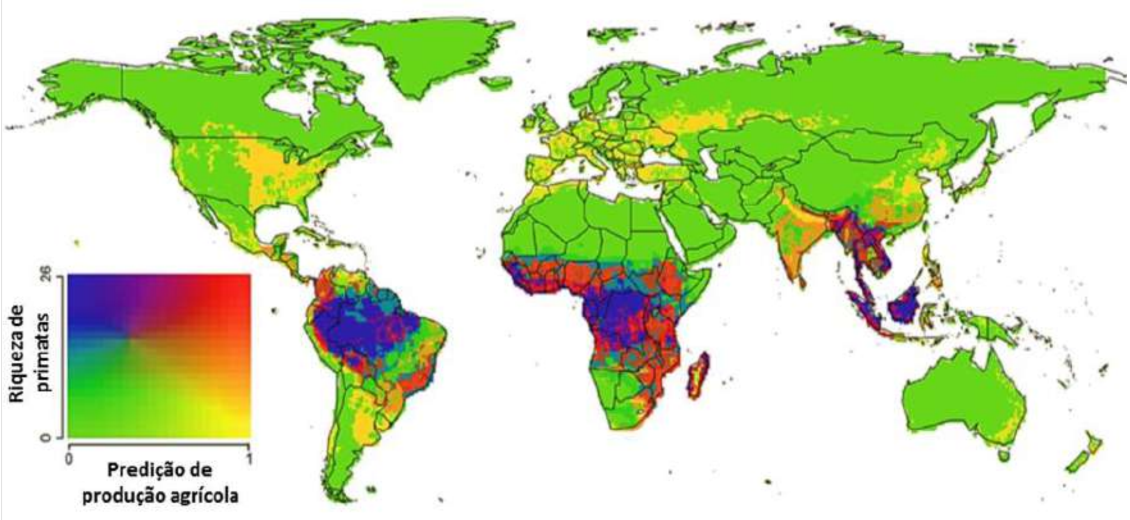

Figura 4 – Padrão global de predição da expansão agrícola nas regiões habitadas por primatas no século XXI. As áreas vermelhas indicam sobreposição entre áreas de expansão agrícola e áreas de alta riqueza de primatas. Áreas azuis indicam zonas de pouco conflito. Adaptado de Estrada et al. (2017).

Os padrões dependentes da área do fragmento também são observados em escalas menores. Como padrão geral em diferentes paisagens da Amazônia brasileira, a riqueza, abundância e ocorrência de espécies aumentam com o tamanho do fragmento (Michalski and Peres 2005, Boyle and Smith 2010a, Benchimol and Venticinque 2014). Similarmente, a ocorrência de primatas é maior conforme a área do fragmento é maior em uma paisagem no *Hotspot* da Mata Atlântica no Brasil (da Silva et al. 2015) e em uma paisagem do México (Arroyo-Rodríguez et al. 2008).

A área do fragmento tem uma influência além da exercida nos padrões de diversidade e ocupação de primatas. Por exemplo, a diminuição do tamanho do fragmento tem um efeito negativo na diversidade genética, e tem um efeito positivo na densidade populacional, prevalência de parasitas e no tempo gasto para se alimentar. Adicionalmente, a redução no tamanho do fragmento deixa menos suscetível à infestação de parasitas as espécies solitárias e de pequeno porte, e contrariamente, mais suscetíveis à infestação de parasitas as espécies de outras estruturas sociais e de grande e médio porte (Carretero-Pinzón et al. 2016).

Por outro lado, fragmentos de formas mais irregulares afetam negativamente a ocorrência e a estrutura populacional de alguns primatas (Arroyo-Rodríguez et al. 2008, Puig-Lagunes et al. 2016). Devido ao efeito de borda gerado pela forma desses fragmentos, a estrutura e composição da vegetação nessas bordas são alteradas (Laurance et al. 1998, Laurance et al. 2006, Liu et al. 2019), como consequência as espécies de primatas podem ser beneficiadas ou não. Por exemplo, primatas do gênero *Alouatta*, os quais têm alta proporção de folhas na sua dieta, podem apresentar maior abundância nas bordas de fragmentos e margens de rios (Peres 1997, Lenz et al. 2014). Entretanto, *Ateles paniscus*, com alta proporção de frutos na sua dieta, apresenta maior abundância no interior dos fragmentos (Lenz et al. 2014).

Na escala da paisagem, entretanto, a quantidade de hábitat (usada como medida de conectividade) e a densidade de fragmentos (usada como medida de fragmentação) têm relação positiva com a riqueza, abundância e ocupação por primatas em paisagens da região de Los Tuxtlas no México (Arroyo-Rodriguez et al. 2008) e de Los Llanos na Colômbia (Carretero-Pinzón et al. 2017, Carretero-Pinzón 2018). Também no México, a cobertura de floresta tem uma relação positiva com o sucesso reprodutivo de *Ateles geoffroyi*, e a permeabilidade da matriz com sua abundância relativa, porém essas relações dependeram da região de estudo, pois tinham diferenças no grau de alteração (Galán-Acedo et al. 2019c).

Não apenas as diferenças no grau de alteração entre paisagens incidem em como os primatas são afetados pelas características da paisagem (Galán-Acedo et al. 2018, Galán-Acedo et al. 2019c), mas também as diferenças da escala na qual a relação primatas-paisagem é estudada (Carretero-Pinzón et al. 2017, Galán-Acedo et al. 2018, Galán-Acedo et al. 2019c, Gestich et al. 2019). Por exemplo, em fragmentos de floresta de uma paisagem da Mata Atlântica, a relação entre a densidade de *Callicebus nigrifrons* e cobertura de floresta, e riqueza de espécies e cobertura de floresta, foi mais forte em um tamanho de paisagem determinada (i.e. uma escala determinada, 28,3 km^2), enquanto em escalas menores a relação foi menos forte (Gestich et al. 2019). Dessa forma, é importante não apenas a seleção de variáveis da paisagem de importância biológica para os primatas como cobertura de floresta, mas também uma escala adequada para o estudo (Arroyo-Rodríguez and Fahrig 2014). Além disso, algumas hipóteses sugerem que as características das espécies, como seu tamanho, área de vida, distância de dispersão, entre outras, podem influenciar a escala do efeito entre uma espécie e alguma característica da paisagem (Miguet et al. 2016).

Por outro lado, embora a relação entre primatas e determinantes de pressão antrópica tem sido pouco estudada, é conhecido que a distância até culturas ou povoados afeta a ocorrência de primatas em paisagens do México e da Amazônia (Michalski and Peres 2005, Arroyo-Rodríguez et al. 2008, Puig-Lagunes et al. 2016). Nesta última região, primatas com maior proporção de frutos na dieta e maior área de vida são menos comuns nos fragmentos (Boyle and Smith 2010a). Por outro lado, primatas com maior tamanho corporal apresentaram maior ocupação de fragmentos em outra paisagem amazônica (Benchimol and Venticinque 2014). Neste ultimo caso, os fragmentos estavam no meio de uma matriz de água devido à construção de uma usina hidrelétrica, pelo que foi sugerido que os primatas maiores tinham mais probabilidade de atravessar essa matriz nadando do que os primatas menores. Adicionalmente, o estudo indica que inclusive matrizes pouco permeáveis como corpos de água não impedem aos primatas trocar de fragmento. De fato, muitas espécies podem usar elementos da matriz através da suplementação da paisagem (Galán-Acedo et al. 2019b).

Em algumas paisagens, os fragmentos de floresta não são produto de intervenções antrópicas, mas de fatores naturais que têm deixado as áreas de floresta imersas em uma matriz também produto de fatores naturais como as savanas (Kankam and Sicotte 2013, Wallace et al. 2013, Carretero-Pinzón 2013). Por exemplo, tanto na África como no Neotrópico, estudos avaliaram os padrões de ocupação e riqueza de espécies de primatas em fragmentos florestais rodeados por savanas (Kankam and Sicotte 2013, Carretero-Pinzón et al. 2017, Carretero-Pinzón 2018) usando os métodos implementados na avaliação de paisagens fragmentadas. Contudo, ainda são necessários mais estudos para conhecer o estado das comunidades de primatas nessas paisagens, principalmente diante de alterações antrópicas na matriz de savana.

1.5. Paisagem de savana no Amapá

Uma porcentagem alta da população humana está distribuída em ecossistemas de savanas tropicais (Scholes and Archer 1997). Estes ecossistemas estão constituídos por manchas de floresta em uma matriz de savana que é caracterizada por uma vegetação mais espalhada e de menor altura (Furley 1999). A região de Los Llanos na Colômbia e Venezuela, e o bioma Cerrado na Bolívia, Paraguai e Brasil representam os maiores ecossistemas de savanas do Neotrópico (Carvalho and Mustin 2017). Porém, também existem outras savanas Neotropicais de menor extensão na região amazônica (Carvalho and Mustin 2017).

As savanas amazônicas estão altamente ameaçadas e são pouco conhecidas (Carvalho and Mustin 2017). Estes ecossistemas estão distribuídos principalmente na Bolívia, Brasil, Guiana, Venezuela e Suriname, e representam uma extensão aproximada de 267.164 km^2, (Carvalho and Mustin 2017). Porém, esse valor não inclui outras savanas amazônicas menores presentes na Colômbia (Llanos del Yarí) e Guiana Francesa (savanas amazônicas da Guiana Francesa) (Menéndez et al. 2012, Stier et al. 2020), de modo que a extensão total das savanas amazônicas é ainda maior.

O Brasil abriga perto de 112.961 km^2 de savanas amazônicas, dos quais 13.000 km^2 estão no estado do Amapá, no extremo nordeste da região amazônica (Carvalho and Mustin 2017). As Savanas do Amapá cobrem aproximadamente 7,2% do estado e são caraterizadas por quatro diferentes tipos de vegetação com variação na composição e número de espécies: savana arborizada, savana florestada, savana gramíneo lenhosa, e savana parque (Mustin et al. 2017). Por sua parte, estas savanas apresentam alto número de espécies de plantas (378 espécies), invertebrados (350 espécies), aves (200 espécies), peixes (26 espécies), anfíbios (41 espécies) e mamíferos não voadores (70 espécies), incluindo várias espécies de primatas (Mustin et al. 2017).

No Amapá ocorrem naturalmente dez espécies de primatas (da Silva et al. 2013) e oito delas estão presentes na área de savana: *Alouatta belzebul*, *Alouatta macconnelli*, *Sapajus apella apella*, *Cebus olivaceus*, *Saimiri sciureus sciureus*, *Pithecia pithecia*, *Saguinus midas* e *Aotus azarae infulatus*. A menor destas espécies é *S. midas* e a maior é *A. belzebul* (Tabela 1), sendo esta última a única espécie de primata das savanas atualmente ameaçada (Vulnerável, Valença-Montenegro et al. 2019). Esta espécie em particular é endêmica do Brasil, sendo sua distribuição restrita apenas a três áreas: uma no Nordeste onde a espécie sobrevive em poucos fragmentos florestais, na margem sul do rio Amazonas na zona chamada de "arco de desmatamento", e na margem norte do mesmo rio no estado do Amapá (Fig. 5) (Valença-Montenegro et al. 2019). Com relação às outras espécies de primatas presentes nas savanas (excluindo *A. azarae infulatus*), suas áreas de distribuição chegam até as Guianas (Fig. 5). Além de *A. belzebul*, existem outras espécies de mamíferos ameaçados nas Savanas do Amapá, como o tamanduá-bandeira (*Myrmecophaga tridactyla*, Vulnerável), o tatu-canastra (*Priodontes maximus*, Vulnerável), a ariranha (*Pteronura brasiliensis*, Em Perigo), a queixada (*Tayassu pecari*, Vulnerável) e a anta (*Tapirus terrestris*, Vulnerável) (da Silva et al. 2013).

Tabela 1 – Espécies de primatas presentes nas Savanas do Amapá e suas características. À respeito da dieta, é apresentado o principal item.

Família	**Espécie**	**Dieta**	**Densidade (indivíduos/km^2)**	**Massa (kg)**	**Área de vida (ha)**
Callitrichidae	*Saguinus midas*	Insetívoro[a]	2 – 30[h]	0,56[m]	35[n]
Aotidae	*Aotus azarae infulatus*	Frugívoro[b]	8,9 – 64[b]	1,21[m]	7[m]
Pitheciidae	*Pithecia pithecia*	Predador de sementes[a]	1 – 13[i]	1,76[m]	9[o]
Cebidae	*Saimiri sciureus sciureus*	Insetívoro, frugívoro[a c]	16 – 528[j]	0,82[m]	153[p]
	Cebus olivaceus	Omnívoro[d]	2 – 19[k]	2,88[m]	270[d]
	Sapajus apella apella	Omnívoro[e]	15 – 55[l]	30,1[m]	320[e]
Atelidae	*Alouatta belzebul*	Frugívoro, folívoro[f g]	Sem informação	6,40[m]	11[g q]
	Alouatta macconnelli	Frugívoro, folívoro[a]	Sem informação	6,37[m]	18[r]

[a]Mittermeier and Roosmalen (1981) [b]Rímoli et al. (2018) [c]Lima and Ferrari (2003) [d]Miller (1996) [e]Zhang (1995) [f]Julliot and Sabatier (1993) [g]Pinto et al. (2003) [h]Snowdon and Soini (1988) [i]Buchanan et al. (1981) [j]Baldwin and Baldwin (1981) [k]Pontes (1999) [l]Freese and Oppenheimer (1981) [m]Galán-Acedo et al. (2019d) [n]Day and Elwood (1999) [o]Oliveira et al. (1985) [p]Defler (2010) [q]Bonvicino (1989) [r]Boubli (2008)

As Savanas do Amapá são habitadas principalmente por colonos e populações tradicionais de Quilombolas (Mustin et al. 2017). Na atualidade, 138 Quilombos estão localizados dentro das savanas (Hilário et al. 2017). Estas populações subsistem da criação de búfalos, pesca e cultivos de mandioca. Além disso, ao longo das savanas são usados produtos como madeira e palmeiras, principalmente açaí (*Euterpe oleracea*) e bacaba (*Oenocarpus* sp.) (Lima 2003). Também a caça é relevante, principalmente perto das cidades (Dias et al. 2014, Silvestre et al. 2020). Além disso, são desenvolvidas algumas atividades de mineração, principalmente de extração de ferro e brita (Governo do Estado do Amapá et al. 2016).

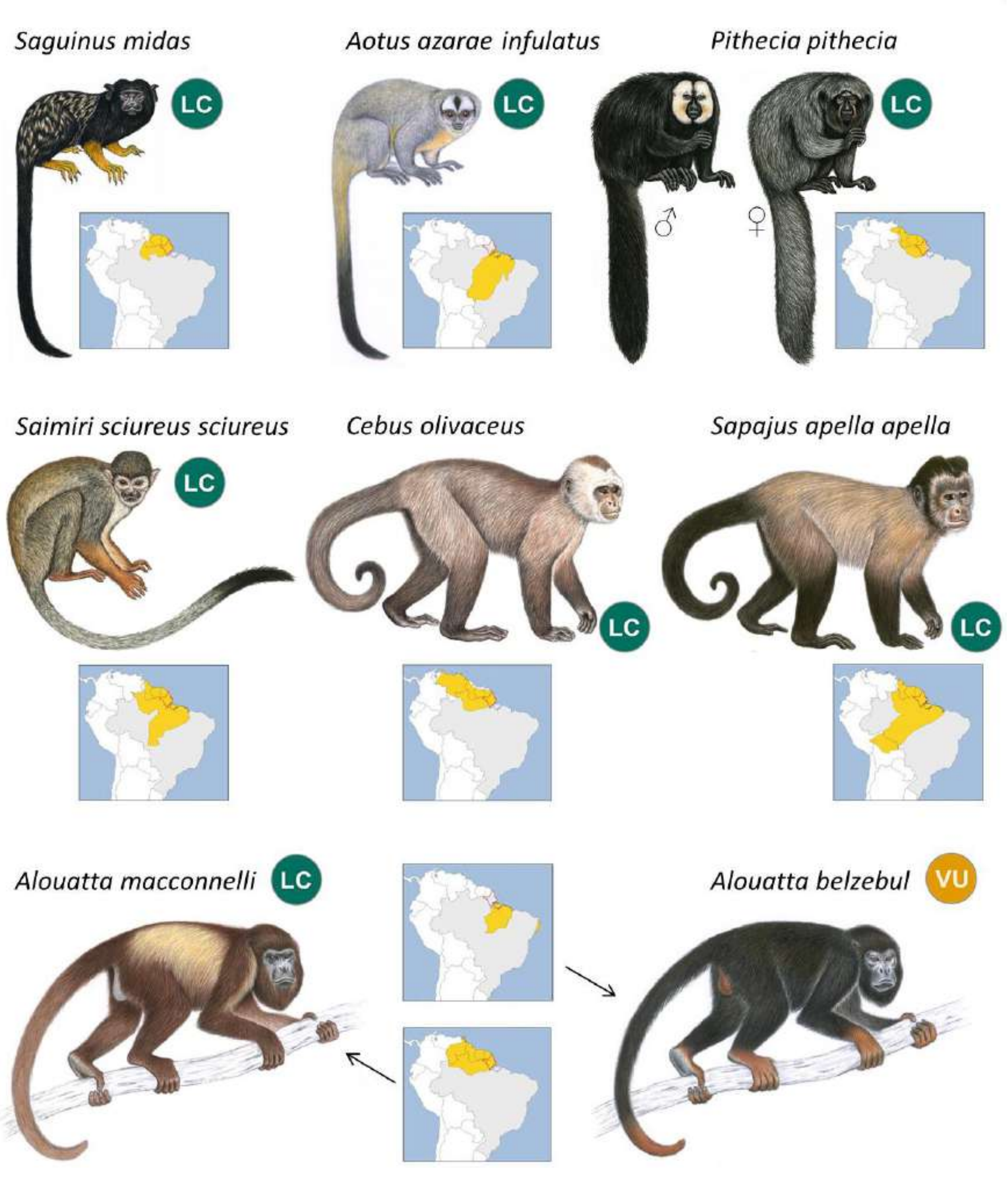

Figura 5 – Espécies de primatas presentes nas Savanas do Amapá, distribuição e risco de extinção (VU-*Vulnerable* [Vulnerável]; LC-*Least Concern* [Preocupação Menor]). As distribuições (em cor amarela dentro de cada mapa) foram obtidas da IUCN (2020), excluindo *C. olivaceus*, que foi obtida de Martins-Junior et al. (2018). Ilustrações de primatas realizadas por Stephen D. Nash e obtidas de Sousa et al. (2008).

As Savanas do Amapá historicamente têm sido ocupadas por plantações de eucalipto (Lima 2003) e atualmente há forte interesse pela produção agrícola de soja (Hilário et al. 2017). A expansão desta última cultura aumentou mais de 100% entre os anos 2013 e 2015, passando de 4.550 até 11.365 ha (IBGE 2017), inclusive no interior de unidades de conservação (Carvalho and Mustin 2017).

Apesar do Amapá ter 19 unidades de conservação, há pouca representatividade destas nas savanas (Drumond et al. 2008, Mustin et al. 2017). Nesse sentido, devido ao crescimento agrícola nas savanas do estado, à presença de fauna ameaçada e pouca representatividade destes ecossistemas em unidades de conservação com categorias mais restritas, faz-se necessário criar novas áreas para a preservação da biodiversidade nessas paisagens.

1.6. Planejamento Sistemático para a Conservação: uma ferramenta para definir áreas prioritárias para a conservação

Há suficiente evidência que sugere que a alteração do hábitat afeta negativamente os primatas (Michalski and Peres 2005, Arroyo-Rodríguez et al. 2008, Boyle and Smith 2010a, Benchimol and Venticinque 2014, da Silva et al. 2015, Puig-Lagunes et al. 2016, Carretero-Pinzón et al. 2017, Galán-Acedo et al. 2019a). Nesse sentido, o planejamento e a gestão são necessários para a proteção dos fragmentos de floresta habitados por primatas, inclusive, a proteção de manchas naturais de floresta onde muitas pressões são exercidas desde a matriz.

Uma das alternativas de proteção da biodiversidade no mundo são as áreas protegidas (Gray et al. 2016). Elas contribuem para diminuir a perda de hábitat florestal, assegurar maior abundância e riqueza de espécies, e diminuir a pegada humana (Geldmann et al. 2013, Gray et al. 2016, Anderson and Mammides 2020). Na atualidade, 15,2% da superfície terrestre estão dentro de alguma área protegida (UNEP-WCMC et al. 2020). Esta proporção está próxima da meta Aichi-11, a qual indica que deveriam ser protegidos pelo menos 17% do território terrestre do planeta (UNEP-WCMC et al. 2018). Contudo, essa meta poderia ser insuficiente, pois a previsão de expansão de áreas agrícolas sugere que seria necessário usar metas maiores (Pouzols et al. 2014). Além disso, ainda existem dúvidas sobre a eficiência das áreas protegidas na proteção de algumas espécies, ecossistemas e serviços ambientais, pois nem sempre as áreas são localizadas nos lugares de maior representatividade (Margules and Pressey 2000, Jenkins and Joppa 2009, Durán et al. 2013, Márquez et al. 2017).

O Brasil é o país com a maior rede de áreas protegidas no mundo (incluindo também terras de populações tradicionais e zonas militares), representando mais de 250 milhões de hectares que correspondem a 29,42% do território (Vieira et al. 2019). Contudo, 19,44% das áreas federais do país estão localizadas em sítios que são considerados como não prioritários (Fendrich et al. 2019). Embora a proporção do território protegido do Brasil tenha aumentado nas últimas duas décadas, houve uma tendência para localizar as novas áreas em ambientes com determinadas características como zonas de baixa intensidade de uso e alta inclinação, e em proporções desiguais entre os diferentes biomas (Vieira et al. 2019). Além disso, a distribuição de cada espécie dentro das áreas protegidas parece ser insuficiente e tem-se deixado fora das áreas espécies endêmicas (Oliveira et al. 2017).

Como opção para o desenho de áreas protegidas e avaliação da sua efetividade, é usado o Planejamento Sistemático para a Conservação (SCP em inglês) (Gutiérrez-Moreno et al. 2008, Pinto and Grelle 2009, Heiner et al. 2011, Lessmann et al. 2014). O SCP oferece um método sistemático para selecionar, desenhar e manejar áreas protegidas (Possingham et al. 2013) obtendo maior amplitude e eficiência. Dentro do processo é importante também inserir outros conceitos chave como a disposição no espaço, flexibilidade, complementariedade, não-substituição, representatividade, idoneidade, e optimização (ver detalhes destes conceitos em Wilson et al. 2013). Para implementar o SCP é necessário realizar oito passos: 1) identificar os atores, 2) definir os objetivos de conservação, 3) localizar espacialmente os objetivos de conservação, 4) definir metas de conservação, 5) identificar áreas atuais e vazios na proteção, 6) selecionar a área a proteger, 7) implementar as ações de conservação, e 8) fazer manutenção e monitoramento (Margules and Pressey 2000, Possingham et al. 2013).

A localização de uma nova área protegida deve considerar algumas limitações sobre onde essas novas áreas deveriam ser localizadas, como aptidão para agricultura (Brandon et al. 2005), densidade de população humana (Pinto and Grelle 2011), impacto ambiental e risco para a biodiversidade (Lessmann et al. 2014), ou indicadores econômicos sobre o custo de manejo e custo de oportunidade (Lessmann et al. 2019). Por sua parte, algumas dessas variáveis podem ser usadas como proxy do contexto socioeconômico com o intuito de minimizar conflitos entre gestores das áreas protegidas e populações locais. Além disso, o estabelecimento de novas áreas protegidas deve considerar o contexto social e econômico do lugar, desta forma é possível obter não só resultados positivos em termos de conservação da biodiversidade, mas também benefícios para as populações locais envolvidas nas novas áreas protegidas (Barrow and Murphree 2001).

No entanto, existem outras possibilidades para a proteção da biodiversidade quando o estabelecimento de áreas protegidas não é desejado (IUCN 2019). O anterior é possível devido a que comunidades locais podem conduzir atividades de conservação nas suas terras, mesmo sem serem áreas protegidas. Também, porque as comunidades locais, mesmo que não tiverem como objetivo levar ações de conservação, desenvolvem atividades de manejo que indiretamente produzem benefícios para o ambiente (IUCN 2019). De fato, há evidencia sobre o importante papel que desempenham as terras comunitárias na proteção da biodiversidade (Garnett et al. 2018; Leiper et al. 2018; Tran et al. 2020). Dessa forma, uma conservação participativa, que envolva tanto terras comunitárias como áreas protegidas, pode gerar melhores resultados na conservação da biodiversidade (Oldekop et al. 2016, Palomo et al. 2014).

A evidência sugere que as áreas protegidas estabilizam as populações de primatas (Rovero et al. 2015). Inclusive, diferentes aproximações sobre SCP têm usado primatas como objetos de conservação (Pinto and Grelle 2011, González 2015, Carretero-Pinzón 2016). Além dos serviços ecossistêmicos que eles desenvolvem (Chapman et al. 2013, Estrada et al. 2017. Andresen et al. 2018), a diversidade de primatas está correlacionada com a diversidade de outros mamíferos (Emmons 1999, Muldoon and Goodman 2015). Dessa forma, o uso de primatas em SCP pode ser uma alternativa para uma conservação mais abrangente da biodiversidade. Porém, é necessário o trabalho com comunidades locais para perpetuar não só a proteção dos primatas, mas também outras espécies e os habitats associados às espécies

(Savage et al. 2010, Franquesa-Soler et al. 2020). Assim, o SCP representa uma ferramenta que pode ser usada em áreas como as Savanas do Amapá. Nesses ecossistemas as mudanças no uso da terra estão se agravando em uma escala da paisagem. Além disso, tanto espécies ameaçadas como comunidades locais precisam dos bens gerados pelo ambiente para subsistir, sendo necessário o manejo sustentável das savanas para a proteção da biodiversidade e perpetuidade de serviços ecossistêmicos.

1.7. A conservação em áreas de conflitos armados

Existem áreas (além das áreas protegidas e terras comunitárias) que exercem um papel de conservação mesmo que a conservação *per se* não seja um dos objetivos (IUCN 2019). As terras militares, por exemplo, são usadas para defender territórios, porém, devido às restrições impostas nessas áreas, essas terras acabam desenvolvendo um papel importante na conservação da biodiversidade (IUCN 2019). Inclusive, terras ocupadas por grupos armados ilegais têm sido consideradas também como áreas nas quais a conservação da biodiversidade tem sido atingida, principalmente devido às restrições impostas por esses grupos para novos empreendimentos (Negret et al. 2017). Assim, essas áreas onde os objetivos são relacionados apenas a questões bélicas acabam desenvolvendo uma conservação acessória (ou chamada de *ancillary conservation* em inglês) com efeitos positivos na biodiversidade (IUCN 2019). Porém, a relação entre biodiversidade e conflitos armados é mais complexa e também pode gerar efeitos contrários (Suarez et al. 2018).

A interação entre biodiversidade e conflito armado depende das diferentes etapas segundo os três estágios do conflito: 1) preparação para o conflito; 2) conflito ou guerra; e 3) pós-conflito (Machlis and Hanson 2008). No primeiro estágio, o estabelecimento de bases militares pode não só oferecer proteção para algumas áreas e espécies, mas também pode provocar efeitos negativos diretos no habitat como poluição e mortalidade de fauna (Hanson 2018). No conflito ou guerra, algumas zonas podem ser abandonadas por populações humanas e pode começar um processo de sucessão natural (Sánchez-Cuervo and Mitchel 2013), porém, atividades ilegais como mineração, caça e narcotráfico, as quais financiam grupos armados ilegais, (Glew and Hudson 2007, Dávalos et al. 2011, Sánchez-Cuervo and Mitchel 2013), e atividades como confrontos armados, nos quais são usadas armas de alto poder de destruição, afetam o ambiente (Lawrence et al. 2015). Já no pós-conflito, surge como uma oportunidade a inclusão de atividades de conservação da biodiversidade, especialmente com as pessoas que estiveram envolvidas no conflito (Baptiste et al. 2017, Negret et al. 2017, Hanson 2018). No entanto, o pós-conflito traz também problemas associados com desmatamento, e aumento da caça e de incêndios nas áreas que eram antigamente ocupadas por grupos armados (Loucks et al. 2009, Armenteras et al. 2019, Clerici et al. 2020).

Um dos exemplos melhor conhecidos sobre o efeito negativo do conflito armado na biodiversidade no estágio de conflito ou guerra é o documentado em Ruanda e a República Democrática do Congo com os gorilas, o maior de todos os primatas (Kanyamibwa 1998, Glew and Hudson 2007). Durante os confrontos armados, muitos indivíduos de gorila-de-grauer (*Gorilla beringei graueri*) e gorila-das-montanhas (*Gorilla berengei berengei*) foram exterminados, inclusive, dentro de áreas protegidas (Glew and Hudson 2007). A respeito do pós-conflito, um dos efeitos negativos mais comuns é o desmatamento, o qual tem sido evidenciado na África (Angola, Burundi, Libéria, Ruanda, e Serra Leoa), na Europa (Bósnia e

Herzegovina) e na América Latina (El Salvador) (Suarez et al. 2018). Esta perda de hábitat no pós-conflito é principalmente por causa da ineficácia no planejamento do uso da terra, o retorno das populações humanas que abandonaram diversas regiões, a demanda de terras para agricultura, as economias extrativistas, e as práticas agrícolas que não são sustentáveis (Suarez et al. 2018). Concomitantemente com a perda de hábitat por causa do pós-conflito, também há diminuição na abundância de algumas espécies de fauna, especialmente de espécies de grande porte, como foi reportado na Camboja para os elefantes-asiáticos (*Elephas maximus*) e duas espécies de veados (*Rucervus eldii* e *Axis porcinus*) (Loucks et al. 2009).

Nos últimos trinta anos houve diferentes acordos de paz no mundo, o que tem causado novos estágios de pós-conflito (Suarez et al. 2018). Muitas dessas zonas de pós-conflito estão em países com *Hotspots* de biodiversidade, por exemplo, a zona de Florestas Afromontanas (Burundi, acordo de paz em 2008; e Ruanda, acordo de paz em 1993), a zona de Florestas da Guiné (Libéria, acordo de paz em 2003; e Serra Leoa, acordo de paz em 2000), a Bacia do Mediterrâneo (Bósnia e Herzegovina, acordo de paz em 1995), e a Mesoamérica (El Salvador, acordo de paz em 1992) (Hanson et al. 2009, Suarez et al. 2018). Um dos exemplos mais recentes é o pós-conflito na Colômbia (Gobierno Nacional and FARC-EP 2016). Este país é reconhecido por apresentar alta diversidade biológica (Andrade-C 2011), ter presença de dois *Hotspost* de biodiversidade (Chocó-Darién, e Andes Tropicais) (Myers et al. 2000), e por ter aproximadamente um terço do seu território em uma região chave como o bioma amazônico (FAO and ITTO 2011).

1.8. O conflito armado da Colômbia e sua relação com a biodiversidade

A Colômbia vem vivendo um período de guerra interna há mais de meio século entre guerrilhas de esquerda contra o governo e grupos paramilitares de direita (Consejería Presidencial para los Derechos Humanos 2015). Os grupos de guerrilha tiveram origem nas zonas rurais como grupos de defesa agrários (Offstein and Aristizábal 2003). Os grupos paramilitares, entretanto, surgiram para combater as guerrilhas e têm sido ajudados por empresários, fazendeiros, e inclusive, o próprio governo através das forças armadas e políticos (Rivera 2007). O conflito interno da Colômbia tem deixado um número alarmante de óbitos, pessoas desaparecidas, e famílias inteiras deslocadas forçosamente das suas terras ou do país (ver detalhes em Consejería Presidencial para los Derechos Humanos 2015).

Apesar do conflito armado da Colômbia ser antigo, apenas no presente século começaram surgir estudos avaliando o efeito do conflito armado sobre a biodiversidade (e.g. Dávalos 2001). Esta relação conflito-biodiversidade tem dependido do contexto econômico e social, e tem variado a diferentes escalas (Dávalos 2001, Dávalos et al. 2011, Sánchez-Cuervo and Mitchel 2013). À escala de bioma (ver Fig. 6), o desmatamento entre os anos 2001 e 2010 no bioma Llanos aumentou nas áreas onde houve maior deslocamento forçado de pessoas, e gerou extensas áreas de agricultura mecanizada (Sánchez-Cuervo and Mitchel 2013). Já à escala de eco-região (ver Fig. 6), a eco-região Vale do Rio Cauca teve um aumento da cobertura de floresta relacionada à maior presença de grupos paramilitares, e a eco-região Andes do Norte teve uma diminuição da cobertura de floresta, também associada à presença de grupos paramilitares (Sánchez-Cuervo and Mitchel 2013). Nesta primeira eco-região (Vale do Rio Cauca), a presença dos paramilitares poderia ter influenciado o estabelecimento de plantações florestais, e na segunda eco-região (Andes do Norte), esses grupos foram associados com atividades de mineração (Sánchez-Cuervo and Mitchel 2013).

Em outras áreas como a eco-região Magdalena-Urabá (Fig. 6), o conflito armado forçou centenas de pessoas a abandonarem as terras e começou um processo de sucessão ecológica até muitas terras se tornarem floresta secundária (Sánchez-Cuervo and Mitchel 2013). Entretanto, em outras áreas como a Serra de San Lucas no extremo norte dos Andes (Fig. 6), as guerrilhas impuseram restrições para evitar o desmatamento, a caça e a mineração, tanto para comunidades locais como para pessoas de outras regiões (Dávalos 2001). De fato, embora alguns grupos de guerrilha forçaram muitas pessoas a abandonarem algumas terras no país, a presença destes grupos não teve relação com o desmatamento na escala de bioma nem na escala de eco-região (Sánchez-Cuervo and Mitchel 2013).

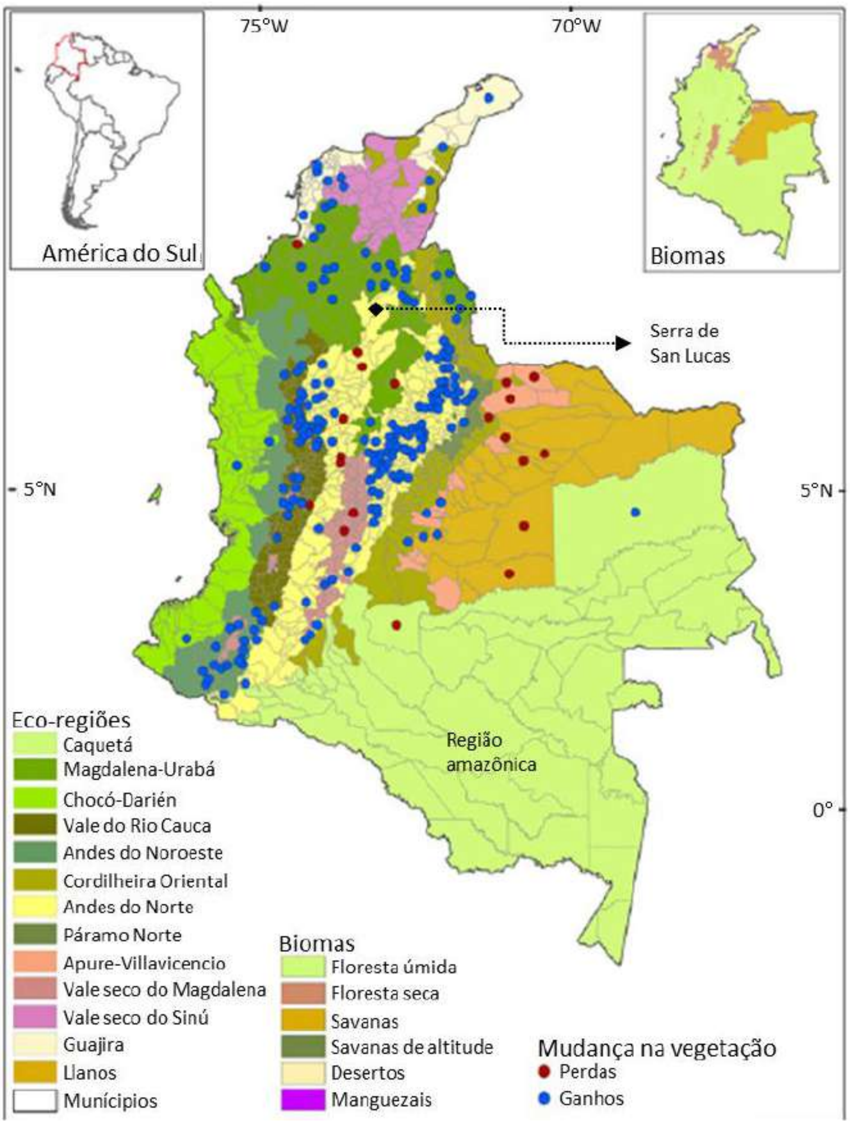

Figura 6 – Biomas e eco-regiões da Colômbia. Os pontos em cada município representam as perdas (em cor vermelha) e ganhos (em cor azul) de vegetação entre os anos 2001 e 2010. Adaptado de Sánchez-Cuervo and Mitchel (2013).

Outra causa de desmatamento associada ao conflito armado tem a ver com o narcotráfico (Dávalos et al. 2011). Em algumas regiões da Colômbia muitas comunidades rurais subsistem cultivando plantas de coca (*Erythroxylum* sp.) para a produção de cocaína (Suárez 2017), o que está associado à presença de grupos armados ilegais tanto de direita como de esquerda (Consejería Presidencial para los Derechos Humanos 2015). No sul do país (região amazônica, Fig. 6), por exemplo, a probabilidade de desmatamento foi maior conforme aumentou a proporção de cultivos de coca na paisagem (Dávalos et al. 2011). Desta forma, o conflito armado da Colômbia tem ocasionado tanto efeitos negativos como positivos na biodiversidade. Estes últimos efeitos têm contribuído para conservar algumas áreas através de uma conservação acessória (*ancillary conservation*), mas devido à dinâmica política do país, esta forma de proteção indireta pode ser alterada.

Após mais de 50 anos de conflito armado entre o governo da Colômbia e a guerrilha das FARC (Forças Armadas Revolucionarias da Colômbia), em 2016 foi assinado um acordo de Paz (Gobierno Nacional and FARC-EP 2016). O Acordo inclui uma reforma agrária com o intuito de fazer uma distribuição das terras produtivas entre as comunidades rurais, incluindo tanto as vítimas do conflito como os ex-combatentes (Gobierno Nacional and FARC-EP 2016).

Embora no estágio de conflito ou guerra da Colômbia tem sido avaliado o efeito do conflito sobre a biodiversidade (principalmente sobre a cobertura de floresta), o efeito do conflito sobre outros elementos da biodiversidade como os mamíferos é desconhecido. A Colômbia tem 518 espécies de mamíferos (Ramírez-Chaves et al. 2016), incluindo 38 espécies e 45 sub-espécies de primatas (APC 2020). Apesar dos efeitos das coberturas do solo sobre os mamíferos, incluindo primatas, terem sido estudados (Marsh et al. 2016, Carretero-Pinzón et al. 2017, Pardo et al. 2018, Borón et a. 2019), são pouco conhecidos os efeitos do conflito sobre suas populações na Colômbia. Esta relação é especialmente importante no estágio de pós-conflito, pois são esperadas mudanças ambientais (e.g. desmatamento) e sociais (e.g. retorno de pessoas que abandonaram as suas terras) (Baptiste et al. 2017, Negret et al. 2017). Além disso, existe pouca representatividade de espécies de vertebrados ameaçadas e endêmicas dentro das áreas protegidas do país (Forero-Medina and Joppa 2010). Assim, é importante identificar as espécies de mamíferos que seriam mais susceptíveis no pós-conflito e as áreas onde poderia haver maiores efeitos negativos sobre suas populações.

Esta tese pretende, primeiramente, avaliar o efeito dos atributos da matriz, do fragmento e do ambiente sobre os primatas na região Neotropical (desde o México até o sul do Brasil) e em algumas sub-regiões Neotropicais (Mesoamérica, Caribe, Tumbes-Chocó-Magdalena, Llanos, Amazônia, Cerrado, Mata Atlântica e Chaco). Além disso, busca entender a escala do efeito da composição da paisagem sobre os primatas nas Savanas do Amapá, e avaliar como os atributos da paisagem, características das manchas e fatores humanos afetam os primatas nessa savana. Por fim, usa dois estudos de caso para identificar tanto áreas como espécies prioritárias para a conservação. O primeiro estudo de caso são as Savanas do Amapá, onde será proposta uma rede de áreas prioritárias para conservar tanto os primatas como o ambiente de savana através do Planejamento Sistemático para a Conservação. O segundo estudo de caso é a Colômbia, onde serão identificados tanto os mamíferos mais sensíveis ao pós-conflito, como as regiões do país onde os efeitos negativos serão mais fortes sobre suas populações.

2. HIPÓTESES

À respeito de como a comunidade de primatas, através da riqueza de espécies e dos traços funcionais, responde aos componentes da matriz, às características do fragmento e aos fatores ambientais na região Neotropical e nas sub-regiões, espera-se que:

- A retenção de espécies, especialmente de primatas de grande porte, será menor em fragmentos de floresta de menor área e rodeados por matrizes que representam maior risco, como infraestrutura e maior densidade de rodovias, devido principalmente a menores tamanhos de população das espécies e baixo fluxo gênico (Oklander et al. 2010, Chaves et al. 2011).
- Espécies de primatas que apresentam alta proporção de partes vegetativas das plantas na sua dieta persistirão nos fragmentos devido à plasticidade da dieta e maior disponibilidade desse item alimentar nos fragmentos de floresta (Benchimol and Peres 2014).
- Espécies de primatas que apresentam alta proporção de presas na sua dieta persistirão nos fragmentos, pois os invertebrados podem se beneficiar dos distúrbios na matriz (Gascon et al. 1999, Uehara-Prado et al. 2009).
- A retenção de espécies de primatas que apresentam alta proporção de partes reprodutivas das plantas na sua dieta declinará conforme diminui a área do fragmento, pois primatas de grande porte e com dietas frugívoras (e.g. *Ateles* spp.) são mais propensos a extinções locais (Boyle and Smith 2010a).
- A persistência de espécies será diferente entre sub-regiões do Neotrópico devido às diferenças na composição de espécies e condições ambientais (Lehman and Fleagle, 2006).
- Em fragmentos dentro de áreas protegidas a retenção de espécies será maior, pois as áreas protegidas podem assegurar a persistência de espécies (Carrillo et al. 2000, Rovero et al. 2015).

Com referência a como opera a escala do efeito (i.e. "a extensão espacial dentro da qual a paisagem afeta uma população", Arroyo-Rodriguez and Fahrig 2014) na relação entre a paisagem e os primatas, e quais são os efeitos dos atributos de composição da paisagem, características das manchas e fatores humanos sobre a comunidade de primatas em uma paisagem de savana amazônica, espera-se que:

- A escala do efeito será maior para espécies com área de vida grande, pois essas espécies interagem com o ambiente em escalas espaciais maiores (Miguet et al. 2016, Galán-Acedo et al. 2018).
- A escala do efeito será maior em áreas de menor distúrbio, pois os movimentos dos primatas são constrangidos por causa das alterações na matriz e os primatas são obrigados a usar apenas os recursos das manchas (Galán-Acedo et al. 2018).
- Tanto a cobertura de floresta como de savana estarão relacionadas positivamente à riqueza e ocorrência de primatas, pois a floresta é o hábitat dos primatas e as savanas podem ser mais permeáveis do que corpos de água (e.g. rios e áreas alagadas) e cobertura antrópica (áreas urbanas, rodovias e campos agrícolas) para a dispersão dos

primatas (Benchimol and Peres 2013, Carretero-Pinzón 2013, Garmendia et al. 2013, Carretero-Pinzón et al. 2017).

- A distância até o bloco de floresta contínua estará negativamente relacionada à ocorrência e riqueza de primatas, pois essas áreas atuam como fonte de espécies (Lawes et al. 2000, Naranjo and Bodmer 2007).
- Manchas de floresta de maior área e maior altura das árvores terão maior riqueza e ocorrência de primatas, pois maior altura da floresta permite uma segregação vertical do nicho e manchas maiores representam maior disponibilidade de recursos (Benchimol and Peres 2014, Gouveia et al. 2014).
- Manchas de formas mais irregulares apresentarão maior ocorrência de espécies com alta proporção de artrópodes na dieta devido ao maior efeito de borda dessas manchas (Murcia 1995).
- Em áreas de maior densidade de população humana, tanto riqueza como ocorrência de primatas serão menores devido à pressão exercida pelas populações humanas sobre os recursos (Laurance et al. 2002, Urquiza-Haas et al. 2009).
- Em áreas mais perto da cidade, tanto riqueza como ocorrência de espécies de grande porte serão menores, pois a frequência de caça é maior perto das cidades e as manchas podem ter maior distúrbio (Michalski and Peres 2005, Silvestre et al. 2020).

Por outro lado, para o primeiro estudo de caso, espera-se que com o uso de primatas como objetos de conservação, será possível identificar áreas prioritárias para a conservação, não só de primatas, mas também de outros elementos da biodiversidade, pois a diversidade de primatas está correlacionada com a diversidade de outros mamíferos (Emmons 1999, Muldoon and Goodman 2015).

Por fim, para o segundo estudo de caso, espera-se que nos municípios da Colômbia onde serão realizadas ações segundo o acordo de paz, haverá mudanças ambientais mais drásticas. Como consequência destas mudanças, os mamíferos nesses municípios (principalmente primatas e ungulados) serão mais afetados do que outras espécies (Gaynor et al. 2016), especialmente por causa de atividades relacionadas às migrações humanas (e.g. caça, degradação do habitat) e à alteração da economia (e.g. demanda de recurso naturais) (Gaynor et al. 2016).

3. OBJETIVOS

3.1. Objetivo geral

Avaliar o efeito dos atributos da paisagem e do fragmento sobre os primatas neotropicais, tanto na escala continental como em uma paisagem de savana amazônica, e usar como estudo de caso a paisagem das Savanas do Amapá como modelo para identificar áreas prioritárias para a conservação dos primatas através do Planejamento Sistemático para a Conservação, e também, usar como estudo de caso o pós-conflito da Colômbia como modelo para identificar tanto os mamíferos mais sensíveis ao pós-conflito, como as regiões do país onde os efeitos negativos serão mais fortes.

3.2. Objetivos específicos

1) Investigar como a comunidade de primatas através da riqueza de espécies e dos traços funcionais responde aos componentes da matriz, às características do fragmento e aos fatores ambientais na região Neotropical e nas sub-regiões.
2) Entender como opera a escala do efeito na relação entre a paisagem e os primatas, e avaliar o efeito dos atributos de composição da paisagem, características das manchas e fatores humanos sobre a ocorrência e riqueza de primatas em uma paisagem de savana amazônica.
3) Identificar áreas prioritárias para a conservação da comunidade de primatas e os tipos de vegetação das savanas usando o Planejamento Sistemático para a Conservação em uma paisagem de savana amazônica.
4) Identificar tanto as espécies de mamíferos mais sensíveis ao pós-conflito na Colômbia, como as regiões do país onde os efeitos negativos serão mais fortes.

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ARTIGO CIENTÍFICO 1

Effect of site attributes and matrix composition on Neotropical primate species richness and functional traits: a comparison among regions

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diversity

Article

Effect of Site Attributes and Matrix Composition on Neotropical Primate Species Richness and Functional Traits: A Comparison Among Regions

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Abstract: Fragmentation threatens biodiversity and forest-dwelling animals can be especially vulnerable. Neotropical primates inhabit forests and play ecological roles in maintaining forest biodiversity. Currently, many primate communities are restricted to forest fragments. We (1) evaluated the influence of environmental, matrix, and site attributes on species richness and functional traits of primates in the Neotropics; and (2) evaluated the effect of the sub-region on the relationships between primates and environmental, matrix, and site attributes. We conducted literature searches to find published data on primate communities in forest fragments throughout the Neotropics. Each fragment was assigned to 1 of 11 sub-regions: Mesoamerica, Tumbes-Chocó-Magdalena, Caribbean, Orinoco, Amazon, Atlantic Forest, Cerrado, Chaco, Andes, Caatinga, and Pampa. Based on actual and expected species occurrences, we calculated the proportion of primate species retained in the fragments, the mass retained, and dietary items retained considering reproductive and vegetative plant parts and prey. We used linear mixed models to correlate primate variables with environmental, matrix, and site attributes. Fragment area was more important for primate retention than environmental, matrix, and site attributes, with primate retention being higher in larger fragments. Fragment size was positively correlated with all primate variables, except for retention of prey consumption, whose retention decreased as water bodies and density of buildings in the matrix increased. Fragments within protected areas retained larger species than unprotected fragments. The proportion of extant mass retained and vegetative plant parts in the diet were highest in Mesoamerica and lowest in the Atlantic Forest. Conservation planning of Neotropical primates should consider both the differences among sub-regions, forest restoration to increase fragment size, and the creation of new protected areas, even in fragmented landscapes.

Keywords: habitat loss; human presence; matrix; Neotropical sub-regions; primate conservation

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1. Introduction

The Earth is in the midst of the sixth mass extinction, making strategies for effective biodiversity conservation increasingly necessary [1]. As a key threat to biodiversity, deforestation is still increasing around the world, leading to reduced species richness and impaired ecosystem functions [2,3]. Habitat fragmentation leads to forest patches of different sizes surrounded by a matrix composed of anthropogenic components [4–8]. Forest patches with remaining populations can suffer local extinctions, as population size alone may not guarantee long-term viability, and organisms may not have the ability to leave the patch and travel through the matrix to colonize other forested areas [3,9,10]. As moving between patches through the landscape may be necessary to maintain populations, species survival may also depend on matrix permeability [11], which can be driven by inherent factors (e.g., climatic conditions, hunting pressure, and differences in agricultural activities) related to regions that host those animals and matrices [12,13].

Although Neotropical primates are primarily forest-dwelling animals, some species are able to use non-forested environments in the matrix for short periods [14,15]. Therefore, it is necessary to understand how the matrix (i.e., the nonhabitat surrounding the fragment [10]) is related to primate occurrence. Globally, primate species richness is highest in the Neotropical region, with 171 species distributed from Southern Mexico to Northern Argentina [16]. Primates are important components of forest biodiversity as seed dispersers, pollinators, and modifiers of both nutrient cycling and forest structure [17–20]. As such, primates occurrence is correlated with the species richness of understory plants [21]. Additionally, primates are important both culturally and as a food resource for many ethnic groups [22], and their extirpation from forests could be related to the loss of aboveground forest biomass [23]. Currently, 36% of Neotropical primates species are threatened and several species are restricted to fragmented landscapes [16].

Studies from fragmented forests in the Neotropical region have shown that fragment size is the primary correlate of primate species richness, abundance, and occurrence [6,24,25]. Higher connectivity between fragments is also associated with primate occurrence [26,27]. The intensity of human impacts (e.g., wildfires, timber extraction, hunting, roads, and agricultural fields) has negative effects on the occurrence and population structure of primates in Neotropical fragmented landscapes [24,28].

The common response of primates to habitat loss, fragmentation, and degradation is population decline; however, the persistence of primate species in fragmented landscapes can be mediated by their functional traits [16]. Species with smaller home ranges, smaller body sizes, and lower proportions of fruit in their diet are able to occupy smaller fragments [6,25]. Loss of primates with certain traits could have negative consequences for ecological processes, such as seed dispersal [20]. Loss of Atelids (primates with large home ranges, bigger body sizes, and higher proportions of fruit in their diet) in different Neotropical sub-regions has been shown to affect recruitment patterns of large-seeded species in the Amazon [29], Orinoco basin [30], and Chocó-Darién [31].

Natural variation in primate species richness shows marked differences between Neotropical sub-regions and continents [16,32]. Such differences depend on both biotic and abiotic attributes. Forest structure (biotic attribute) is the main driver of primate diversity in the Neotropics, but precipitation (abiotic attribute) is the main driver in Asia [32]. Environmental conditions inherent to each sub-region can influence the economic, social, political, and cultural context, and consequently modify the nature of matrices that surround forest patches that host primate species [12,33].

Therefore, attributes of the regions need to be considered to make robust primate conservation plans. Whereas large-scale studies have assessed the effect of patch size, fragment age, and connectivity on primates across the Neotropics [34–36], at a continental scale, little is known about the effects of matrix attributes such as length of roads and number of human settlements. Attributes such as these have, at least locally, been shown to affect the occurrence of Neotropical large mammals [37,38]. Notwithstanding protected areas being recognized as preserving primate populations locally [39,40], no large-scale evaluation of their effectiveness for primate conservation has been conducted.

In this study, we aimed to investigate how primate communities respond to matrix components (e.g., human settlements and roads) surrounding the forest fragments, site-level attributes (e.g., forest height, net primary productivity, and protection status), and environmental factors (temperature and precipitation), in the Neotropical region and between Neotropical sub-regions. We evaluated the influence of environmental features, matrix components, and site attributes on species richness and functional traits of primates in the Neotropical region, considering the effect of the Neotropical sub-region on the relationships between primates and matrix components and site attributes. We expected that species retention, especially the larger ones, will be lower in small fragments and in those fragments surrounded by matrices that are more hostile to primates (e.g., more infrastructure and higher roads density) due to smaller population sizes and reduced gene flux, leading to genetic deterioration [41,42]. We predicted that primates that consume higher amounts of vegetative plant parts will persist in small fragments due the plasticity in their diet and higher availability of this food item [43]. The same trend may be expected regarding primates that heavily rely on prey, which may benefit from the fact that disturbances in the matrix increase populations of invertebrate prey [44,45]. Retention of reproductive plant part consumption will decline sharply because large-bodied frugivorous primates (e.g., spider monkey) are the first going extinct in small fragments [25]. Finally, we predicted that species persistence will be different among sub-regions due to differences both environmental conditions and species composition, and that fragments within protected areas will retain more species than unprotected fragments.

2. Materials and Methods

2.1. Literature Review

We conducted literature searches in Web of Science, Scopus, Scielo, and Google Scholar to find studies that reported on primate species composition in forest fragments in the Neotropical region. We used three key words ('primates', 'habitat loss', and 'fragmentation') in English, Spanish, and Portuguese in combination with 19 Neotropical primate genera [46]: *Alouatta*, *Aotus*, *Ateles*, *Brachyteles*, *Cacajao*, *Callicebus*, *Callimico*, *Callithrix*, *Cebuella*, *Cebus*, *Chiropotes*, *Lagothrix*, *Leontopithecus*, *Mico*, *Oreonax*, *Pithecia*, *Saguinus*, *Saimiri*, and *Sapajus*.

The initial search returned 3491 studies (journal articles, theses, and technical reports) published from 1960 to September 2016. Firstly, duplicates were removed from the 3491 studies, and then the results were filtered based on title alone and the abstract, discarding papers that were clearly unrelated to the purposes of this study. We also discarded studies that did not present sufficient geographical information to identify precisely each forest fragment. The selected studies included data collected through interviews, surveys and behavioral studies (direct observations), playback [36,43], and camera traps in combination with any other method. Studies that used camera traps alone were discarded because they may miss certain primate species, even when they are located on tree branches [47,48]. We only included in the analysis forest patches and fragments with an area ≤11,570 ha (hereafter, fragments), including both those from anthropogenically-fragmented forest landscapes and naturally patchy landscapes (e.g., savannas) with anthropogenic components in the matrix. This size was chosen since it is the "minimum area of suitable habitat" for the biggest Neotropical primate (*Brachyteles* spp.) [49]. Whenever possible, start and ending years of fieldwork were also recorded for each study. At the end of the selection process, a total of 110 studies were found that reported information regarding the primate communities in 512 forest fragments.

2.2. Geographic Information System (GIS) Analysis

The coordinates of each selected fragment were uploaded into Google Earth Pro (version 7.1.5.1557; Google Inc., Mountain View, CA, USA). If the image available for the fragment was of sufficiently high resolution, then a polygon was drawn around it to quantify its area and perimeter. We also delineated and removed vegetation-free areas inside the fragments to obtain the real area of forest available for the primates. We used the best image available with the date closest to the year in which fieldwork was conducted. We preferred the use of Google Earth Pro instead of other alternatives for measuring forest cover (e.g., Hansen et al. [2]), because this software provides readily available images covering most of the Neotropical region. Google Earth Pro is a tool that has been used in the classification of landscapes in other studies of Neotropical primates [36,50] and landscape analyses in the Neotropics [51].

For each fragment, we calculated a shape index as:

$$shape = \frac{p}{200\left[(\pi A)^{1/2}\right]}, \tag{1}$$

where p is the perimeter in meters and A is the area in hectares [52]. A value of 1 indicates a perfectly circular fragment; the higher the value, the more irregular the shape.

Each forest fragment was assigned to 1 of the following 11 Neotropical sub-regions, following author descriptions from the original studies and shapefiles from the Critical Ecosystem Partnership Fund (CEPF) [53] and the Instituto Brasileiro de Geografia e Estatística (IBGE) [54]: Mesoamerica, Tumbes-Chocó-Magdalena (TCM), Caribbean, Andes, Orinoco, Amazon, Atlantic Forest, Cerrado, Caatinga, Pampa, and Chaco. Amazon and TCM are regions dominated by rainforest, although some areas from Peru and Ecuador present other vegetation (dry forest) [55]. Cerrado, Orinoco, and Pampa are predominately areas of savanna and grasses with some forest patches [27,56,57]. Caribe and Caatinga are areas of dry forest [58,59]. The Andes region is composed of montane forests in elevations above 1,000 m in altitude [60]. Atlantic Forest and Mesoamerica include tropical and subtropical forest [61,62], and elevation and latitude determine the vegetation type. Chaco is a forested area in the center of South America, with both dry and wet areas and a dominant vegetation characterized mostly by deciduous trees and shrubs in the dry season [63].

Two fragments at the northern extreme of the TCM sub-region were classified within the Caribbean sub-region as their features are markedly different from those of the TCM in Colombia in terms of precipitation and vegetation, being significantly drier areas [59]. Seven fragments located between the limits of the Andes and TCM sub-regions in Colombia were classified as TCM as they are along the inter-Andean valley of the Magdalena River and are located below 1,000 m in altitude. Three fragments from Brazil classified as Atlantic Forest by the authors were located in the Cerrado according to the Brazilian biome shapefile [54].

We imported the polygons created in Google Earth into QGIS (version 2.14.8-Essen; QGIS Development Team 2014, Essen, Germany), saved them as a shapefile and re-projected all in WGS84 datum in the Universal Transversal Mercator (UTM) coordinate system. We generated a 1-km buffer from the border of the fragment to characterize the matrix within the buffer, a method that has been used for small mammals and primates in Neotropical studies [7,8,64,65]. We selected this buffer size because it is the mean travel distance in the matrix reported for some Neotropical primates [66–68]. From a landscape perspective, the effect of the matrix considers the fragments size [69]; however, because Neotropical primates are primarily arboreal and non-forested areas outside the fragments are not habitat for them, we preferred a buffer from the fragment perimeter, contrary to a circular buffer as used in the patch-landscape approach [12]. Our objective was to understand how the components beyond the border of the fragment (i.e., where the primates leave the habitat and start a "non-natural" movement) affect the primates.

We exported the buffers to Google Earth Pro and manually classified the areas within the buffer into five types using the 'polygon' tool. We then calculated the percentage of (1) forest vegetation (Ve), as a proxy of functional connectivity since primates can use the non-habitat (matrix), expressing a different movement pattern to arrive to another forest fragment [11]; (2) water bodies (Wa), such as seas, lagoons, and rivers; (3) residential areas (RA), defined as groups of houses forming urban or rural areas; (4) tree and palm plantations (Pl); and (5) non-forested areas (NF) as all those areas without structures of connection for primates. NF specifically included land without vegetation (rocks and beaches) and areas with crops, grass, or savanna. Although some areas such as crops have different effects on primates than open areas because they can serve as source of secondary resources to some primate species [14,15], they are not structures providing connection for Neotropical primates. It is difficult to distinguish those areas using the available images in all the Neotropical regions. We counted the number of isolated individual roofs inside the buffer to calculate the density of buildings (DB) and calculated the length of roads using the 'path' tool to estimate the density of roads (DR). To balance the time taken to conduct the manual classification of the matrix with the number of patches available for the analysis, first, we randomly selected 10 sites per sub-region for classification. For TCM and Chaco, we included all nine fragments that achieved our selection criteria (see below) in each sub-region. For the Atlantic Forest and Mesoamerica, we selected five additional fragments in each sub-region given the larger set of fragments available. For the Amazon, we selected 10 additional fragments considering both the larger set of fragments available and the larger extension of the sub-region. We considered the distribution of the sites throughout the sub-regions to include these additional fragments, selecting those fragments located mostly away from other selected sites. Finally, a total of 97 fragments were included in this study from studies conducted between 2000 and 2016 (Table S1).

We extracted data on other predictors from the center of each forest fragment using raster images. We used a global map of forest height (FH) at a 1 km^2 spatial resolution [70] as a proxy of vertical forest structure [32]. We downloaded net primary productivity (NPP) data at a 1 km^2 spatial resolution from the NASA Earth Observations to represent a measurement of the total amount of carbon dioxide up taken by plants [71]. Because NPP is temporally variable, we used a sequence of raster images of June and December from 2000 to 2010, then we used the sequence to calculate a mean NPP for each fragment over this time period. Finally, we obtained temperature annual range (TAR) and precipitation seasonality (PS) data at ~1 km^2 spatial resolution via WorldClim version 2 [72]. To understand the effect of the reserves on primate communities, we identified if each fragment was within a protected area (PA) according to the information from the study site.

2.3. Primate Variables

We calculated the proportion of extant species retained for each fragment (*sp*) as:

$$sp = sp_{ext} / sp_{max}, \tag{2}$$

where sp_{ext} is the current species richness reported in each fragment and sp_{max} is the maximal species richness expected, considering the natural geographic distribution of all primate species for each fragment [36], based on distributions from the IUCN (International Union for Conservation of Nature, Red List of Threatened Species) [73] and reports from each study. The genus *Aotus* was only included in the calculation of sp_{max} when the study reported its presence, since it is more difficult to detect these nocturnal primates. Introduced or reintroduced primate species were not considered in sp_{max} or sp_{ext}.

Each primate species was also classified according to an updated list of functional classification of ecospecies [74]. Ecospecies are classifications of platyrrhine primates based on functional traits of species that are ecologically equivalent [75]. This classification allows gathering more information about different taxa to understand the primate response to changes in the habitat [43]. We obtained the body mass of each species from the All the World's Primates database [76]. We used the average value of male and female body mass for those species in which the information was provided separated by sex. For those species without information in that database (13%), we used the average body mass of the ecospecies [74]. The proportion of extant mass retained (*M*) was calculated using the following equation:

$$M = \frac{\sum_{i=1}^{n} m_i}{\sum_{j=1}^{N} m_j}, \tag{3}$$

where m_i is the body mass of species *i* considering the current species reported in each fragment (*n*), and m_j is the body mass of the species *j* considering the complete primate assemblage (*N*) according to the natural geographic distribution of primates for each fragment. As such, *M* allows "to examine broad patterns of species deletion across the body size spectrum" [36].

To understand the variation in species responses according to diet, we assessed the proportion of the following items in the diet of each ecospecies [74]: (1) reproductive plant parts ($diet_{RP}$: fruits, seed, and flowers); (2) vegetative plant parts ($diet_{VP}$: leaves and buds); and (3) animal prey ($diet_{Pr}$) (Table S2). First, the contribution of each ecospecies in a dietary category for each fragment (p_{xi}) was calculated as:

$$p_{xi} = \frac{d_{xi}}{\sum_{i=1}^{N} d_{xi}}, \tag{4}$$

where d is the proportion of an item x (RP, VP, or Pr) in the diet of ecospecies i present in each fragment according to the values from Hawes and Peres [74], and N is the maximal number of species found in the fragment. Finally, for each fragment, the proportion of each extant consumption of a dietary item retained ($diet_x$) was calculated as:

$$diet_x = \sum_{i=1}^{n} p_{xi}, \tag{5}$$

where n is the number of species found currently in the fragment and x is the item in a dietary category (RP, VP, or Pr). As the indices related to functional traits used here consider the ecospecies composition, they can provide insights into how the predictor variables operate among the different sub-regions because species composition is different among them.

2.4. Data Analysis

We used an ANOVA to test for significant differences in matrix components (Ve, Wa, RA, DB, Pl, and DR) and fragment size between sub-regions. We used linear mixed-models (LMM) from the package 'nlme' [77] to analyze the influence of environmental variables (TAR and PS), site (FH, ln(NPP), shape, ln(area), and PA) and matrix components ($\text{Ve}^{1/2}$, Wa, RA, DB, Pl, and DR) on the proportion of species retained (sp) and retention of functional traits (M, $diet_{RP}$, $diet_{VP}$, and $diet_{Pr}$) considering forest fragments as sampling units. We used LMM to deal with the possible spatial autocorrelation, controlling for the effect of the sub-region by placing it as a random factor, and using the environmental variables, site attributes, and matrix components as fixed factors to test their effect on the proportion of species retained and the ecological characteristics of primates. Only those fragments with $sp_{max} > 1$ and $sp_{ext} \neq 0$ were included in the analysis. These criteria excluded all fragments from the Pampa sub-region, some from Mesoamerica (El Salvador and the Sumidero canyon in Mexico), all from the Argentinian Chaco, and from the Andes. We used Akaike's information criterion corrected for small samples (AICc) to select the most plausible model for each dependent variable applying the Maximum Likelihood (ML) method in accordance with Zuur et al. [78] and using the package 'MuMIn' [79]. We used a 'Random Intercept Model' instead of a 'Random Intercept and Slope Model' in the LMM [78] due to the large number of explanatory variables and assuming that the rate of the effect of the predictor variables does not change between sub-regions. After, we ran the most parsimonious model applying the restricted maximum likelihood (REML) method [78]. We checked for spatial autocorrelation in the residuals of each most parsimonious model with Moran's I correlograms in the package 'ncf' [80] and detected spatial autocorrelation in all models, at least in the first two distance classes (Figure S1). As such, we then used the 'corr' argument available in the 'nlme' package to create the same models, but adding different classes of spatial correlation structures, such as spherical, exponential, Gaussian, linear, and rational. We used the Akaike's information criterion (AIC) to compare those models applying the ML method. Once the most parsimonious model was chosen (i.e., model with the lowest AIC), we refitted the original model with the spatial correlation structure applying the REML method [78]. Although it was possible to assess the effect of the random factor (i.e., Neotropical sub-region) plus fixed factors (i.e., environmental variables, site attributes and matrix components) on primates using the conditional R^2 in the LMM [81], the 'Random Intercept Model' does not allow detection of shifts in the slope (i.e., interaction of predictors with sub-region). Therefore, we used ANCOVA's to assess such effects using only predictors detected by our most parsimonious models. All analyses were performed in R software, version 3.5.1 [82]. Because some fragments from Mesoamerica did not provide values for the diet of animal prey due to the presence of species that feed exclusively on plant parts (*Alouatta* and *Ateles*), resulting in only three fragments with values for this dependent variable, we excluded Mesoamerica in the model of $diet_{Pr}$. In the final database, all but four studies involved direct observation (Table S1); for that reason, we think that detectability is not a problem here.

3. Results

3.1. *Matrix Differences Among Neotropical Sub-Regions*

The 97 fragments selected from 50 studies were distributed in eight minor sub-regions with at least nine fragments per sub-region (Mesoamerica, Tumbes-Chocó-Magdalena, Caribbean, Orinoco, Amazon, Atlantic Forest, Cerrado, and Chaco) (Figure 1, Tables S1 and S3). In these 97 fragments, size ranged between 0.8 and 8897 ha, and varied equally across sub-regions ($F = 1.43$, p-value = 0.203). The proportion of some matrix components in the 1-km buffer around each fragment differed significantly among sub-regions: forest vegetation ($F = 4.887$, p-value = 0.0001), water bodies ($F = 4.726$, p-value = 0.0001), residential areas ($F = 3.319$, p-value = 0.003), non-forested areas ($F = 7.45$, p-value < 0.0001), density of roads ($F = 5.7$, p-value < 0.0001), and density of buildings ($F = 5.587$, p-value < 0.0001). Specifically, the highest proportion of forest surrounding the fragments was found in the Amazon sub-region. The Amazon also had the greatest proportion of water in the matrix, mainly due to dams. The Cerrado, Orinoco, and Atlantic Forest sub-regions had a greater proportion of plantations in the buffer area, composed of oil palms and eucalyptus. The Cerrado had the highest proportion of residential areas. The Chaco and Atlantic Forest sub-regions had the highest density of roads and houses (Figure S2).

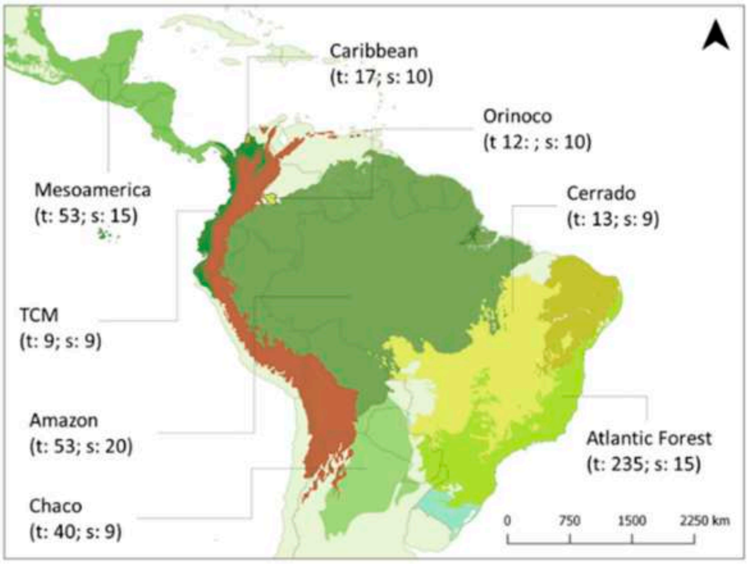

Figure 1. Distribution of the nine sub-regions in the Neotropics, the total number of fragments (t) found in the literature search, and the number of fragments included in our analyses (s) for each sub-region.

3.2. *Effects of Matrix Components, Environmental Conditions, and Site Attributes on Primates*

For species retention and consumption of reproductive parts, the most parsimonious model included only fragment size as predictor, indicating that larger fragments hold a greater proportion of the original assemblages and species with diets composed more heavily of fruits, seeds, and flowers (Table 1). For mass retention, the most parsimonious model included density of buildings, fragment size, and protected areas as predictors (Table 1), indicating that large and protected fragments retain larger species, but increased human presence in the matrix (density of buildings) negatively affects these larger primates (Table 1). The most parsimonious model for consumption of vegetative plant parts indicated a positive effect of fragment size and protected areas (Table 1). Finally, for diets based on animal prey, the best model included density of buildings, fragment shape, and water bodies (Table 1). Thus, retention of animal prey consumption decreased significantly in fragments surrounded by higher proportions of water bodies and increased human presence in the matrix (density of buildings) (Table 1).

Table 1. Results of model selection using linear-mixed models (LMM) explaining the proportion of species retained and ecological characteristics of primates in forest fragments in the Neotropical region through environment, landscape, and fragment attributes. Marginal R^2 values (mR^2) only consider fixed effects, and conditional R^2 (cR^2) includes both fixed and random effects. $\hat{\alpha}$ and $\hat{\beta}$ are the intercept and slope, respectively, of the fixed effects and $\hat{d}$ is the variance for the random intercept.

Model	mR^2	cR^2	$\hat{\alpha}$	Predictors	$\hat{\beta}$	p-Value	$\hat{d}$
sp [a]	0.09	0.12	0.397	Area	0.041	0.0005	0.041
M [b]	0.09	0.17	0.427	Area	0.020	0.040	0.089
				DB	−0.009	0.055	
				PA	0.166	0.019	
$diet_{RP}$ [c]	0.09	0.09	0.364	Area	0.044	0.0008	0.00001
$diet_{VP}$ [b]	0.09	0.28	0.402	Area	0.037	0.001	0.147
				PA	0.121	0.13	
$diet_{Pr}$ [b]	0.12	0.12	0.590	DB	−0.022	0.045	0.000008
				Shape	0.039	0.081	
				Wa	−0.416	0.011	

Note: Primate variables are species retention (sp), mass retention (M), species retention with diet of reproductive parts of the plant ($diet_{RP}$), species retention with diet of vegetative parts of the plant ($diet_{VP}$), species retention with diet of preys ($diet_{Pr}$). Predictors are density of buildings (DB), water (Wa) and protected area (PA). [a] Exponential spatial correlation, [b] Rational quadratic spatial correlation, [c] Spherical spatial correlation.

3.3. *Effect of Sub-Region on the Relationship between Primates and Site and Matrix Attributes*

Results of conditional R^2 indicated that sub-region plus fragment size had an effect on some primate-site relationships (Table 1), although there were no changes in slope detected by the ANCOVA tests. For species and mass retention, and for retention of diets based on vegetative parts, the proportion of variance explained by fragment size and sub-region (conditional R^2) was higher than the proportion of variance explained only by fragment size (marginal R^2) (Table 1). For retention of diets based on reproductive parts of the plant and animal prey, fixed factors explained the same variation as the fixed and random factors together (conditional R^2 = marginal R^2); values of the variance for the random intercept ($\hat{d}$) were close to zero (Table 1). There was variation among sub-regions in the relationship between fragment size and species retention, mass, and diet based on vegetative plant parts, with the highest variation for diet ($\hat{d}$ = 0.147) and lowest for retention of species ($\hat{d}$ = 0.041) (Table 1). As such, for the same fragment size, retention of primate attributes would be highest in Mesoamerica and the Amazon, and lowest in the Atlantic forest and Chaco (Figure 2).

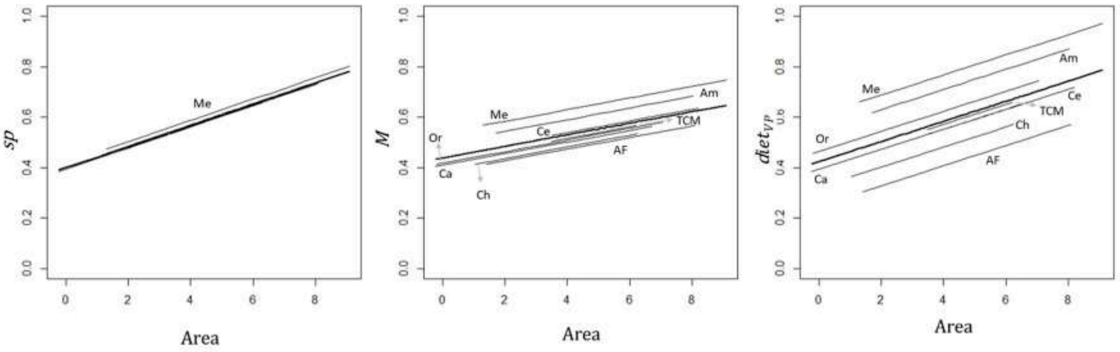

Figure 2. Relationship between species retention (sp), mass retention (M) species retention with diet of vegetative parts of the plant ($diet_{VP}$) and fragment size (ln(area)). Models are based on a 'Random Intercept Model' using LMM. Thick line represents the fixed component and Neotropical sub-regions are Atlantic Forest (AF), Amazonia (Am), Caribbean (Ca), Cerrado (Ce), Chaco (Ch), Mesoamerica (Me), Orinoco (Or), and Tumbes-Chocó-Magdalena (TCM).

4. Discussion

This is the first study to compare how matrix components, including quantitative measures of anthropogenic attributes and environmental conditions, affect the retention of primates in fragmented landscapes across the Neotropical region. Although matrix composition was included as a potential predictor, a clear general pattern emerged, in which fragment size is a key determinant of species persistence and of the retention of traits of Neotropical primates. We found that primate persistence within forest fragments depends on their functional traits and on inherent aspects of the biogeographic sub-regions.

4.1. Relationship Between Matrix and Site Attributes and Primate Species Richness and Functional Traits

Our results show that fragment size was the most important predictor of the retention of primate species in the Neotropical region, which is consistent with previous global and Neotropical analyses for primates and other vertebrates [34,36,83]. Larger areas not only support larger primate populations, but also maintain an adequate forest structure [84]. Larger fragments of tropical forest may provide a greater diversity of food resources, different canopy strata, and shelter to support viable populations of different animal species [85]. Larger fragments host more tree species and more stable availability of food resources through the year [85]. Death of larger trees increases sharply along the fragment edges [86] and smaller trees become more frequent in smaller fragments exposed to chronic edge effects [87]. Therefore, in smaller fragments, resource quantity and quality may change dramatically.

Fragment size also explained a significant part of the retention of functional traits of primates. The higher retention of body mass in larger fragments is consistent with previous studies in the Neotropics [36]. As larger species are more prone to local extinctions [88], we expected this pattern from our results. In forest fragments from the Amazon, body mass predicted the occurrence rate of primates [6], suggesting that larger primates need larger areas. Considering the body size spectrum within the forest fragments [36], the smaller fragments are retaining small-sized primate species, and this could have negative consequences for frugivory and therefore for plant diversity. For example, due to the positive correlation between body mass and percentage of frugivory [74], we think that, independent of the ecospecies present in a certain fragment, fruit consumption will be higher where mass retention is higher. Frugivory has connotations for plant species richness. As such, it is expected that larger fragments will have higher species richness than smaller fragments. This pattern was observed in fragments from the Amazon, where a reduction in species richness of seedling communities was detected in smaller fragments [89]. This makes even more sense, since we also detected a positive relationship between fragment size and retention of consumption of reproductive plant parts (fruits, seeds, and flowers). Those fragments within protected areas can retain larger primate species. Protected areas are recognized by their role in maintaining higher abundance and species richness by diminishing forest loss [90,91], and evidence suggests that reserves maintain stable populations of primates by avoiding hunting [39,40].

We found that persistence of folivorous primates was affected by fragment size in all Neotropical regions. Foliage is a resource present in both smaller and larger forest fragments, and its availability do not seem to be limiting for primates in small fragments. Smaller fragments have higher edge effects, allowing herbivores to find plant species with leaves containing higher nutritional quality content [92]. However, habitat loss could be affecting the quantity and quality of other resources that are more variable over time (e.g., fruits), with consequences for primate persistence. The majority of Neotropical primates include certain proportions of leaves in their diets, and even the most folivorous species do not feed exclusively on leaves [74]. The effect of area on the retention of folivorous primates could be a reflection of the loss of primates, such as *Alouatta* and *Brachyteles*, since these primates include the largest proportions of leaves, but also fruits, in their diets [74]. *Brachyteles* spp. for example, is present in the Atlantic Forest, one of the most fragmented regions in the Neotropics [93]. These primates are highly sensitive to habitat loss and showed low occupancy rates in their distribution area [43]. *Alouatta* spp. is a widely distributed genus, found from Mexico to Argentina. Their species are commonly reported to persist in fragmented landscapes and they occupy fragments (even small fragments) throughout the Neotropical region [43]. However, each case regarding this genus needs to be analyzed with caution, as *Alouatta* has been reported to be locally extinct in some areas, and in others, it is necessary to maintain a minimum fragment size to reduce the extinction probability [94,95]. The important issue regarding this relationship is that the reduction in fragment size decreases the diets based on vegetative parts. Therefore, this could reduce ecosystem services provided by primates, such as increase the amount of foliage due the removal of buds and nutrient cycling, with negative effects on the forest structure [19].

Some primates are considered to be 'ecosystem engineers' as they modify plant community structure through their feeding behaviors [19]. Specifically, primates can reduce the reproductive success of some tree species through feeding on flowers [96], or could increase the reproductive success of other plants through pollination [17] and seed dispersal [21], and contribute to nutrient movement within and between habitats through feeding on fruits and subsequent defecation [97]. The higher retention of diets based on reproductive parts of the plant in larger fragments has important implications for seed dispersal and, as such, has key conservation implications. If small areas are retaining fewer primates that feed on plant reproductive parts, there will be a disruption in seed dispersal leading to a decrease in plant species richness in the understory [21,29–31]. Consequently, large forest patches are necessary to maintain these primates and the ecological services they and other species provide [98]. Contrary to the other traits, the retention of prey consumption was not explained by area. Instead, it showed a negative association with the density of buildings. A higher density of buildings may be correlated with more intensive agricultural activities, and this may modify the arthropod communities as a result of increased use of pesticides and fertilizers compared with less densely populated areas [99,100]. Another possible reason could be pet-keeping and hunting, as carnivorous and insectivorous primates are represented mainly by Cebids, which are frequently used for those purposes (e.g., *Cebus capucinus*, *Saguinus nigricollis*, and *Saguinus leucopus* as pets; and *Cebus kaapori* and *Sapajus xanthosternos* as hunting targets) [101–105]. Although empirical evidence exists to support the idea of negative effects of reservoirs (the main type of water body in our study areas) on primates and other vertebrates [106,107], the negative relationship between area of water bodies in the matrix and diets based in animal prey may also be explained by a negative effect of water bodies on prey species. Invertebrates are the main prey fed upon by Neotropical primates [74], and they are also sensitive to dams and alterations in water flow [108,109].

Other studies have shown that the matrix matters more than fragment size for small mammals [8,64]; however, for some Neotropical primates, the pattern is contrary, and fragment size is more important than components in the matrix [7]. Here, we present empirical support to show that in the entire Neotropical region, fragment size is more important than matrix components for primate species. Nevertheless, fragment size alone should not completely explain how primates are responding to habitat loss, since we detected spatially-structured residuals in the LMMs before adding the spatial correlation structures. This means that other spatially-structured ecological processes or historical events may be influencing the primate populations but not represented by the variables in our analyses [110], such as differences in levels of endemism or beta-diversity as a consequences of geological legacies [111,112]. Hence, large-scale studies should include spatial covariates as surrogates for other ecological processes or historical events because the assemblages of many vertebrates can be more related to spatial effects than environmental conditions [113].

4.2. *Effect of the Neotropical Sub-Region on Primate Species Richness and Functional Traits*

The relationships between fragment size and retention of mass, diets of vegetative parts, and species varied between sub-regions. Although such variation was weak for species retention, this was consistent in a global-scale study in which South America showed higher species richness than Madagascar for a given fragment size, and that species richness in Africa has no significant relationship with fragment size [34]. Primates from Madagascar face a limited dietary quality and this could decrease the likelihood of their persistence in small fragments [114]. The non-relationship in Africa is due to the extant taxa being resistant to anthropogenic landscape alterations [34]. These results suggest there are regional mechanisms that act synergistically with the relationship between primate retention and site attributes, such as resource availability and species traits.

We found a general pattern where primates from Mesoamerica seem to be the least sensitive to fragment size changes, and those in the Atlantic Forest, the most sensitive. Although both sub-regions are highly fragmented and have historically coped with habitat loss [61,62,93], they are distinctly different in primate composition. Several species occupy the Atlantic Forest, and large portions of this sub-region (and also the Chaco sub-region) are below the Tropic of Capricorn. Globally, there is a positive relationship between latitude and geographic range of primates (Rapoport effect), but such relation is negative in the Neotropical region [115]. Species of narrow geographic ranges are more prone to extinction [116] and, consequently, those primates from Chaco and Atlantic Forest would be more vulnerable than primates from Mesoamerica. Thus, primates may face some challenges to survive in higher latitudes and fragmentation may be adding to these challenges, leading to a lower retention of primates in small fragments at higher latitudes.

The highest variation between sub-regions was found for the relationship between fragment size and diets based on vegetative parts, and this was mainly due to differences between Mesoamerica and the Atlantic Forest. This may be explained by the greater persistence of Atelids in Mesoamerica. In this sub-region, *Alouatta*, the most folivorous primate in the Neotropics, is present in 86% of the fragments, whereas in the Atlantic Forest, *Alouatta* was reported only in 33% of the fragments. *Brachyteles*, another genus that includes large amounts of leaves in its diet, was absent from all fragments in the Atlantic Forest included in our analyses. The pattern in the Chaco was similar to that in the Atlantic Forest, with two species of *Alouatta*, one of which is locally extinct [95], contributing to the lower retention of the diet based on vegetative parts. The pattern in the Amazon was more similar to that in Mesoamerica, with the sub-region not only having the highest maximum species richness in the Neotropics, but also a fauna including ecospecies with relatively high contributions of vegetative parts in their diets such as howler monkeys (*Alouatta*, 54%), Amazonian dusky titi monkeys (*Callicebus*, 34%), and tufted capuchins (*Sapajus apella*, 16%) [74]. A Neotropical analysis showed that these ecospecies are less sensitive to changes in fragment size (e.g., *Alouatta* and *Callicebus*) and have the highest occupation rates (e.g., *Alouatta* and *Sapajus apella*) in fragments along their geographic distribution [43]. Mesoamerica, in contrast, although showing lower species richness, hosts *Alouatta*, the most folivorous genus and the genus most resistant to human alterations [117–119], which could explain the higher retention of diets based in vegetative parts in this sub-region.

Another important variation between sub-regions was observed in the relationship between fragment size and mass, which could also be explained by differences in primate faunas, with less loss of mass in primate communities in the Amazon and in Mesoamerica than in the other sub-regions. In both cases, this is seemingly being driven by the persistence of species of the largest genera including *Alouatta* and *Ateles* in both sub-regions, and *Lagothrix* in the Amazon only. For example, more than 50% of the analyzed fragments in Mesoamerica retained *Alouatta* and *Ateles*, all fragments from the Amazon had *Alouatta*, and 50% had *Ateles* or *Lagothrix* too.

5. Conclusions

Our approach of using functional traits to compare actual and expected species occurrences is useful for evaluations on large scales; however, differences among sub-regions need to be considered. Studies like this could be conducted in other areas such as Africa, clustering fragments into the biodiversity hotspots [120] and ecoregions [121]. Africa (including Madagascar island) has a total of 214 primate species, with more than one-third of them threatened, and with body masses ranging from 0.03 kg (Madame Berthe's mouse lemur, *Microcebus berthae*) to 200 kg (western and eastern gorillas, *Gorilla* spp.) [16]. Other biological orders could be targeted, since there is information about current occurrence available in published studies, the expected species occurrences using the IUCN distribution, and information about functional traits from PanTHEIRA [122]. However, we recommend using the patch-landscape approach for studies of terrestrial mammals, since those animals do not exclusively inhabit forest fragments.

As some variation exists between species included within the same ecospecies, or even within some taxonomic species (e.g., differences in fruit consumption; see Strier [123] and Carvalho et al. [124]), the use of values of diet for ecospecies may have prevented the detection of some relationships in the present study. Nevertheless, various species included in this study did not have specific data for these variables. More detailed studies should be conducted whenever these data are available in a species-specific, or even site-specific, basis.

Finally, conservation planning for primates communities should consider both the regional context and the fragment size. At the regional level, the economic, social, political, and cultural context can have different influences on the matrix. For example, post-conflict areas can modify the land uses and make some areas within biodiversity hotspots more sensitive for primates [125]. For species with broad geographic range distributed in more than one sub-region (e.g., *Ateles belzebuth*, present in the Amazon and Orinoco; *Alouatta belzebul*, in the Amazon and Atlantic Forest; and *Alouatta palliata* in Mesoamerica and Tumbes-Chocó-Magdalena) [126], we need to consider that deforestation rates are different among countries and forest types, and the amount of remaining natural habitat changes from one region to another [127,128]. At the fragment level, however, it is necessary to conduct forest restoration programs aimed at increasing the current forest extension and fragment sizes or connecting remaining forest patches. The creation of new protected areas, even in fragmented landscapes, is also an important conservation strategy, as evidence suggest that in the Neotropical region, protected areas are efficient in retaining larger primates. Considering these aspects could help to prevent the loss of primates—one of the most charismatic animals—during Earth's sixth mass extinction.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/11/5/83/s1, Figure S1: Moran's I correlograms of the residuals of each model, Figure S2: Proportion of matrix attributes among eight sub-regions in the Neotropics, Table S1: Species composition of each forest fragment, Table S2: Proportion of dietary items for each ecospecies, Table S3: List of 97 fragments used in the analysis.

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SUPPORTING INFORMATION

Effect of Site Attributes and Matrix Composition on Neotropical Primate Species Richness and Functional Traits: a Comparison Among Regions

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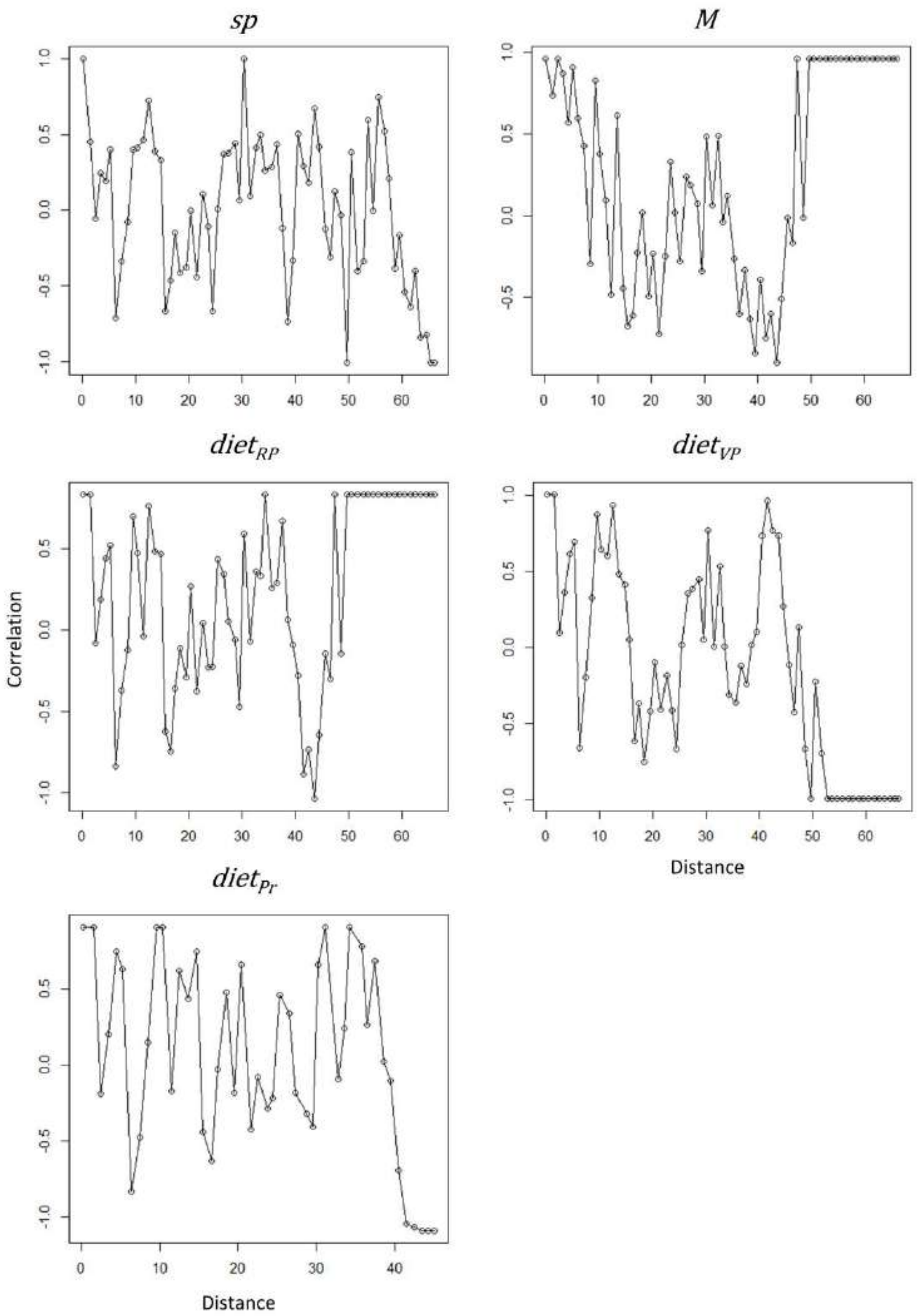

Figure S1. Moran's I correlograms of the residuals of each model. Species retention (sp), mass retention (M), species retention with diet composed of reproductive parts of the plant ($diet_{RP}$), species retention with diet composed of vegetative parts of the plant ($diet_{VP}$), species retention with diet composed of prey ($diet_{Pr}$).

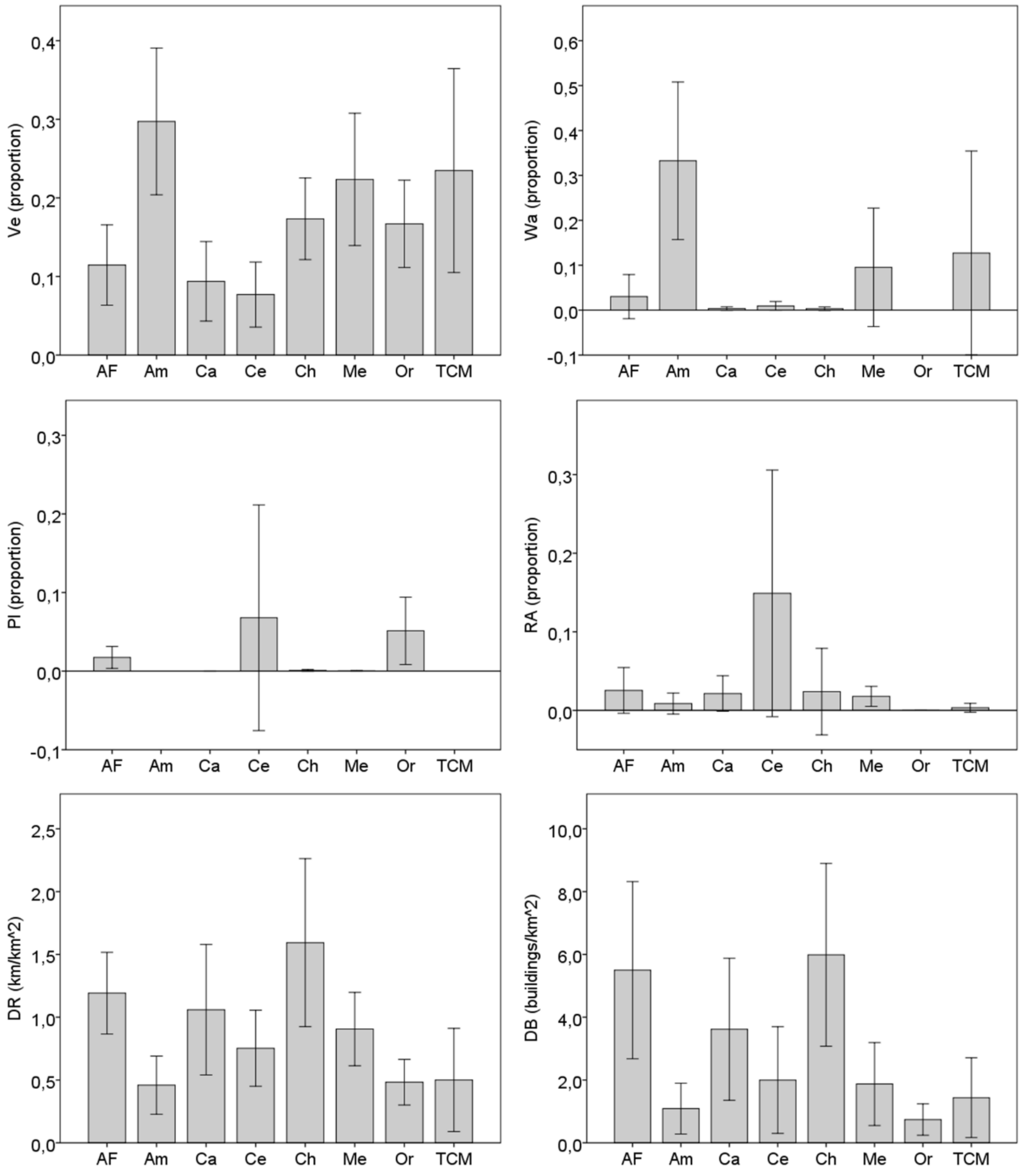

Figure S2. Proportion of matrix components among eight sub-regions in the Neotropics. Landscape attributes: forest vegetation (Ve), plantations (Pl), water bodies (Wa), residential areas (RA), density of buildings (DB) and density of roads (DR). Sub-regions: Atlantic Forest (AF), Amazonia (Am), Caribbean (Ca), Cerrado (Ce), Chaco (Ch), Mesoamerica (Me), Orinoco (Or), Tumbes-Chocó-Magdalena (TCM).

Table S1. List of 97 fragments (Fr) and species used in the analysis. Sub-regions are Amazonia (Am), Caribbean (Ca), Cerrado (Ce), Atlantic Forest (AF), Mesoamerica (Me), Orinoco (Or), Chaco (Ch) and Tumbes-Chocó-Magdalena (TCM). PA indicate if the fragment is within a protected area. Methods used in each work were based on direct observation (do), such as transect lines, behavior studies and walks; auditory records (ar), such as playbacks and interviews (in). The number 1 and 0 in each species indicate the presence or absence, respectively. Countries are Colombia (Co), Mexico (Mx), Costa Rica (CR), Peru (Pe), Brazil (Br), Belize (Be), Panama (Pa) and Bolivia (Bo). NI is no information.

Fr	Sub-region	Country	PA	Year image	Year field	Method	Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	Species 7	Species 8	Species 9
1	AF	Br	yes	2008	2007	do	*Callithrix penicillata 0*	*Alouatta guariba 1*	*Cebus nigritus 0*	*Callicebus nigrifrons 0*					
2	AF	Br	yes	2008	2007	do	*Callithrix penicillata 1*	*Alouatta guariba 1*	*Cebus nigritus 0*	*Callicebus nigrifrons 1*					
3	AF	Br	yes	2013	2013	do	*Callicebus sp 1*	*Callithrix penicillata 1*	*Alouatta guariba 0*	*Sapajus nigritus 0*					
4	AF	Br	no	2011	2008	do	*Cebus nigritus 1*	*Alouatta caraya 1*							
5	AF	Br	no	2012	2011	do	*Callithrix penicillata 0*	*Callicebus nigrifrons 1*	*Alouatta guariba clamitans 0*	*Sapajus nigritus 0*	*Brachyteles hypoxanthus 0*				
6	AF	Br	no	2013	2013	do	*Sapajus flavius 1*	*Callithrix jacchus 1*	*Alouatta belzebul 0*						
7	AF	Br	no	2016	2000	do/in/ar	*Callithrix sp 1*	*Callicebus melanochir 1*	*Cebus sp 1*	*Alouatta guariba 0*	*Leontopithecus chrysomelas 0*				
8	AF	Br	no	2015	2000	do/in/ar	*Callithrix sp 1*	*Callicebus melanochir 1*	*Cebus sp 1*	*Alouatta guariba 0*	*Leontopithecus chrysomelas 1*				
9	AF	Br	no	2010	2010	do/ar	*Alouatta guariba clamitans 0*	*Callithrix aurita 0*	*Callithrix penicillata 0*	*Sapajus nigritus 1*	*Callicebus nigrifrons 1*				
10	AF	Br	no	2010	2010	do/ar	*Alouatta guariba clamitans 1*	*Callithrix aurita 1*	*Callithrix penicillata 0*	*Sapajus nigritus 0*	*Callicebus nigrifrons 1*	*Brachyteles arachnoides 0*			
11	AF	Br	no	2013	2010	ar	*Callithrix aurita 0*	*Callicebus nigrifrons 1*	*Sapajus nigritus 0*	*Alouatta caraya 0*					
12	AF	Br	no	2013	2009	in	*Sapajus*	*Alouatta*	*Callithrix*						

							flavius 1	*belzebul 0*	*jacchus 1*						
13	AF	Br	no	2013	2009	in	*Sapajus flavius 1*	*Alouatta belzebul 0*	*Callithrix jacchus 1*						
14	AF	Br	no	2013	2009	in	*Sapajus flavius 1*	*Alouatta belzebul 0*	*Callithrix jacchus 1*						
15	AF	Br	no	2012	2002	do/in	*Callithrix* sp *1*	*Callicebus* sp *1*	*Cebus* sp *1*	*Alouatta guariba 1*	*Leontopithecus chrysomelas 0*				
16	Am	Pe	no	2005	2004	do	*Saguinus fuscicollis leucogenys 1*	*Callicebus oenanthe 1*	*Cebus albifrons 0*	*Ateles belzebuth 0*	*Oreonax flavicauda 0*	*Sapajus macrocephalus 0*	*Alouatta seniculus 0*	*Saimiri sciureus 0*	
17	Am	Br	no	2017	2001	do	*Alouatta belzebul 1*	*Cebus apella 1*	*Chiropotes satanas 0*	*Saimiri sciureus 0*	*Saguinus midas 0*	*Cebus kaapori 0*			
18	Am	Co	no	2013	2008	do	*Lagothrix lagotricha 1*	*Alouatta seniculus 1*	*Saimiri sciureus 1*	*Callicebus torquatus lugens 1*	*Saguinus inustus 1*	*Cebus albifrons 1*	*Sapajus apella 1*	*Aotus* sp *1*	
19	Am	Br	no	2017	2002	do	*Chiropotes satanas 1*	*Cebus apella 1*	*Alouatta belzebul 1*	*Saimiri sciureus 1*	*Saguinus niger 0*	*Callicebus moloch 0*			
20	Am	Br	no	2017	2002	do	*Chiropotes satanas 1*	*Cebus apella 1*	*Alouatta belzebul 1*	*Aotus infulatus 0*	*Saimiri sciureus 0*	*Saguinus midas 0*	*Cebus kaapori 0*		
21	Am	Br	no	2002	2000	do	*Alouatta macconnelli 1*	*Saguinus midas 1*	*Pithecia chrysocephala 1*	*Chiropotes satanas chiropotes 1*	*Ateles paniscus 0*	*Sapajus apella 0*	*Cebus olivaceus 0*		
22	Am	Br	no	2002	2000	do	*Alouatta macconnelli 1*	*Saguinus midas 0*	*Pithecia chrysocephala 0*	*Chiropotes satanas chiropotes 0*	*Ateles paniscus 0*	*Sapajus apella 0*	*Cebus olivaceus 0*		
23	Am	Br	yes	2007	2008	do	*Alouatta macconnelli 1*	*Cebus apella 1*	*Ateles paniscus 1*	*Chiropotes sagulatus 0*	*Pithecia pithecia 0*	*Saguinus midas 0*	*Saimiri sciureus 0*	*Cebus olivaceus 0*	
24	Am	Br	yes	2007	2008	do	*Alouatta macconnelli 1*	*Cebus apella 1*	*Ateles paniscus 1*	*Chiropotes sagulatus 1*	*Pithecia pithecia 0*	*Saguinus midas 0*	*Saimiri sciureus 0*	*Cebus olivaceus 0*	
25	Am	Br	yes	2007	2008	do	*Alouatta macconnelli 1*	*Cebus apella 1*	*Ateles paniscus 1*	*Chiropotes sagulatus 1*	*Pithecia pithecia 0*	*Saguinus midas 1*	*Saimiri sciureus 0*	*Cebus olivaceus 0*	
26	Am	Br	yes	2007	2008	do	*Alouatta macconnelli 1*	*Cebus apella 1*	*Ateles paniscus 1*	*Chiropotes sagulatus 1*	*Pithecia pithecia 1*	*Saguinus midas 1*	*Saimiri sciureus 0*	*Cebus olivaceus 0*	
27	Am	Br	yes	2007	2008	do	*Alouatta macconnelli 1*	*Cebus apella 1*	*Ateles paniscus 1*	*Chiropotes sagulatus 1*	*Pithecia pithecia 1*	*Saguinus midas 0*	*Saimiri sciureus 0*	*Cebus olivaceus 0*	
28	Am	Br	yes	2013	2009	do	*Sapajus apella 1*	*Saguinus weddelli 1*	*Aotus nigriceps 1*	*Callicebus cf. moloch 1*	*Pithecia irrorata 1*	*Alouatta puruensis 1*	*Ateles chamek 1*	*Saimiri ustus 1*	*Chiropotes albinasus 1*

29	Am	Br	no	2010	2007	do	*Cebus apella 0*	*Mico argentatus 0*	*Saguinus niger 0*	*Saimiri sciureus 0*	*Aotus azarae 0*	*Callicebus moloch 0*	*Chiropotes albinasus 0*	*Alouatta belzebul 1*	*Ateles marginatus 0*
30	Am	Br	no	2010	2009	do	*Cebus kaapori 1*	*Alouatta belzebul 1*	*Saimiri sciureus 1*	*Sapajus apella 1*	*Chiropotes satanas 0*	*Saguinus midas 0*			
31	Am	Br	no	2015	NI	do	*Alouatta belzebul 1*	*Ateles marginatus 0*	*Callicebus moloch 0*	*Cebus apella 1*	*Chiropotes albinasus 0*	*Mico argentatus 1*	*Saimiri sciureus 0*		
32	Am	Br	no	2016	NI	do	*Alouatta belzebul 1*	*Ateles marginatus 1*	*Callicebus moloch 1*	*Cebus apella 1*	*Chiropotes albinasus 1*	*Mico argentatus 1*	*Saimiri sciureus 1*		
33	Am	Br	no	2012	NI	do	*Alouatta belzebul 1*	*Ateles marginatus 1*	*Callicebus moloch 1*	*Cebus apella 1*	*Chiropotes albinasus 1*	*Mico argentatus 1*	*Saimiri sciureus 1*		
34	Am	Br	no	2012	NI	do	*Alouatta belzebul 1*	*Ateles marginatus 0*	*Callicebus moloch 1*	*Cebus apella 1*	*Chiropotes albinasus 1*	*Mico argentatus 1*	*Saimiri sciureus 1*		
35	Am	Br	yes	2008	2008	do/in	*Ateles chamek 1*	*Alouatta seniculus 1*	*Cebus apella 1*	*Chiropotes albinasus 1*	*Callicebus sp 1*	*Pithecia irrorata 1*	*Saimiri ustus 1*	*Aotus nigriceps 1*	*Saguinus fuscicollis weddelli 1*
36	Ca	Co	no	2007	2005	do	*Alouatta seniculus 1*	*Saguinus oedipus 1*	*Cebus capucinus 0*						
37	Ca	Co	no	2004	2005	do	*Alouatta seniculus 1*	*Saguinus oedipus 1*	*Cebus capucinus 1*	*Alouatta palliata 0*					
38	Ca	Co	no	2011	2010	do	*Alouatta seniculus seniculus 1*	*Saguinus oedipus 1*	*Cebus capucinus capucinus 1*	*Alouatta palliata 0*	*Ateles fusciceps 0*				
39	Ca	Co	no	2011	2010	do	*Alouatta seniculus seniculus 1*	*Saguinus oedipus 1*	*Cebus capucinus capucinus 1*	*Alouatta palliata 0*	*Ateles fusciceps 0*				
40	Ca	Co	no	2012	2010	do	*Alouatta seniculus 1*	*Saguinus oedipus 1*	*Ateles geoffroyi 0*	*Cebus capucinus 0*	*Alouatta palliata 0*				
41	Ca	Co	no	2011	2010	do	*Alouatta seniculus 1*	*Saguinus oedipus 0*	*Ateles geoffroyi 0*	*Cebus capucinus 0*	*Alouatta palliata 0*				
42	Ca	Co	no	2011	2010	do	*Alouatta seniculus 1*	*Saguinus oedipus 0*	*Ateles geoffroyi 0*	*Cebus capucinus 0*	*Alouatta palliata 0*				
43	Ca	Co	no	2011	2010	do	*Alouatta seniculus 1*	*Saguinus oedipus 1*	*Ateles geoffroyi 0*	*Cebus capucinus 0*	*Alouatta palliata 0*				
44	Ca	Co	no	2011	2010	do	*Alouatta seniculus 1*	*Saguinus oedipus 0*	*Ateles geoffroyi 0*	*Cebus capucinus 0*	*Alouatta palliata 0*				
45	Ca	Co	no	2011	2010	do	*Alouatta seniculus 1*	*Saguinus oedipus 1*	*Ateles geoffroyi 0*	*Cebus capucinus 0*	*Alouatta palliata 0*				
46	Ce	Br	yes	2003	1992	do	*Callicebus personatus 1*	*Alouatta caraya 1*	*Callithrix penicillata 1*	*Sapajus nigritus 0*					
47	Ce	Br	yes	2009	2009	do	*Alouatta*	*Sapajus*	*Callithrix*						

							caraya 1	*libidinosus 1*	*penicillata 0*					
48	Ce	Br	no	2002	1998	do	*Callithrix penicillata 1*	*Cebus apella 1*	*Alouatta caraya 0*	*Callicebus nigrifrons 0*				
49	Ce	Br	yes	2002	2002	do	*Callithrix geoffroyi 1*	*Alouatta caraya 1*	*Callicebus nigrifrons 0*	*Callithrix penicillata 0*				
50	Ce	Br	no	2015	2015	do	*Callithrix penicillata 1*	*Sapajus libidinosus 0*	*Alouatta caraya 0*	*Callicebus nigrifrons 0*				
51	Ce	Br	yes	2012	NI	do	*Cebus apella nigritus 1*	*Callithrix penicillata 1*	*Alouatta caraya 0*	*Callicebus nigrifrons 0*				
52	Ce	Br	no	2007	2000	do	*Callithrix aurita 0*	*Callicebus personatus 0*	*Cebus apella 1*	*Alouatta guariba 1*	*Brachyteles arachnoides 0*			
53	Ce	Br	no	2007	2000	do	*Callithrix aurita 1*	*Callicebus personatus 1*	*Cebus apella 1*	*Alouatta guariba 1*	*Brachyteles arachnoides 1*			
54	Ce	Br	no	2007	2000	do	*Callithrix aurita 0*	*Callicebus personatus 1*	*Cebus apella 1*	*Alouatta guariba 1*	*Brachyteles arachnoides 1*			
55	Ch	Bo	yes	2006	2005	do	*Callithrix melanura 1*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis 0*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
56	Ch	Bo	yes	2006	2005	do	*Callithrix melanura 1*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis 0*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
57	Ch	Bo	no	2006	2005	do	*Callithrix melanura 1*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis 1*	*Alouatta caraya 1*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
58	Ch	Bo	no	2010	2005	do	*Callithrix melanura 0*	*Cebus libidinosus juruanus 0*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis 0*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
59	Ch	Bo	no	2010	2005	do	*Callithrix melanura 0*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis 1*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
60	Ch	Bo	no	2010	2005	do	*Callithrix melanura 0*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*

										0				
61	Ch	Bo	no	2012	2005	do	*Callithrix melanura 1*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 0*	*Aotus azarae boliviensis 0*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
62	Ch	Bo	no	2010	2005	do	*Callithrix melanura 1*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 0*	*Aotus azarae boliviensis 0*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
63	Ch	Bo	no	2010	2005	do	*Callithrix melanura 1*	*Cebus libidinosus juruanus 1*	*Callicebus donacophilus 1*	*Aotus azarae boliviensis 0*	*Alouatta caraya 0*	*Saimiri boliviensis 0*	*Alouatta sara 0*	*Ateles chamek 0*
64	Me	Mx	no	2006	2003	do	*Alouatta palliata mexicana 1*	*Ateles geoffroyi vellerosus 1*						
65	Me	CR	yes	2011	2005	do	*Ateles geoffroyi 1*	*Alouatta palliata 1*	*Cebus capucinus 1*					
66	Me	Mx	no	2017	2010	do	*Alouatta pigra 1*	*Ateles geoffroyi 1*						
67	Me	Mx	no	2012	2002	do	*Ateles geoffroyi 1*	*Alouatta pigra 1*						
68	Me	Mx	no	2004	2002	do	*Alouatta pigra 0*	*Ateles geoffroyi yucatensis 1*						
69	Me	Mx	no	2009	2002	do	*Alouatta pigra 1*	*Ateles geoffroyi yucatensis 1*						
70	Me	Mx	no	2011	2002	do	*Alouatta pigra 1*	*Ateles geoffroyi yucatensis 1*						
71	Me	Mx	no	2011	2002	do	*Alouatta pigra 1*	*Ateles geoffroyi yucatensis 0*						
72	Me	Mx	no	2011	2002	do	*Alouatta pigra 0*	*Ateles geoffroyi yucatensis 1*						
73	Me	Mx	no	2005	1995	do	*Alouatta palliata 1*	*Ateles geoffroyi 0*						
74	Me	Mx	yes	2012	2010	do	*Ateles geoffroyi 1*	*Alouatta pigra 1*						

75	Me	Be	no	2012	2007	do	*Ateles geoffroyi 0*	*Alouatta pigra 1*					
76	Me	CR	yes	2005	2005	do	*Alouatta palliata 1*	*Ateles geoffroyi 1*	*Cebus capucinus 0*				
77	Me	Mx	no	2003	2004	do	*Alouatta palliata 1*	*Ateles geoffroyi 0*					
78	Me	Pa	yes	2017	2000	do	*Cebus capucinus 1*	*Saguinus geoffroyi 1*	*Ateles geoffroyi 0*	*Alouatta palliata 1*			
79	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 1*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
80	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 1*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
81	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 0*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
82	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 0*	*Aotus brumbacki 0*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
83	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 0*	*Aotus brumbacki 0*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
84	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 1*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
85	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 0*	*Callicebus ornatus 1*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
86	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 1*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
87	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 1*	*Aotus brumbacki 1*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
88	Or	Co	no	2014	2011	do	*Alouatta seniculus 1*	*Sapajus apella 1*	*Saimiri sciureus albigena 1*	*Callicebus ornatus 0*	*Aotus brumbacki 0*	*Lagothrix lugens 0*	*Ateles belzebuth 0*
89	TCM	Co	no	2017	2010	do	*Alouatta seniculus 1*	*Cebus capucinus 1*	*Saguinus oedipus 1*	*Ateles fusciceps 0*			
90	TCM	Co	no	2013	2008	do	*Saguinus leucopus 0*	*Alouatta seniculus 1*	*Ateles hybridus 0*	*Cebus albifrons 0*			
91	TCM	Co	no	2013	2008	do	*Saguinus leucopus 1*	*Alouatta seniculus 0*	*Ateles hybridus 0*	*Cebus albifrons 0*			
92	TCM	Co	no	2007	2008	do	*Saguinus leucopus 1*	*Alouatta seniculus 1*	*Ateles hybridus 0*	*Cebus albifrons 0*			

93	TCM	Co	no	2013	2008	do	*Saguinus leucopus 1*	*Alouatta seniculus 0*	*Ateles hybridus 0*	*Cebus albifrons 0*	
94	TCM	Co	no	2017	2008	do	*Ateles hybridus 1*	*Alouatta seniculus 1*	*Cebus albifrons 1*	*Aotus* sp 1	
95	TCM	Co	no	2017	2010	do	*Saguinus leucopus 1*	*Ateles hybridus 0*	*Cebus albifrons 0*	*Lagothrix lugens 0*	*Alouatta seniculus 0*
96	TCM	Co	no	2017	2010	do	*Saguinus leucopus 1*	*Ateles hybridus 0*	*Cebus albifrons 0*	*Lagothrix lugens 0*	*Alouatta seniculus 0*
97	TCM	Co	yes	2007	2006	do	*Alouatta seniculus 1*	*Cebus spp 1*	*Ateles hybridus 1*		

Table S2. Proportion of reproductive parts, vegetative parts and preys in the diet of each ecospecies. Information from Hawes and Peres (2014).

Cod	Ecospecies	Species	Reproductive parts (%)	Vegetative parts (%)	Prey (%)
Cj*	uakaries	*Cacajao* spp.	93	3	2
Ct	collared titi monkeys	*C. torquatus*, *Callicebus* spp.	90	7	3
Pi	saki monkeys	*Pithecia* spp.	89	9	1
Ch	bearded saki monkeys	*Chiropotes* spp.	93	1	3
Cf	white-fronted capuchins	*Cebus albifrons*, *C. capucinus*	82	1	17
Cp	Atlantic forest dusky titi monkeys	*C. personatus*, *Callicebus* spp.	81	16	0
At	spider monkeys	*Ateles* spp.	83	12	0
Ao	owl monkeys	*Aotus* spp.	91	3	6
Le	lion tamarins	*Leontopithecus* spp.	87	0	9
La	woolly monkeys	*Lagothrix* spp., *Oreonax flavicauda*	76	13	9
Sx*	moustached tamarins	*S. mystax* , *S. labiatus* , *S. imperator*	75	0	15
Sm	midas tamarins	*S. midas*, *S. niger*	67	0	30
So	bare-faced tamarins	*S. bicolor*, *S. geoffroyi*, *S. leucopus*, *S. martinsi*, *S. oedipus*	63	1	25
Co	wedge-capped capuchins	*C. kaapori*, *C. olivaceus*	61	6	33
Sf	saddle-back tamarins	*Saguinus fuscicollis*, *S. inustus*, *S. melanoleucus*, *S. nigricollis*, *S. tripartitus*	58	0	29
Cm	Amazonian dusky titi monkeys	Callicebus moloch, Callicebus spp.	57	34	8
Ca	brown capuchins	*C. apella*, *Cebus* spp.	52	16	30
Br	woolly spider monkeys	*Brachyteles* spp.	52	46	0
Sa	squirrel monkeys	*Saimiri* spp.	42	0	58
Al	howler monkeys	*Alouatta* spp.	43	54	0
Cg*	Goeldi's monkeys	*Callimico goeldii*	29	0	13
Mi	Amazonian marmosets	*Mico* spp.	19	0	19
Cx	Atlantic forest marmosets	*Callithrix* spp.	18	0	22
Cb*	pygmy marmosets	*Cebuella pygmaea* , *Callibella humilis*	0	0	23

*Ecospecies absents in the analysis.

Table S3. List of 97 fragments used in the analysis and their geographic coordinates in decimal degrees. Sub-regions: Amazonia (Am), Caribbean (Ca), Cerrado (Ce), Atlantic Forest (AF), Mesoamerica (Me), Orinoco (Or), Chaco (Ch), Tumbes-Chocó-Magdalena (TCM).

Fragment	Latitude	Longitude	Country	Sub-region	References
1	-22.80855376	-46.99288454	Brazil	AF	1
2	-22.77891695	-47.00155041	Brazil	AF	1
3	-21.193466	-43.699189	Brazil	AF	2
4	-23.753629	-53.13647	Brazil	AF	3
5	-20.687425	-42.8733	Brazil	AF	4
6	-6.566738	-35.131221	Brazil	AF	5
7	-13.952823	-39.451174	Brazil	AF	6
8	-15.926917	-39.635883	Brazil	AF	6
9	-21.36861111	-46.27888889	Brazil	AF	7
10	-22.89472222	-46.32361111	Brazil	AF	7
11	-21.42333618	-46.09480468	Brazil	AF	8
12	-6.758444444	-35.10827778	Brazil	AF	9
13	-8.525270448	-35.05341867	Brazil	AF	9
14	-9.757241667	-36.240175	Brazil	AF	9
15	-16.042222	-40.058889	Brazil	AF	10
16	-6.025528	-76.992694	Peru	Am	11
17	-4.30787	-49.494389	Brazil	Am	12
18	2.372988	-72.640968	Colombia	Am	13
19	-3.869943	-49.642028	Brazil	Am	14
20	-4.273274	-49.504488	Brazil	Am	15
21	-2.342269	-60.095024	Brazil	Am	16
22	-2.404463	-59.871321	Brazil	Am	16
23	-1.783361111	-59.68769444	Brazil	Am	17
24	-1.831416667	-59.68719444	Brazil	Am	17
25	-1.739361111	-59.44230556	Brazil	Am	17
26	-1.741694444	-59.70322222	Brazil	Am	17
27	-1.592694444	-59.62730556	Brazil	Am	17
28	-11.488094	-61.438953	Brazil	Am	18
29	-3.403467	-51.7363	Brazil	Am	19
30	-4.141411	-49.511967	Brazil	Am	20
31	-2.94698215	-54.80584365	Brazil	Am	21
32	-3.365571073	-54.87861993	Brazil	Am	21

33	-4.059984246	-54.91029614	Brazil	Am	21
34	-3.95	-54.86805556	Brazil	Am	21
35	-11.715918	-61.486929	Brazil	Am	22
36	10.04	-74.974944	Colombia	Ca	23
37	10.635422	-75.246621	Colombia	Ca	24
38	9.459337	-75.361197	Colombia	Ca	25
39	9.473889	-75.348889	Colombia	Ca	25
40	9.587543181	-75.33680657	Colombia	Ca	26
41	9.498810544	-75.38619036	Colombia	Ca	26
42	9.576150463	-75.46742552	Colombia	Ca	26
43	9.435677532	-75.37333609	Colombia	Ca	26
44	9.426915127	-75.45255531	Colombia	Ca	26
45	9.940501976	-75.10090395	Colombia	Ca	26
46	-21.580303	-47.807235	Brazil	Ce	27
47	-20.392896	-54.587635	Brazil	Ce	28
48	-21.11421	-47.66381	Brazil	Ce	29
49	-19.257778	-43.516944	Brazil	Ce	30
50	-18.925748	-48.154949	Brazil	Ce	31
51	-21.218923	-47.846245	Brazil	Ce	32
52	-22.633639	-48.289997	Brazil	Ce	33
53	-22.665924	-48.192556	Brazil	Ce	33
54	-22.694422	-48.084542	Brazil	Ce	33
55	-17.92374794	-63.16547971	Bolivia	Ch	34
56	-17.92697204	-63.14819431	Bolivia	Ch	34
57	-17.78021498	-63.06639822	Bolivia	Ch	34
58	-17.81188633	-62.95304426	Bolivia	Ch	34
59	-17.82122383	-62.95192874	Bolivia	Ch	34
60	-17.84435341	-62.92806677	Bolivia	Ch	34
61	-17.91027807	-62.93607955	Bolivia	Ch	34
62	-17.89008947	-62.91511188	Bolivia	Ch	34
63	-17.88716937	-62.90817504	Bolivia	Ch	34
64	18.37934037	-94.76922254	Mexico	Me	35
65	10.467944	-83.954119	Costa Rica	Me	36
66	16.181003	-90.874028	Mexico	Me	37
67	18.273611	-90.731944	Mexico	Me	38
68	18.46666667	-91.18333333	Mexico	Me	39
69	18.15	-91.61666667	Mexico	Me	39

70	18.58333333	-88.45	Mexico	Me	39
71	17.93333333	-88.86666667	Mexico	Me	39
72	21.23333333	-88.55	Mexico	Me	39
73	18.686792	-95.188451	Mexico	Me	40
74	17.305222	-88.446236	Belize	Me	41
75	16.370667	-88.494479	Belize	Me	41
76	10.411715	-84.114233	Costa Rica	Me	42
77	17.79458	-93.109908	Mexico	Me	43
78	9.154959	-79.843718	Panama	Me	44
79	3.608744	-73.638841	Colombia	Or	45
80	3.616664	-73.646057	Colombia	Or	45
81	3.61726	-73.641334	Colombia	Or	45
82	3.59999	-73.625466	Colombia	Or	45
83	3.593552	-73.633222	Colombia	Or	45
84	3.594236	-73.624502	Colombia	Or	45
85	3.599476	-73.64619	Colombia	Or	45
86	3.578006	-73.444488	Colombia	Or	45
87	3.565448	-73.448329	Colombia	Or	45
88	3.561927	-73.475485	Colombia	Or	45
89	7.943641	-76.251857	Colombia	TCM	46
90	5.67503	-74.7744	Colombia	TCM	47
91	5.641332	-74.836359	Colombia	TCM	47
92	5.57532	-74.95763	Colombia	TCM	47
93	5.33933	-74.73547	Colombia	TCM	47
94	6.712071	-74.14557	Colombia	TCM	48
95	6.897457	-74.578329	Colombia	TCM	49
96	6.907453	-74.572368	Colombia	TCM	49
97	6.048338	-74.265375	Colombia	TCM	50

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ARTIGO CIENTÍFICO 2

Drivers of primate richness and occurrence in a naturally patchy landscape in the Brazilian Amazon

Artigo submetido ao periódico "Biodiversity and Conservation"

Drivers of primate richness and occurrence in a naturally patchy landscape in the Brazilian Amazon

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Abstract

We assessed the spatial extent at which the species-landscape relationship is strongest (i.e. the scale of effect – SE) on primate occurrence (*Alouatta belzebul*, *Saguinus midas*, *Saimiri sciureus*, and *Sapajus apella* and *Cebus olivaceus*, the last two considered together in the analysis) and species richness and evaluated which landscape, patch, and human variables influence primate distribution in a savanna ecosystem in Brazil. We used nested buffers to measure the landscape attributes, and used these data to assess the SE of the species-landscape relationships. We explored the relative contributions of landscape, patch, and human variables to species richness and occurrences by using Generalized Linear Mixed Models and logistic regression. We found that the SE did not differ between primates, but did between two regions with different matrix composition. At the landscape level, occurrence of all species was higher as the distance to the nearest block of continuous forest decreased, but was lower as the amount of water bodies and anthropogenic cover in the matrix increased. The occurrence of *S. apella*, *C. olivaceus* and *A. belzebul* was positively related to forest cover, and all species but *A. belzebul* had higher occurrence in taller forest. The occurrence of *S. apella*, *C. olivaceus* and *A. belzebul* decreased closer to the city, and *S. apella* and *C. olivaceus* presence increased with the number of residents. Richness was negatively related to the number of residents and anthropogenic cover, but positively to forest height. We concluded that conservation planning for primates should follow a “functional landscape” perspective, by maintaining higher forest cover and minimizing the anthropogenic alterations in the matrix.

Key words Amapá · Habitat amount · Human-modified landscape · Primate conservation · Savanna · Scale of effect

Introduction

Forest loss and the area occupied by human-modified landscapes are increasing rapidly around the world due to deforestation, wildfire, forestry and agriculture (Melo et al. 2013; Curtis et al. 2018). This has resulted in increasingly fragmented landscapes, where forest remnants are reduced and disconnected (Arroyo-Rodríguez and Fahrig 2014), being surrounded by matrices of non-natural landscape components, such as agricultural fields, roads and human settlements (Anderson et al. 2007; Laurance et al. 2009; Tee et al. 2018). Understanding how such landscape components affect species within those fragments is crucial for the formulation of robust conservation plans (Fahrig and Merriam 1994; Arroyo-Rodríguez and Fahrig 2014). Furthermore, an understanding of both the spatial extent at which the species-landscape relationship is strongest (i.e. the scale of effect) (Arroyo-Rodríguez and Fahrig 2014) and how other features related to human presence (e.g. hunting) affect the species are necessary to build a more holistic knowledge of how animal communities are affected in human-modified landscapes (Cardillo et al. 2004; Urquiza-Haas et al. 2009).

Primates are among the most threatened animals globally, and currently many species inhabit human-modified landscapes (Estrada et al. 2017; Galán-Acedo et al. 2019a). They are sensitive to climate change and are threatened by land-use changes (Graham et al. 2016; Estrada et al. 2017; Calle-Rendón et al. 2018). Primates play important roles in sustaining ecological processes such as seed dispersal, and as such, in the maintenance of a high diversity of forest plants (Chapman et al. 2013; Andresen et al. 2018). Some species are important for human populations as food, pets and medicines, and for aspects related to myth, folklore, magic, and religion (Cormier 2006; Parathian and Maldonado 2010). From a landscape perspective (see Fahrig 2005), primate occurrence and richness are positively related to both higher forest cover and matrix permeability (Benchimol and Peres 2014; Carretero-Pinzón et al. 2017; Galán-Acedo et al. 2019b), and additional spatial components, such as distance to the nearest fragment negatively affect the ratio of adult females to adult males (Puig-Lagunes et al. 2016). Some patch characteristics such as fragment size and forest height positively affect both primate occurrence and richness (Michalski and Peres 2005; Arroyo-Rodríguez et al. 2008; Boyle and Smith 2010; Benchimol and Venticinque 2014; Gouveia et al. 2014; da Silva et al. 2015; Puig-Lagunes et al. 2016; Calle-Rendón et al. 2019), but others such as irregular fragment shape negatively affect primate occurrence and population structure (Arroyo-Rodríguez et al. 2008; Puig-Lagunes et al. 2016), as in such fragments edge effects drive environmental changes related to vegetation structure (Laurance et al. 1998; Laurance et al. 2006) and composition (Liu et al. 2019), affecting the availability of food for primates. Indeed, although some species are negatively affected by these changes (e.g. *Ateles paniscus*), others may benefit from it (e.g. *Alouatta macconnelli*) (Lenz et al. 2014). Furthermore, while variables related to human presence, such as distance to the city and hunting pressure, have been shown to negatively affect primate occurrence (Arroyo-Rodríguez et al. 2008; Urquiza-Haas et al. 2009), the effects of human density on primate distributions are complex, and not yet well-understood.

A large part of the world's human population lives within tropical savanna ecosystems (Scholes and Archer 1997). These ecosystems represent mosaics of forest patches occurring in a non-forested matrix (Furley 1999). Historical and continued human use of these areas has led to many highly modified ecosystems (Scholes and Archer 1997). The Savannas of Amapá, in the far north of Brazil, covers an area of approximately 10,000 km^2, and is the least protected complex of Amazonian savannas, being currently highly threatened by the expansion of large-scale agriculture (Carvalho and Mustin 2017; Hilário et al. 2017; Mustin et al. 2017). Eight primate species are present in this ecosystem (*Aotus infulatus*, *Saguinus midas*, *Saimiri sciureus*, *Pithecia pithecia*, *Cebus olivaceus*, *Sapajus apella*, *Alouatta macconnelli* and *Alouatta belzebul*) and one of them (*A. belzebul*) is listed globally (Valença-Montenegro et al. 2019) and nationally (Valença-Montenegro et al. 2012) as threatened (Vulnerable). Amapá's savannas are under-studied (Carvalho and Mustin 2017; Mustin et al. 2017), and few studies have previously related species richness and abundance of mammals –including primates– to conversion of savannas into anthropogenic environments (but see Coelho et al. 2014; Piña et al. 2019). The Savannas of Amapá are naturally patchy, containing patches of riparian forests, immersed in a matrix of savannas and flooded fields, and particularly in the south of the state, they are being increasingly replaced by anthropogenic cover. This spatial configuration presents an opportunity to study the effects of patch-level attributes, landscape composition and human activities on non-human primates, via a landscape perspective. Most of the knowledge about the effect of landscape composition on primates comes from studies in anthropogenically fragmented landscapes, and little is known about these processes in naturally patchy landscapes. Moreover, due to the cultural and ecological roles played by primates, using them as a model could help in the conservation of naturally patchy landscapes (Estrada et al. 2017; Galán-Acedo et al. 2019c), including the Savannas of Amapá.

Here, we address two key questions. Firstly, we seek to understand the scale of effect (SE) of landscape composition on primate occurrence and primate species richness in the Savannas of Amapá. The SE is "the spatial extent within which the landscape affects a population" (Arroyo-Rodriguez and Fahrig 2014), and as such, we will test if the amount of forest cover and matrix attributes affect primates over short or long distances. Due to accelerated land use change over large areas in the Savannas of Amapá, a better comprehension of the spatial extent over which such changes affect primates will allow us to identify whether land use change will actually impact populations (i.e. occurs within the SE radius), allowing for better species and habitat management plans to prevent population losses. Thus, we expect that i) the SE will increase with increasing species' home range size because species with larger home ranges interact with the environment over large spatial extents (Miguet et al. 2016; Galán-Acedo et al. 2018); and ii) the SE in more disturbed areas will be lower than in less disturbed areas, because in disturbed areas, movements are disrupted due to alterations in the matrix and primates are forced to depend on resources from the focal patch (Galán-Acedo et al. 2018). Our second key question concerns the relative importance of landscape attributes, patch characteristics, and human factors in driving patterns of primate species richness and occurrence in the Savannas of Amapá. We predict that, in terms of landscape attributes, forest cover and savanna area will be positively related to primate occurrence and species richness, as forests represent habitat for feeding and reproduction, whereas savannas may be more suitable for primate dispersal than water bodies (e.g. rivers and flooded fields) and anthropogenic cover (e.g. urban areas, roads and agricultural fields) (Benchimol and Peres 2013; Carretero-Pinzón 2013; Garmendia et al. 2013; Carretero-Pinzón et al. 2017; Galán-Acedo et al. 2019a). We also expect that the distance to the nearest large block of continuous forest will be negatively related to primate occurrences and species richness, as such forested areas may act as sources (Lawes et al. 2000; Naranjo and Bodmer 2007). In terms of patch-level characteristics, we predict that both larger patches and taller forests will have higher occurrences and species richness of primates (Benchimol and Peres 2014; Gouveia et al. 2016; Calle-Rendón et al. 2019), as taller forests may allow vertical niche segregation between primates and both taller forests and larger forest areas may represent higher resource availability. We further predict that patches that are more irregularly shaped will have higher rates of occurrence of primates with a higher proportion of arthropods in their diets because such patches have more edge effect (Murcia 1995). Finally, in terms of human factors, since human population density is related to the loss of some biodiversity components (Thompson and Jones 1999; Cardillo et al. 2004; Urquiza-Haas et al. 2009), we predict that overall primate richness and rates of occurrence of larger primates will be lower in landscapes with higher numbers of residents, due to increased hunting and clearing of native vegetation

(Laurance et al. 2002; Urquiza-Haas et al. 2009). As a second proxy for these types of disturbances, we also used distance to the capital city, predicting that patches closer to the city will be less species rich and have lower rates of occurrence of larger primates, as hunting pressure will be greater than in more isolated patches (Silvestre et al. 2020), and the patches are likely to be more highly disturbed (Michalski and Peres 2005).

Methods

Study area

We conducted this study in three locations (Curiaú, Pedreira and BR-156) in a savanna ecosystem in the Brazilian state of Amapá, in the northeastern part of the Amazon (Fig. 1). The savanna complex in this region is often referred to as the "Cerrado of Amapá" or "Savannas of Amapá" (here after Savannas of Amapá – SOA). The climate in this region is wet and hot, the annual mean temperature is 26.5 °C and average annual precipitation is 2570 mm, with a dry season between August and November (Tavares 2014). The SOA are characterized by a mosaic of natural, open, grassy areas with sparse shrub and tree cover, and flooded fields, interspersed with patches of riparian forest and non-natural areas such as commercial plantations of maize, soybean and manioc (Hilário et al. 2017; Mustin et al. 2017). Currently, the SOA is inhabited by colonists and *Quilombolas* (the descendants of escaped African slaves, who have special land rights in Brazil). This region has been occupied for centuries, and as such, forest patches in this landscape are disturbed, in part as a result of timber extraction to build settlements (Lima 2003). However, one of the main drivers of land conversion in the SOA is to make way for agricultural plantations (Hilário et al. 2017; Mustin et al. 2017). The increase in area planted with soybeans in recent years was higher in the municipality of Macapá, where the Curiaú and Pedreira locations are situated. BR-156 is situated in the municipality of Santana, where the area planted with soybeans is lower compared with Macapá (Hilário et al. 2017). For that reason, we assumed that the anthropogenic disturbance is higher in Curiaú and Pedreira than in BR-156.

Study species

There are seven diurnal primate species that have part of their distributions in the SOA, but there are no published data on their specific ecology in the SOA. However, studies from other parts of their range show that both the weeper capuchin (*Cebus olivaceus*) and the brown capuchin (*Sapajus apella*) are omnivorous, groups present a home ranges between 270 and 320 ha (Zhang 1995; Miller 1996), and population densities range between 6 and 55 individuals/km^2 (Freese and Oppenheimer 1981). The squirrel monkey (*Saimiri sciureus*) is mainly insectivorous-frugivorous, groups have a home range varying from 65 to 280 ha (Mittermeier and Roosmalen 1981; Lima and Ferrari 2003; Defler 2010), and population densities range between 16 and 528 individuals/km^2 (Baldwin and Baldwin 1981). The red-handed tamarin (*Saguinus midas*) is the smallest primate in the SOA, is mainly insectivorous, group home range size is 31-42 ha (Mittermeier and Roosmalen 1981; Day and Elwood 1999), and population densities range between 2 and 30 individuals/km^2 (Snowdon and Soini 1988). The Guiana red howler (*Alouatta macconnelli*) and the red-handed howler (*Alouatta belzebul*) are the largest primate species in the SOA, their home ranges vary between 6-45 and 9-18 ha, respectively (Bonvicino 1989; Pinto et al. 2003; Boubli et al. 2008). Howler monkeys are folivorous-frugivorous (Mittermeier and Roosmalen 1981; Julliot and Sabatier 1993; Pinto et al. 2003). Population density of these *Alouatta* species are unknown in their distributional range, however, *A. seniculus* (a close species to *A. macconnelli*, Cortés-Ortiz et al. 2003) is present in forest patches of a savanna ecosystem in the Orinoco basin in densities between 23 and 54 individuals/km^2 (Defler 2010). Meanwhile, *A. belzebul* seems to be common in some areas of continuous forest from the Amazon and less common in the Atlantic Forest, where less than 500 individuals survive in some forest fragments, with no information about the species in savanna areas (Valença-Montenegro et al. 2019). The white-faced saki (*Pithecia pithecia*) is mainly a seed predator and its group home range size is the smallest among the species in the SOA, approximately 8-9 ha (Mittermeier and Roosmalen 1981; Oliveira et al. 1985). Population densities range between 1 and 13 individuals/km^2 (Buchanan et al. 1981).

Primate survey

Across a total area of approximately 2300 km^2, we selected 70 forest patches by using images from Google Earth Pro (version 7.3.2.5776). We produced maps of these forest patches, their access roads and any nearby buildings, which were then printed for use in the field. Between October 2017 and February 2018, we visited the buildings marked on the map to carry out interviews with local inhabitants and gather information about the occurrence of primate species. We were able to conduct 77 interviews that provided information on primate presence in 43 forest patches (13 patches in Pedreira, 17 in Curiaú and 13 in BR-156) across a total area of approximately 1700 km^2. In some cases, interviews were not possible either because houses marked on the map were not inhabited, locals declined to participate in the interview, or the buildings marked on the map were not actually houses. During the interviews, we used the map as a reference to identify the forest patch of interest. We then showed participants photographs of the 10 primate species known to be present in the state of Amapá (*Alouatta belzebul*, *Alouatta macconnelli*, *Ateles paniscus*, *Chiropotes sagulatus*, *Pithecia pithecia*, *Cebus olivaceus*, *Sapajus apella*, *Saimiri sciureus*, *Aotus infulatus*, and *Saguinus midas*) (Silva et al. 2013) and one Neotropical primate species not present in the study region (*Callithrix jacchus* from the Atlantic Forest and Caatinga), included as a control (Bezerra et al. 2018). Participants were asked to identify which species they had seen in that forest patch.

Interviews with locals have been commonly used to gather information about occurrence of several mammal species, including primates, and are especially useful in large areas (Michalski and Peres 2005; Urquiza-Haas et al. 2009; Martínez-Marti et al. 2016; Camino et al. 2020). Moreover, interviews and methods based on local knowledge (e.g. locally-based surveys) have a higher detection probability than standard methods such as transects and camera traps and represent a useful and cost-effective approach (Camino et al. 2020). However, to validate the data on primate presence and absence obtained in the interviews, we performed playback sessions in at least 30% of forest patches in each study location (9 in Curiaú, 9 in Pedreira and 4 in BR-156) between July and December 2018.

We established transects of 800 m in length in each forest patch using Google Earth Pro, standardizing the sampling effort according to the patch area: area < 25 ha (2 transects), 25 < area < 50 ha (3 transects), 50 < area < 100 ha (4 transects) and area > 100 ha (5 transects). Five playback stations were established along each transect at intervals of 200 m. We broadcast a playback session from each station, consisting of a sequence of vocalizations of seven diurnal primates in the following order: *A. belzebul*, *S. midas*, *P. pithecia*, *A. macconnelli*, *S. sciureus*, *S. apella* and *C. olivaceus*. Vocalizations of each species were broadcast for 3 minutes, except *Alouatta* genus, which was broadcast for 7 minutes because the vocalizations of these species are longer than those of other species (Drubbel and Gautier 1993). Playbacks of vocalizations were followed by a 7-minute interval without playback which was used to listen for any response (except *Alouatta* genus, where the interval was 8 minutes). Playback sessions began at 07:00 h, 09:00 h, 10:30 h, 15:10 h, and 16:40 h. We broadcast vocalizations of *Alouatta* only at the first and the last playback station of each transect (07:00 h and 16:40 h), because they generally vocalize at sunrise and sunset (Drubbel and Gautier 1993; Oliveira and Ades 2004). Between playback sessions, the distance between stations was walked slowly (40 minutes), either following our own transect in a Global Positioning System (Garmin eTrex 20) or using human and cattle paths, to detect any primate occurrences and to check the forest floor for primate fecal matter. In eight of the 43 forest patches it was not possible to establish transects of 800 m in length due to patch size and shape, and in these cases we performed just two or three playback sessions per day (i.e. transects of 200 m and 600 m in length respectively).

The data from the playback sessions was only used to "correct" the interview data in two cases: 1) where species identified as absent in the interviews were recorded as present using playback (N = 1); and 2) where species presence or absence was recorded as unknown during the interview (because the interviewee was unsure), in which case presence was considered to be established by the playback data (N = 2). Three opportunistic confirmations of presence (made outside of playbacks) were used to evaluate the veracity of the interview data. Specifically, two presences of *A. belzebul* (a vocalization from Curiaú and a sighting from Pedreira) and one of *S. sciureus* (a sighting in Curiaú). Finally, as participants frequently reported both *C. olivaceus* and *S. apella* to be present in patches in which only one was recorded during playback, records of the presence of both species were joined. As such, absences of *C. olivaceus* and *S. apella* were only recorded in those patches in which participants reported both species as absent, and where neither species was recorded during playback.

The vocalizations used were obtained from Emmons et al. (1997). In the case of *A. macconnelli*, the vocalization used was of *A. seniculus*, as until recently these taxa were considered to be a single species (Boubli et al. 2008). The vocalizations were edited to standardize the total playback time, and also to reduce the background noise not related to the primate vocalizations. Each vocalization was saved as an MP3 file and broadcast using a Max Print 601205-3 speaker (frequency range: 50 to 20,000 Hz, output power: 100 RMS). Before carrying out the playback sessions, we tested the speaker and established that the maximum distance at which we could still hear the vocalizations was approximately 100 m. The same person carried out all of the playback sessions to avoid biases in species detection.

Landscape composition

We adopted a patch-landscape approach (Arroyo-Rodríguez and Fahrig 2014) in which response variables are measured in a focal patch, and landscape attributes are measured within a specific radius (buffer) from the focal patch. For each of the 43 forest patches we generated 10 nested buffers using QGIS (Version 2.14.9-Essen). The smallest landscape size was a buffer of 300 m radius (28 ha landscape), and the largest landscape size was a buffer of 1200 m radius (452 ha landscape), as larger radii would have led to overlapping landscapes around the different forest patches. The smallest landscape created is larger than the home range size reported for at least two primate species present in the study site (*P. pithecia* and *A. belzebul*), and the largest landscape is larger than the home range reported for the species with the largest home ranges in the study site (*C. olivaceus* and *S. apella*). We nested eight additional buffers between the smallest and largest buffers, at intervals of 100 m: 400 m (50.3 ha landscape), 500 m (78.5 ha), 600 m (113.1 ha), 700 m (153.9 ha), 800 m (201.1 ha), 900 m (254.5 ha), 1000 m (314.2 ha) and 1100 m (380.1 ha).

We carried out a supervised classification for each study location using Landsat 8 OLI images from 2017 and 2018 at a 30 m spatial resolution, retrieved from the U.S. Geological Survey (https://earthexplorer.usgs.gov/). We used the Semi-Automatic Classification Plugin (Version 5.4.2) in QGIS (Version 2.14.9-Essen), combining bands 2 to 8. We separated the area into four general attributes of landscape composition: 1) forest cover (FC), which included forest environments and palm corridors; 2) savanna (Sav), including some cleared areas used for cattle ranching which were not distinguishable from savannas areas; 3) water bodies (WB), including rivers, lakes and flooded fields; and 4) anthropogenic cover (AC), including urban areas, roads, open areas (e.g. bare ground) and agricultural fields (mainly soybeans, maize and manioc plantations). We used a total of 2122 points based on field observations and from Google Earth Pro images to make the classification in the three regions, and used between 28% and 38% of those points to validate the classification. Overall, classification accuracy was between 89% and 98%.

We calculated the distance between each forest patch and the nearest block of forest considered as a possible source of species (DF). To do so, we first identified in Google Earth the blocks of continuous forest that could be sources of individuals, based on the information on presence of primates gathered in the interviews with locals. We then drew a polygon of each block, exported the polygon into QGIS, and calculated the Euclidean distance between each forest patch and the nearest block of forest. Although DF is not a landscape attribute according to the landscape perspective, it was included as landscape predictor since it is representing a measure of the space in the landscape.

Patch characteristics

We imported the forest patches delineated in Google Earth Pro into QGIS and calculated the patch area (PA). We then calculated a shape index (SI) as:

$$SI = p/\sqrt{(\pi \times PA)}$$

where p and PA are the perimeter and patch area, respectively, in meters (Carretero-Pinzón et al. 2017). Higher values of SI represent forest patches that are more irregular and a value of 2 represents a forest patch that is perfectly circular. We calculated forest height in each playback station by using the difference between X-band and P-band from Synthetic-Aperture Radar (SAR) images of 5 m spatial resolution, obtained from the *Secretaria de Estado do Meio Ambiente* (State's Secretariat of the Environment) of Amapá. We then used the average among points to calculate the forest height (FH) of each patch.

Human factors

We used a shapefile based on data from the 2010 census, obtained from the *Instituto Brasileiro de Geografia e Estatística* (Brazilian Institute of Geography and Statistics) (IBGE 2019). We used the nested buffers from the landscape evaluation to extract the values of number of residents (NR) in each buffer. Additionally, we calculated the distance by road of each forest patch to Macapá (DC), the most populated city and capital of the state of Amapá, by delineating in Google Earth the roads using the 'path tool'. DC was used as a proxy of hunting frequency (Silvestre et al. 2020).

Statistical analysis

All analyses were performed in R (version 3.5.1) (R Core Team 2018). We calculated the Cohen's kappa coefficient to measure the concordance of presence-absence data between interviews and playbacks, by using the 'irr' package (Gamer et al. 2012). Concordance was high for *A. belzebul* (Kappa = 0.83) and *P. pithecia* (Kappa = 1), and moderate for *S. midas* (Kappa = 0.529). Although concordance was low for *S. sciureus* (Kappa = 0.188), and *C. olivaceus* and *S. apella* (Kappa = 0.253), there were no false positives for these species (i.e. an interview participant reporting an absence when a playback reported a presence) (Table S1). Indeed, there was only one false positive (for *S. midas*). As such, we are confident in the reliability of the interviews to inform primate occurrence in the study area, because such differences between interviews and playback likely reflect low detectability of those species using playback, rather than a low quality of information provided by the interview participants. Once a species is detected, its presence is assured, while it may take a number of surveys without detection to be sure about the absence of a species. Therefore, it is more common to have false absences (i.e. imperfect detection or false negatives) than false presences (i.e. false positives). Considering this, we think that playback sessions may have missed some species, but these species may have been detected by locals, as they have spent far more time within the forest patches. Moreover, no participant reported the presence of the species used as a control. While species richness was modeled using all reported species, we only used the data of *A. belzebul*, *S. midas*, *S. sciureus*, and *C. olivaceus* and *S. apella* (together) to model occurrence, as *A. macconnelli* and *P. pithecia* were only present in one and six forest patches, respectively.

We used an ANOVA to test for significant differences in landscape attributes (FC, Sav, WB and AC) among regions using the amount calculated in the largest radius (1200 m). Following Jackson and Fahrig (2012), we identified the spatial extent that maximized the strength of the relationship (i.e. the scale of effect) between primate richness and occurrence and landscape attributes and only one human factor measured using a landscape perspective (NR). We used pairwise Generalized Linear Models (GLM) to relate primate occurrence (binomial distribution) and species richness (poisson distribution) to each attribute of landscape composition (FC, WB, Sav and AC) and NR (transformed as ln[1+NR]) in a specific radius. The scale of effect was considered to be the radius of the buffer for which the AIC (Akaike's information criterion) value of the model was lowest (Jackson and Fahrig 2015).

To answer our first question about the scale of effect, we calculated the ΔAIC for each model by computing the difference between the AIC of each model and the AIC of the most supported model (i.e. the model with the lowest AIC). We considered that models with ΔAIC < 2 could have the same empirical support, and where all models had ΔAIC < 2, we inferred that there was no definable scale of effect (Gestich et al. 2019). Then we plotted the radius of each landscape against the ΔAIC of forest cover, considering the occurrence models of all species (prediction 1), and against the ΔAIC of forest cover considering models of species richness (prediction 2). In this second prediction, pairwise GLMs were implemented for each location separately (BR-

156, Pedreira and Curiaú). For these models, we selected only 11 forest patches per location to increase the spatial separation between Pedreira and Curiaú, as these two locations were 3.8 km apart from each other, thus we excluded four landscapes at the northern limit of Curiaú. We also excluded an additional six patches for which the presence of some species was unknown (i.e. the interviewee could not confirm the presence of the species) (Fig. 1). After this process, the distance between the closest forest patches of Curiaú and Pedreira was 11 km.

To answer our second question, we used a multimodel inference approach to assess the relative effect of each predictor on each response variable (Burnham and Anderson 2002). For species occurrence data we fitted logistic regression models using Firth Logistic Regression from the 'logistf' package (Heinze et al. 2018), as data exploration revealed problems of perfect separation (Heinze and Schemper 2002). Then we assessed the effect of the attributes of landscape composition (FC, WB, Sav, and AC measured at the scale of effect, and DF), patch characteristics (FH, ln[PA], and SI) and human factors (ln[1+NR] measured at the scale of effect, and DC) on occurrence of each species through full models. As we detected differences in the SE among locations (see results concerning our second prediction in Results section), we used Generalized Linear Mixed Models (GLMM) to assess the effect of landscape composition (FC, WB, Sav, and ln[1+AC], and DF), patch characteristics (FH, ln[PA], and SI) and human factors (ln[1+NR] and DC) on species richness. We implemented the GLMM using the 'lme4' package (Bates et al. 2018) with the Laplace approximation (Bolker et al. 2009), and each location (Curiaú, Pedreira and BR-156) as a random factor. The SE used in this GLMM were those detected in each location in the evaluation of the second prediction related to our first question. Additionally, we assessed the effect of the random factor (i.e. the effect of the location) plus fixed factors (i.e. landscape attributes, patch characteristics and human factors) on species richness using the conditional R^2 (Nakagawa and Schielzeth 2013). We used the 'MuMIn' package (Bartoń 2018) to obtain a set of models for the occurrence of each species and species richness and ranked them according to the AICc, considering only those models with ΔAICc < 2. Variance inflation factors (VIF) were calculated for each model using the package 'car' (Fox et al. 2018). If a VIF > 3 was detected, then we ran a new analysis with the 'subset' argument to exclude models with collinear variables. The performance of each logistic regression from the set of models was assessed with the area under the ROC curve (AUC) using the 'pROC' package (Robin et al. 2019). We checked for spatial autocorrelation in the residuals of all models with ΔAICc < 2 through Moran's I correlograms in the package 'ncf' (Bjørnstad and Cai 2018). We obtained the Akaike weights (w_i) of each model in the set of models and hence, the relative importance of each predictor variable (i.e. the sum of the weights: $\sum w_i$). We used a threshold of $\sum w_i = 0.4$ to decide whether a predictor was important or not (Burnham 2015). Additionally, we calculated the average relative importance of each group of variables (landscape, patch and human) for the occurrence of each species, and for species richness (Carretero-Pinzón et al. 2017).

Results

Difference in landscape composition between locations

We found that anthropogenic, forest and savanna cover were significantly different between the three locations (ANOVA: p = 0.008, p = 0.02 and p = 0.03, respectively), however the *post hoc* analysis showed that the differences were only significant between BR-156 and Curiaú (Fig. S1). Anthropogenic cover was higher in Curiaú (mean 86.3 ± 80 SD) and lower in Pedreira (mean 44.7 ± 37.9 SD) and BR-156 (mean 18.5 ± 17.3 SD) (Fig. S1). The average forest cover in BR-156 was approximately 30% higher than forest cover in both Curiaú and Pedreira (Fig. S1). Savanna cover from BR-156 was 34% and 40% higher than in Pedreira and Curiaú, respectively (Fig. S1). Patch size did not differ significantly between localities, and the mean area was 38 ± 32.3 ha, 46.6 ± 51.6 ha and 57.5 ± 63.4 ha in BR-156, Curiaú and Pedreira, respectively.

Primate surveys

Alouatta belzebul was recorded in 48% of the patches, and *C. olivaceus* and *S. apella* in 57%, and were present mainly in Pedreira and BR-156. *Saguinus midas* was recorded in 64% of the patches and was present mainly in BR-156 and Curiaú. *Saimiri sciureus* was present in 61% of patches and occupied the three locations in similar proportions. *Pitecia pithecia* and *A. macconnelli* were present only in the BR-156 and occupied six and one patch respectively. Species richness ranged between zero and five species per patch. The location BR-156 had the highest mean species richness (mean 3.9 ± 1.5 SD) followed by Pedreira and Curiaú (mean 2.3 ± 1.2 SD and mean 1.8 ± 1.4 SD, respectively).

Scale of effect of landscape composition on primate occurrences and species richness

We found that the scale of effect (SE) varied widely across the buffer radius (Fig. 2). There was no clear positive relationship between home range size and the SE (first prediction). The SE for occurrence of *A. belzebul* (species with smallest home range in our analysis) varied from 500 to 800 m, while the SE for *C. olivaceus* and *S. apella* (species with the largest home range) varied from 500 to 1100 m. For *S. sciureus*, the SE was plausible at distances between 300 and 1100 m and there was no definable SE for *S. midas* (Fig. 2a). Finally, the SE of forest cover on species richness in the most disturbed location (Curiau, between 800 and 1200 m) was higher than the SE of the least disturbed location (BR-156, between 300 and 500 m), which was contrary to our second prediction (Fig. 2b).

Relative importance of landscape attributes, patch characteristics and human factors on primate occurrence and species richness

Models showed that occurrence of all species but *S. sciureus* may be explained by landscape, patch and human variables (Table S2). For *C. olivaceus* and *S. apella*, *A. belzebul*, and *S. midas* all models in the set of models were significant and the AUC ranged between 0.90 and 0.98, but for *S. sciureus* models were not significant and AUC ranged between 0.76 and 0.77 (Table S2). Landscape attributes were more important than patch characteristics and human factors in explaining the occurrence of all species, however, human factors were more important than landscape attributes and patch characteristics for species richness (Fig. 3).

At the landscape level, both the probability of occurrence of all species and species richness were lower where landscapes had higher anthropogenic cover ($\sum w_i = 1$ for occurrence of all species and $\sum w_i = 48$ for species richness - Fig. 4), and the probability of occurrence of all species was also lower where the matrix contained higher proportions of water bodies ($\sum w_i = 1$ for all species - Fig. 4). The probability of occurrence of *A. belzebul* ($\sum w_i = 1$) and *S. midas* ($\sum w_i = 0.85$) were lower where landscapes had larger areas of savanna (Fig. 4). Forest cover was positively related to the occurrence of *S. sciureus* ($\sum w_i = 1$), *C. olivaceus* and *S. apella* ($\sum w_i = 0.68$), and *A. belzebul* ($\sum w_i = 1$) (Fig. 4). The distance to the nearest block of forest was negatively related to the occurrence of all species ($\sum w_i = 0.85$ for *S. midas*, $\sum w_i = 1$ for *S. sciureus*, $\sum w_i = 0.72$ for *C. olivaceus*, *S. apella*, and *A. belzebul* - Fig. 4). At the patch level, forest height was important and positively related to species richness ($\sum w_i = 0.48$) and occurrence of *S. midas* ($\sum w_i = 1$), *S. sciureus* ($\sum w_i = 0.79$), and *C. olivaceus* and *S. apella* ($\sum w_i = 0.63$) (Fig. 4), but was negatively related to *A. belzebul* ($\sum w_i = 0.71$) (Fig. 4). *Saimiri sciureus* and *A. belzebul* had a higher probability of occurrence in more irregularly shaped patches ($\sum w_i = 0.8$ and $\sum w_i = 0.45$, respectively - Fig. 4). In terms of human factors, distance from the city was important and positively related to the occurrence of *S. sciureus*, *A. belzebul*, and *C. olivaceus* and *S. apella*, but was negatively related to the occurrence of *S. midas* ($\sum w_i = 1$ for all species - Fig. 4). Species richness was lower ($\sum w_i = 0.94$) and the probability of occurrence of *C. olivaceus* and *S. apella* higher ($\sum w_i = 0.4$) in areas with more residents (Fig. 4).

Eleven models of species richness had empirical support (Table S3). Fixed factors explained the same variation as the fixed and random factors together (i.e. marginal R^2 = conditional R^2) in all models in the set of models (Table S3). In fact, values of the variance for the random intercept ($\hat{d}$) were zero or close to zero (Table S3). This means, there is no effect of the locality in explaining species richness when considering landscape, patch and human variables together. However, when considering only one landscape attribute (e.g. anthropogenic cover or forest cover), the random factor (i.e. the locality) and the fixed factor (i.e. the landscape attribute) together explain a higher variation in species richness (i.e. conditional R^2 > marginal R^2), but these models had low empirical support.

Discussion

To the best of our knowledge, this study represents the first assessment of patterns of occurrence and species richness of Neotropical primates from a naturally patchy landscape to include human factors alongside landscape attributes and patch characteristics. Our key findings include that, while landscape variables, particularly matrix composition, are the most important correlates of occurrence of all species, the number of residents is the most important correlate of species richness. The probability of occurrence of the large-bodied primates (*A. belzebul*, and *C. olivaceus* and *S. apella*) also decreased with increasing proximity to the state capital, Macapá. Beyond this, we found that *C. olivaceus* and *S. apella*, *A. belzebul*, and *S. midas* were less frequent in patches in Curiaú, the most disturbed region, than in the other two regions, and that *P. pithecia* and *A. macconneli* were restricted to BR-156, the least disturbed region, where overall species richness was also higher. Taken together, these results seem to indicate that anthropogenic use and disturbance are influencing the primate community in the Savannas of Amapá. Indeed, the proportion of anthropogenic cover (urban areas, roads, bare ground and agricultural fields) in the landscape was found to be an important predictor, and negatively related to species richness and the probability of occurrence of all primate species. Given the precipitous increase in anthropogenic cover in the region in recent years, and the likely continuing trend towards the expansion of large-scale agriculture (Hilário et al. 2017; Mustin et al. 2017), our results have important implications for the conservation of Neotropical primates in the Savannas of Amapá.

Scale of effect

The only factor that influenced SE was the location, which is likely due to variation in disturbance levels, with SE of forest cover being higher in Curiaú (more disturbed) than in BR-165 (least disturbed). This result may indicate that in Curiaú primates use habitat further away from the focal patch and that as such they need to travel larger distances than in the less disturbed regions. This result is consistent with another study regarding Neotropical primates where the SE was larger in the most disturbed region and where animal movements among fragments seemingly follow metapopulation dynamics (Galán-Acedo et al. 2018). From an ecological perspective, these results suggest that the primate community in the SOA may be modulated by a metacommunity dynamic, such that a set of local communities are interacting through dispersal among patches (Livingston et al. 2013). At the species level (i.e. metapopulation dynamics), similar processes have been suggested to occur for *Alouatta palliata* in a highly fragmented landscape in Mexico (Galán-Acedo et al. 2018), as many individuals were recorded switching between fragments to obtain resources (Anzures-Dadda and Manson 2007; Galán-Acedo et al. 2018). In another savanna ecosystem from Colombia, four primate species have been recorded using live fences to move between patches (Carretero-Pinzón 2010), and indeed this could also be occurring in the SOA. Given these results, conservation planning for primates in the SOA must take into account locality when considering forest cover, as the SE of forest cover varied between localities. However, when other variables are included, differences in SE between localities disappear, suggesting that conservation planning does not need to be carried out in separate regional units, unless strong changes occur in the landscape. That being said, the smaller proportion of anthropogenic cover in BR-156 compared with Pedreira and Curiaú might call for different conservation priorities between the localities. Specifically, avoiding the conversion of savannas into agricultural fields, such as has been anticipated in the *Zoneamento Socioambiental do Cerrado do Amapá* (Socioenvironmental Zoning of the Savannas of Amapá) (Hilário et al. 2017), is urgent to maintain primate species richness in the BR-156. While this is also crucial in the more highly disturbed location, there the primate community could also benefit from further conservation actions such as increasing connectivity using live fences. In addition, species home range size had no effect on the SE. This may reflect the importance of other spatio-temporal processes, such as migration and source-sink dynamics, in determining species occurrences (Jackson and Fahrig 2015; Galán-Acedo et al. 2018), as has previously been suggested for Atelids in Mexico (Galán-Acedo et al. 2018).

Influence of landscape scale processes on primates

Anthropogenic cover was the only important landscape correlate of the probability of occurrence of all primate species, as well as overall species richness. Roads, agricultural fields and human settlements denote hostile, less permeable and low quality matrices that act to increase isolation of primates in the forest patches (Michalski and Peres 2005). However, according to our results, the effects of anthropogenic cover operate mostly over short distances (scale of effect up to 400 m). This may indicate that primate dispersal might be affected not only by the anthropogenic cover in and of itself (i.e. roads, agriculture and human settlements), but also by other human-environment interactions that may be taking place, such as persecution from people and domestic animals (Michalski and Peres 2005), and degradation of forest vegetation (Lewis et al. 2015).

While anthropogenic cover was an important correlate for all species, forest cover was only important for the larger primates (*A. belzebul*, *C. olivaceus* and *S. apella*). In general, studies in fragmented landscapes have shown that forest cover is important not only for primates (Benchimol and Peres 2013; Carretero-Pinzón et al. 2017), but also for bats, carnivores, rodents, marsupials and forest specialist birds (Carrara et al. 2015; Arroyo-Rodríguez et al. 2016; Melo et al. 2017; Rabelo et al. 2019). This is consistent with the habitat amount hypothesis which posits that species richness (or occurrence) increases as the patch size and the natural habitat surrounding the patch increase (Fahrig 2013). Our study indicates that the same pattern is true for patchy non-fragmented environments, indicating that similar mechanisms are probably operating. This reinforces the significance of forests as reservoirs of biodiversity and highlights the importance of maintaining forest patches to support primate communities and the ecological services they provide (Chapman et al. 2013; Estrada et al. 2017; Andresen et al. 2018). Although deforestation is not a common process in the SOA, wildfires are common there (Mustin et al. 2017) and could reduce the extension and the quality (reducing forest height, tree diversity, increasing lianas and pioneer species) of the forest patches (Hoffman et al. 2003) with negative consequences for primates and other species.

At the landscape level, and contrary to our expectations, the probability of occurrence of two primate species declined with increasing savanna cover, which may suggest that the savannas are not very permeable for these species. Indeed, savannas generally seem to represent poor structural connectivity for mammals (Piña et al. 2019). Additionally, and consistent with our prediction, water bodies have a negative effect on the occurrence of all primate species in the SOA. Large seasonal lakes (mainly found in Curiaú) may reduce primate movements between forest patches because of the physical impediment, but also due to disturbances caused by fishing and rearing of African buffalo. Small dams are frequently made to provide water for cattle, and to be used for fish farming and recreation, which may also increase disturbance levels, acting as deterrents to primates.

Finally, the large block of forest that surrounds the SOA may act as source of individuals of all primate species as occurrence rate is higher as distance to the block decrease. The mainland-island model from metapopulation theory assumes that the mainland (the block of forest) is a source of individuals that migrate to habitat islands (the forest patches) (Hanski and Gyllenberg 1993). Patterns of occurrence of some mammal species have been consistent with this theory (Lawes et al. 2000). This has implications for the conservation of wild populations since such blocks of forest, when protected, can act as a source of species in the landscape (Naranjo and Bodmer 2007). The state of Amapá is the most protected in Brazil, and its protected areas generally encompass continuous forest. It is possible that immigration to forest patches is necessary to keep viable primate populations in the SOA and thereby, effort must be made to optimize landscape connection in order to keep the movements of fauna through riparian forest, palm corridors and forest patches.

Influence of patch scale processes on primates

For all but *A.belzebul*, probability of occurrence was higher in patches where the forest is taller, which is a reflection of higher habitat quality in these patches (Anzures-Dadda and Manson 2007; Gouveia et al. 2014; Carretero et al. 2017; Piña et al. 2019), and possibly of vertical stratification of the primate community (Peres 1993). The fact that *A.belzebul* is more likely to be found in patches where the forest is not so tall does not however mean that this species prefers low-quality habitat, but rather likely reflects the importance of other environmental variables (e.g. soils) in influencing forest characteristics related to high-quality habitat, such as fruit production. In the Colombian Llanos, occupancy of both *Alouatta seniculus* and *Sapajus apella* has been shown to decrease with increasing forest height, which it has been suggested reflects the importance of topography and forest composition, rather than canopy height, in determining habitat quality for these species (Carretero et al. 2017). Indeed, our results show that at the patch level, the probability of occurrence of *A.belzebul* is related to patch shape, increasing with irregularity of the patch. *Alouatta belzebul* has a relatively high proportion of leaves in its diet (Pinto et al. 2003), and irregular forest patches have a higher edge proportion, leading to edge effects that include modified plant species composition in the patch border (Liu et al. 2019), ultimately increasing the representation of plant species with higher nutrient content (Poorter and Bongers 2006), with obvious benefits to *A. belzebul*. These findings are consistent with another Amazonian areas where *Alouatta* prefers forest edges (in fragmented forests) and river borders (in continuous forest) instead of the forest interior (Peres 1997; Lenz et al. 2014). However, such results may depend on site context or even depend on species specificity, since another *Alouatta* species (*A. palliata*) did not present preference for either edge or interior environments in Costa Rica (Bolt et al. 2018; Johnson et al. 2020). Similarly, we found higher occurrence of *S. sciureus*, a species with a higher proportion of arthropods in its diet, in irregular forest patches. However, models of this species were not reliable, which may suggest that other factors not considered in this study, such as site level variables (e.g. number of trees with fruits, Carretero-Pinzón et al. 2017), are more important correlates of the occurrence of *S. sciureus*.

Influence of human processes on primates

The probability of occurrence of the largest bodied primates in the SOA increased with distance from the most populated city (Macapá). The occurrence of *Alouatta* genus has also been shown to be positively correlated with distance to the city in forest fragments in the southern Amazon (Michalski and Peres 2005). This pattern may reflect increased hunting pressure on large bodied mammals, which are often preferred by hunters (Jerozolimski and Peres 2003). In the SOA, hunting is a common activity closer to the city (Silvestre et al. 2020). Indeed, eight interviewees indicated that primates were among their target hunted species during the data collection for this study, with a focus on the larger species (*A. belzebul* 50%, *A. macconnelli* 12.5%, and *C. olivaceus* and *S. apella* 37.5%). Moreover, two interviewees told us they had eaten *A. belzebul* during the three weeks prior to the interview. In contrast to this pattern for the larger primates, and contrary to our prediction, we found that the probability of occurrence of *S. midas* –the smallest primate– increased with proximity to the city. This could reflect a pattern of reduced inter-specific competition as larger-bodied species are absent from these patches (likely due to hunting), meaning that smaller species can occupy the fragments (Peres and Dolman 2000), though this has not been assessed specifically in the SOA.

While the occurrence of most species is not related to the number of residents in the landscape, we found that overall species richness is lower where the number of residents is higher, and that the probability of occurrence of *C. olivaceus* and *S. apella* is actually higher in more densely populated areas. Human population density has previously been related to low probability of occurrence of mammals and low species richness (Parks and Harcourt 2002; Urquiza-Haas et al. 2009). The number of residents is a driver of biodiversity loss mainly at small scales, reducing species richness, and it is associated with other human activities such as road kills, persecution and low habitat quality (Urquiza-Haas et al. 2009). In terms of *C. olivaceus* and *S. apella*, their increased occurrence may reflect increased resource availability as areas with higher numbers of residents are associated with more shifting cultivation of manioc and small-scale fruit plantations, and *Cebus* and *Sapajus* can feed actively on such crops (Freitas et al. 2008; Spagnoletti et al. 2017).

Conservation implications and future directions

Amazonian savannas, including the SOA, are being cleared for large-scale agribusiness plantations at a fast pace, before conservationists and researchers are truly able to characterize their biodiversity and ecosystem processes, and as such, understanding their role for biodiversity conservation (Carvalho and Mustin 2017). As we found no difference in the scale of effect between primate species, conservation strategies for primates in this landscape can focus on the primate community as a whole, rather than on particular species. Given that landscape attributes are the most important correlates of primate occurrence in the SOA, conservation actions for primate populations should follow a "functional landscape" perspective by maintaining both higher forest cover and structural connectivity (see Melo et al. 2013). Possible strategies to increase the conservation value of forest fragments in the SOA for primates include protecting against the spread of large-scale agriculture and infrastructure projects, the planting of live fences to promote dispersal throughout the landscape, and reduction of disturbance associated with water bodies via fishing, pastoralism and recreational activities. These actions can, in theory, be achieved in collaboration with private landowners or through the establishment of protected areas. Conservation strategies for primates, and even other animals, outside of protected areas could include planning for their sustainable use through agreements of use with local communities, and enhancing connectivity through protection of native vegetation on private properties, including individual trees that may be used as stepping-stones in agricultural fields, and tree-lines or palm corridors that act as elements of structural connectivity between forest patches across crop fields and non-forest environments. The establishment of protected areas may be particularly important in landscapes such as the SOA, as forest patches are currently surrounded by extensive areas of natural environments (e.g. savannas), but anthropogenic cover is increasing quickly (Mustin et al. 2017). Planning and implementation of potential new protected areas must take into account both the biodiversity value of the SOA, and also their importance for the well-being, livelihoods and traditions of local communities, and the process through which such areas are planned must be open, transparent, participatory and respectful of local land and resource use rights and customary tenure.

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Fig. 1 The three study locations (Pedreira, Curiaú and BR-156) in a savanna ecosystem in the state of Amapá (Brazil), in the northeastern part of the Amazon. Buffers with dotted lines represent the forest patches that were not included in the analyses to test the second prediction about the scale of effect, nor in the analysis of species richness

Fig. 2 Association between landscape size (radius in a circular landscape) and difference in Akaike's Information Criterion (ΔAIC) between forest cover and two response variables: (a) primate occurrence, and (b) species richness. ΔAIC was obtained from generalized linear models. The range of scale of effect is indicated with a gray horizontal line (Ab: *A. belzebul*; Cap: Capuchins (*C. olivaceus* and *S. apella*); Ss: *S. sciureus*; Sm: *S. midas*; Cur: Curiaú; BR: BR-156; and Ped: Pedreira). Dotted horizontal line indicate the limit in which models are considered to have equivalent support. Black symbols indicate ΔAIC ≥ 2

Fig. 3 Average relative importance for each group of variables (landscape, patch and human) for four primate species and species richness in a Brazilian Amazonian savanna. For *S. midas* and *A. belzebul* only one variable related to human factors was present in the set of models, impeding the calculation of the average. Capuchins are *C. olivaceus* and *S. apella*

Fig. 4 Relative Importance of landscape attributes, patch characteristics and human factors for four primate species (capuchins are *C. olivaceus* and *S. apella*) and species richness in a Brazilian Amazonian savanna. Numbers within bars of landscape attributes and NR are the scale of effect. Note that for species richness the scale of effect depends on each locality (Ped: Pedreira; Cur: Curiaú; and BR: BR-156). Symbols indicate whether the relationship is positive (+) or negative (–). Predictors are anthropogenic cover (AC), water bodies (WB), forest cover (FC), savanna (Sav), distance to block of forest (DF), patch area (PA), forest height (FH), shape index (SI), distance to city (DC), and number of residents (NR). Vertical line is the threshold ($\sum w_i = 0.4$) above which the variable is considered to be an important correlate of primate occurrences and richness

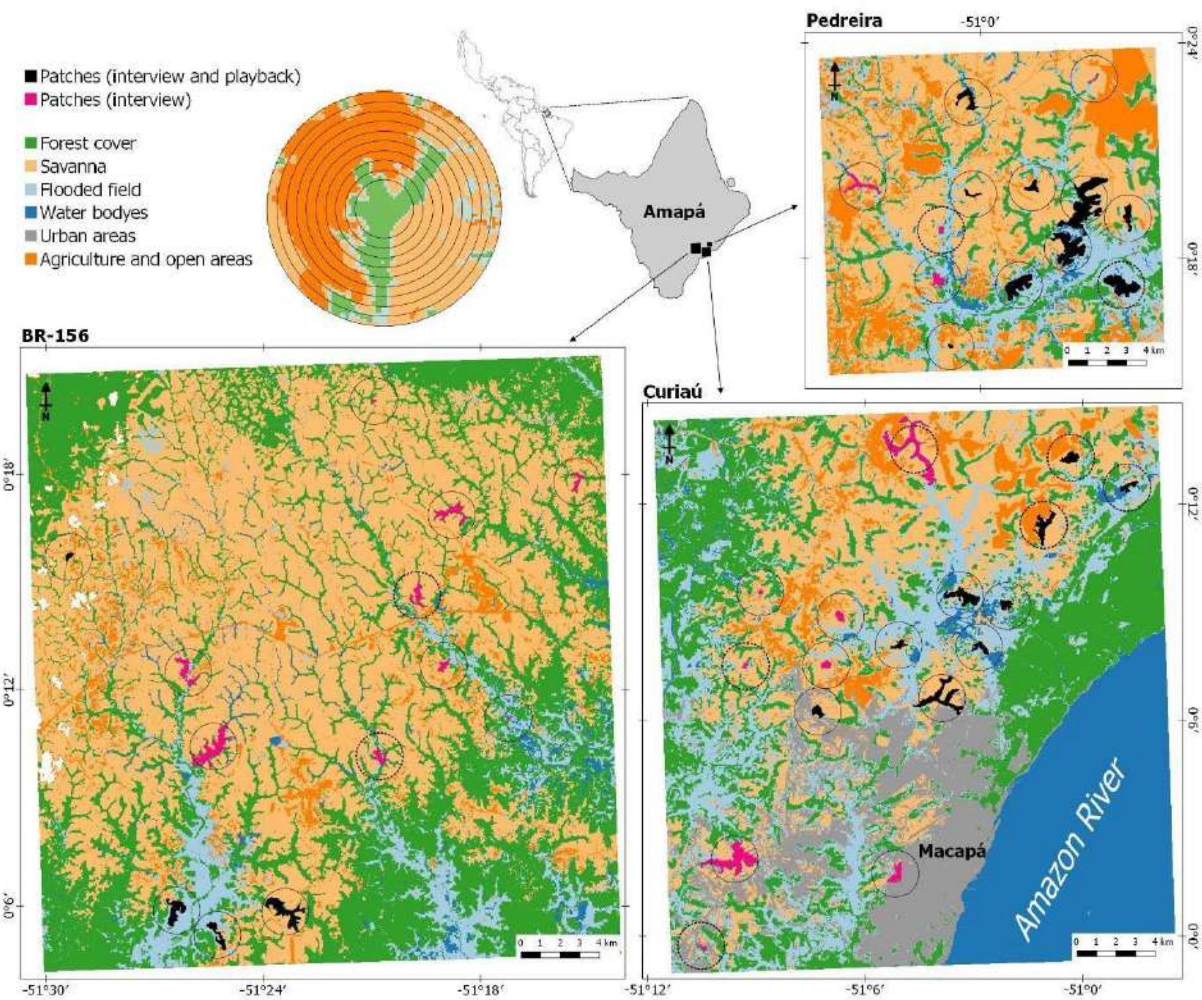
Patches (interview and playback)
Patches (interview)
Forest cover
Savanna
Flooded field
Water bodyes
Urban areas
Agriculture and open areas
Amapá
Pedreira
-51°0′
0°24′
0°18′
BR-156
0°18′
0°12′
0°6′
-51°30′
-51°24′
-51°18′
Curiaú
0°12′
0°6′
0°0′
-51°12′
-51°6′
-51°0′
Macapá
Amazon River
N
0 1 2 3 4 km

Fig. 1

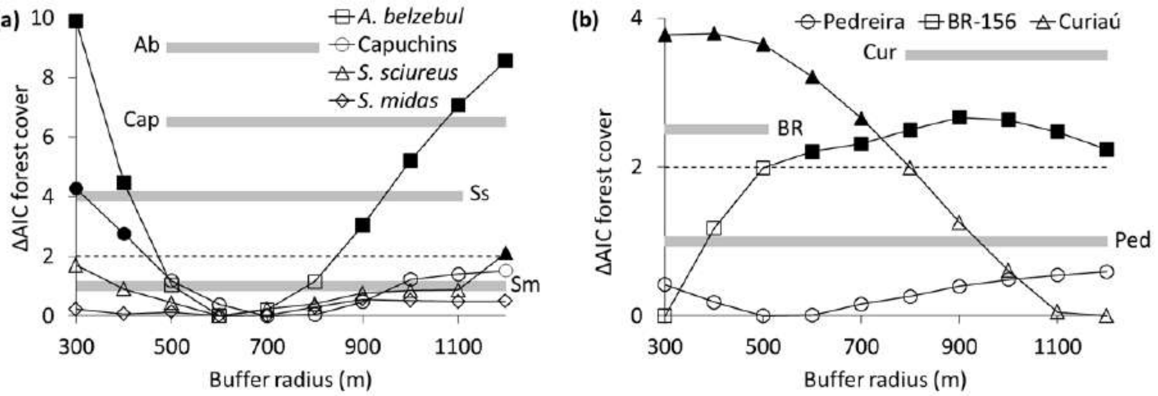
(a)
A. belzebul
Capuchins
S. sciureus
S. midas
Ab
Cap
Ss
Sm
ΔAIC forest cover
10
8
6
4
2
0
300
500
700
900
1100
Buffer radius (m)
(b)
Pedreira
BR-156
Curiaú
Cur
BR
Ped
ΔAIC forest cover
4
2
0
300
500
700
900
1100
Buffer radius (m)

Fig. 2

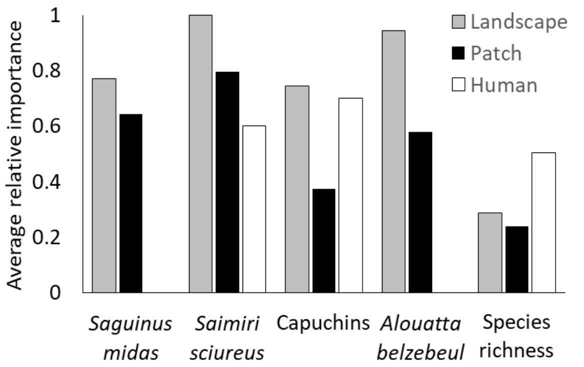
1
0.8
0.6
0.4
0.2
0
Average relative importance
Landscape
Patch
Human
Saguinus midas
Saimiri sciureus
Capuchins
Alouatta belzebeul
Species richness

Fig. 3

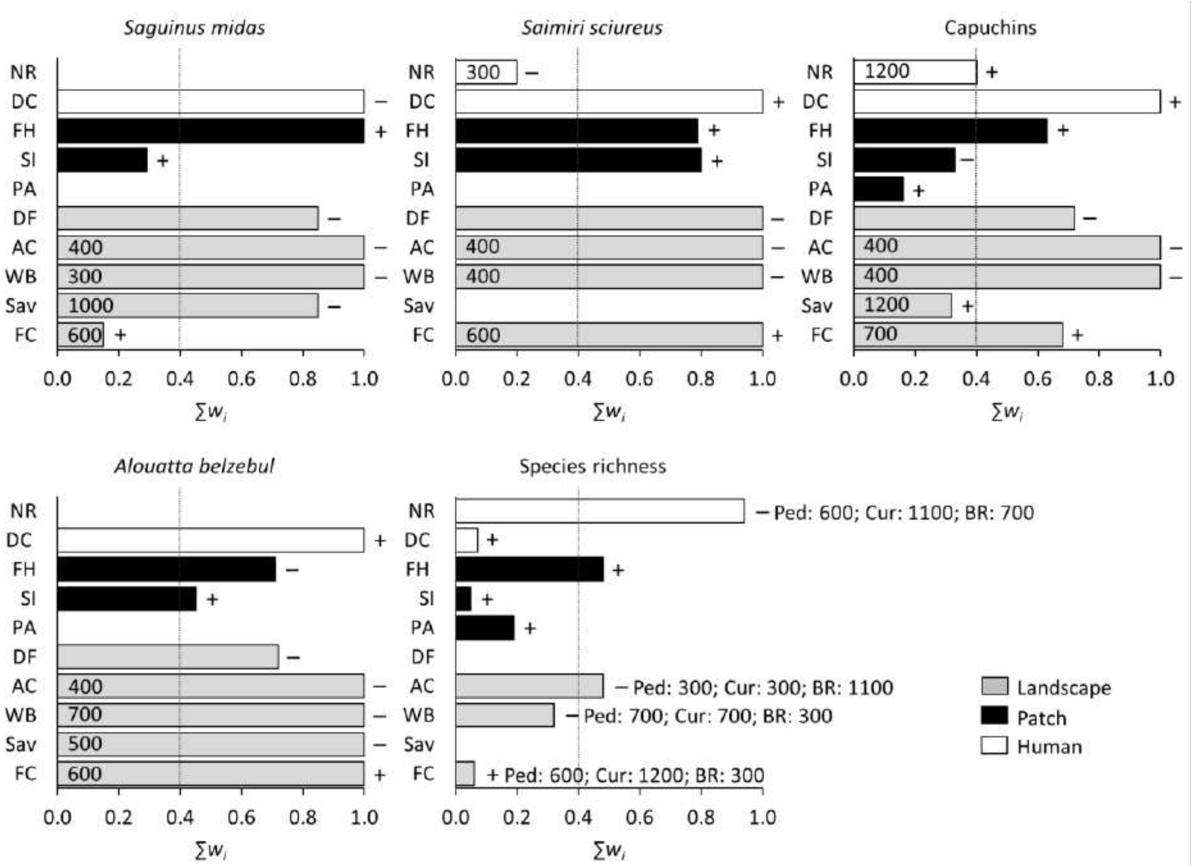
Saguinus midas
Saimiri sciureus
Capuchins
Alouatta belzebul
Species richness
NR
DC
FH
SI
PA
DF
AC
WB
Sav
FC
400
300
1000
600
1200
700
500
– Ped: 600; Cur: 1100; BR: 700
– Ped: 300; Cur: 300; BR: 1100
– Ped: 700; Cur: 700; BR: 300
+ Ped: 600; Cur: 1200; BR: 300
Landscape
Patch
Human
0.0
0.2
0.4
0.6
0.8
1.0
$\sum w_i$

Fig. 4

Drivers of primate richness and occurrence in a naturally patchy landscape in the Brazilian Amazon

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Table S1 Matrix of inputs to run the Cohen's kappa to measure the concordance of presence-absence data between interviews and playbacks of four species of primates. E_0 and PB_0 are absences in the interview and playback, respectively, and E_1 and PB_1 are presences in the interview and playback, respectively. Coefficients were high for *A. belzebul* (Kappa = 0.83; p = 0.00003), and *P. pithecia* (Kappa = 1; $p < 0.00001$), moderate for *S. midas* (Kappa = 0.529; p = 0.01), and small for *S. sciureus* (Kappa = 0.188; p = 0.131) and Capuchins (Kappa = 0.253; p = 0.08).

	S. midas		*A. belzebul*		*S. sciureus*		Capuchins		*P. pithecia*	
	PB_0	PB_1	PB_0	PB_1	PB_0	PB_1	PB_0	PB_1	PB_0	PB_1
E_0	9	1	9	0	7	0	8	0	17	0
E_1	4	7	2	13	11	4	9	4	0	3

Table S2 Set of models of landscape attributes, patch characteristics and human factors related to the occurrence of four primate species. Attributes of landscape are forest cover (FC), water bodies (WB), savanna (Sav), anthropogenic cover (AC) and distance to block of forest (DF). Patch characteristics are forest height (FH), patch area (PA) and shape index (SI). Human factors are distance to the city (DC) and number of residents (NR). *p*-value according to the Likelihood ratio test, AUC is the Area Under the ROC Curve, and w_i is the weight of each model.

Species	Predictors								*p*-value	AUC	AICc	ΔAICc	w_i
Saguinus midas	AC	FH	DC	DF	WB	Sav			0.007	0.92	11.44	0.00	0.40
	AC	FH	DC	DF	WB	Sav	SI		0.02	0.92	12.09	0.64	0.29
	AC	FH	DC	WB	Sav				0.004	0.90	13.36	1.91	0.15
	AC	FH	DC	DF	FC	WB			0.007	0.93	13.43	1.99	0.15
Saimiri sciureus	AC	FH	DC	DF	WB	Sav			0.23	0.77	11.44	0.00	0.40
	AC	FH	DC	DF	WB	Sav	SI		0.15	0.76	12.09	0.64	0.29
	AC	FH	DC	WB	Sav				0.23	0.77	13.36	1.91	0.15
	AC	FH	DC	DF	FC	WB			0.33	0.77	13.43	1.99	0.15
Capuchins	AC	FH	DC	DF	FC	WB			0.0002	0.97	7.37	0.00	0.08
	AC	DC	DF	FC	WB				< 0.0001	0.98	7.75	0.38	0.06
	AC	FH	DC	FC	WB				< 0.0001	0.98	7.88	0.51	0.06
	AC	FH	DC	DF	WB	PA	Sav		0.001	0.96	8.13	0.76	0.05
	AC	FH	DC	DF	FC	WB	NR		0.0009	0.98	8.19	0.82	0.05
	AC	FH	DC	DF	FC	WB	SI		0.0009	0.97	8.22	0.85	0.05
	AC	FH	DC	DF	WB	Sav			0.001	0.95	8.34	0.97	0.05
	AC	DC	DF	FC	WB	NR			0.0002	0.97	8.39	1.02	0.05
	AC	DC	DF	FC	WB	SI			0.0002	0.97	8.40	1.03	0.05
	AC	DC	DF	WB	PA	Sav			0.0004	0.96	8.42	1.05	0.05
	AC	FH	DC	FC	WB	NR			0.0002	0.97	8.51	1.14	0.04
	AC	DC	FC	WB					< 0.0001	0.97	8.52	1.15	0.04
	AC	FH	DC	DF	WB	NR	Sav		0.002	0.95	8.52	1.15	0.04
	AC	FH	DC	FC	WB	SI			0.0002	0.98	8.57	1.20	0.04
	AC	FH	DC	DF	WB	Sav	SI		0.003	0.94	8.72	1.35	0.04
	AC	DC	FC	WB	NR				< 0.0001	0.97	8.96	1.60	0.03
	AC	DC	FC	WB	SI				< 0.0001	0.97	8.97	1.60	0.03
	AC	FH	DC	DF	WB	NR	Sav	SI	0.006	0.95	9.07	1.71	0.03
	AC	DC	DF	WB	NR	PA	Sav		0.001	0.96	9.14	1.77	0.03
	AC	FH	DC	DF	WB	NR	PA	Sav	0.003	0.96	9.16	1.79	0.03
	AC	DC	DF	FC	WB	NR	SI		0.0008	0.97	9.19	1.82	0.03
	AC	FH	DC	DF	FC	WB	NR	SI	0.002	0.97	9.21	1.84	0.03
	AC	FH	DC	FC	WB	NR	SI		0.0008	0.97	9.35	1.98	0.03
Alouatta belzebul	AC	FH	DF	DC	FC	WB	Sav		0.0003	0.97	5.58	0.00	0.24
	AC	FH	DF	DC	FC	WB	Sav	SI	0.0009	0.97	6.13	0.55	0.18
	AC	DF	DC	FC	WB	Sav			0.0001	0.96	6.44	0.86	0.16
	AC	FH	DC	FC	WB	Sav			0.0001	0.96	6.48	0.89	0.15
	AC	DF	DC	FC	WB	Sav	SI		0.0003	0.97	6.75	1.17	0.13
	AC	FH	DC	FC	WB	Sav	SI		0.0003	0.96	6.80	1.22	0.13

Table S3 Set of models of landscape attributes, patch characteristics and human factors related to primate species richness. Attributes of landscape are forest cover (FC), savanna (Sav), water bodies (WB), and anthropogenic cover (AC). Patch characteristics are forest height (FH), patch area (PA) and shape index (SI). Human factors are distance to the city (DC) and number of residents (NR). Marginal R^2 values (mR^2) only consider fixed effects (predictors), and conditional R^2 (cR^2) includes both fixed and random effects (localities). The variance for the random intercept is $\hat{d}$, and w_i is the weight of each model.

	Predictors			mR^2	cR^2	$\hat{d}$	AICc	ΔAICc	w_i
Models with empirical support (i.e. ΔAICc < 2)	FH	NR		0.45	0.45	0	111.65	0.00	0.14
	AC	NR	PA	0.51	0.51	0	111.70	0.05	0.13
	AC	NR		0.49	0.49	0	111.88	0.23	0.12
	FH	WB	NR	0.51	0.51	0	111.97	0.32	0.12
	FH	AC	NR	0.48	0.48	< 0.000001	112.11	0.46	0.11
	WB	NR		0.55	0.55	0	112.56	0.91	0.09
	DC	AC	NR	0.48	0.48	0	113.05	1.40	0.07
	FH	WB		0.40	0.40	0	113.23	1.58	0.06
	WB	NR	PA	0.55	0.55	0	113.28	1.63	0.06
	FH	FC	NR	0.49	0.49	0	113.28	1.63	0.06
	AC	NR	SI	0.50	0.50	0	113.64	1.99	0.05
Models without empirical support (i.e. ΔAICc > 2)	WB			0.48	0.48	0	115.27	3.62	
	AC			0.13	0.32	0.13	122.27	10.62	
	Sav			0.44	0.44	0	122.94	11.29	
	Null model						123.31	11.66	
	FC			0.09	0.48	0.35	123.88	12.23	

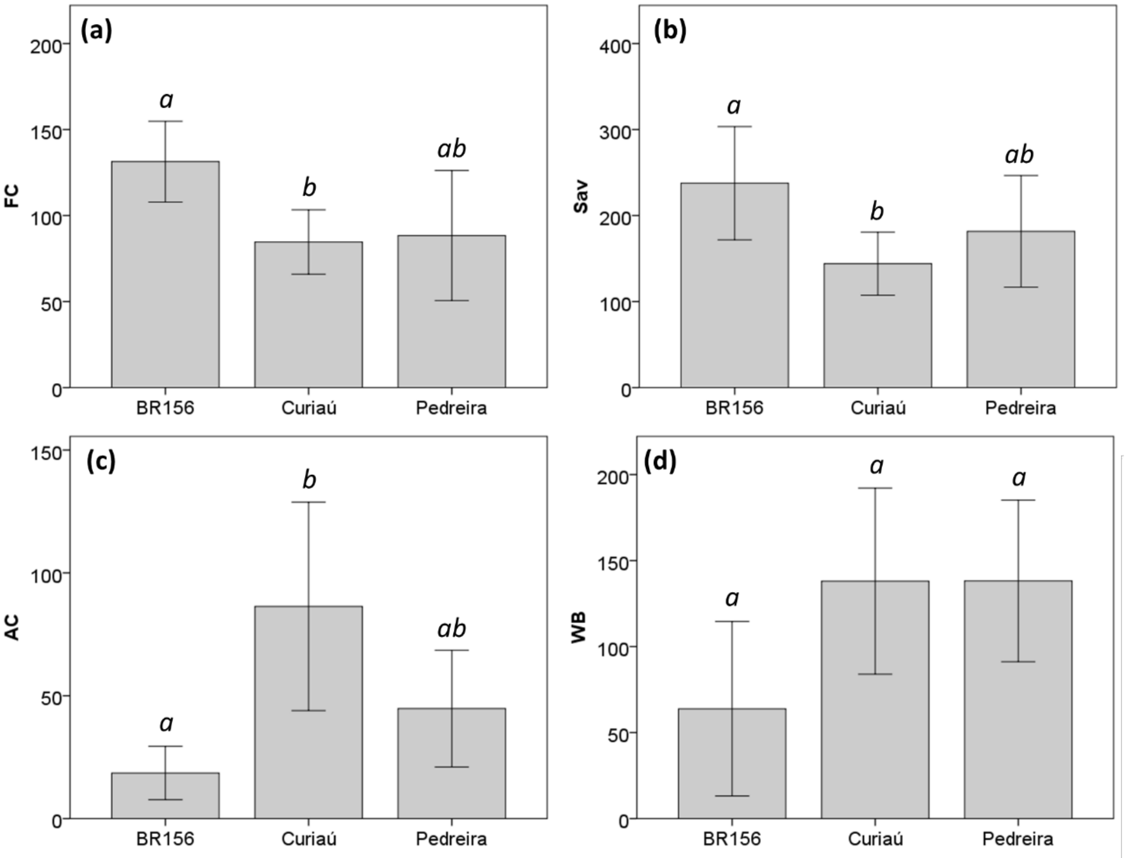

Fig. S1 Comparison landscape attributes (a: FC-forest cover; b: Sav-savanna; c: AC-anthropogenic cover; and d: WB-water bodies) among three locations (BR-156, Curiaú and Pedreira). Measurements were made in radius of 1200 m from the center of each forest patch. Bars with the same letter (*a* or *b*) indicate locations that are not significantly different ($P < 0.05$) according to Tukey's multiple comparison test. Bars and whiskers represent the mean and 95% confidence intervals, respectively.

ARTIGO CIENTÍFICO 3

Priority areas for conservation of primates in a threatened Amazonian savanna

Artigo para ser submetido ao periódico

“Journal of Environmental Planning and Management”

Priority areas for conservation of primates in a threatened Amazonian savanna

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We used the distribution of six primate taxa and four vegetation types to identify a network of priority areas to conserve an Amazonian savanna in Brazil, using a Systematic Conservation Planning approach. We constructed species distribution models (SDM) for the primates and defined as conservation targets the proportion of the distribution of each primate within the network according to their vulnerability and 30% of each vegetation type. We created a map of potential use of the land for agriculture and another of environmental risk, and together with the SDMs and vegetation types, identified the network of priority areas by using the software Marxan. Conservation targets for primates and vegetation types were met by protecting 3,240 km^2 in the savannas. These priority areas represent a starting point for a participatory process that includes all stakeholders in the savannas to design a conservation programme that involves new PAs and conservation on community lands.

Key words: Amapá; Brazil; community lands; environmental risk; potential use of the land for agriculture; protected areas; Systematic Conservation Planning

1. Introduction

Worldwide, protected areas (hereafter referred to as PAs) continue to be the key tool used to conserve biodiversity (Gray *et al*. 2016). However, the extent to which these areas are effective is still in dispute (Rodrigues *et al*. 2004a; Rodrigues *et al*. 2004b; Watson *et al*. 2014), as they tend to be placed in areas that are more politically acceptable (Joppa and Pfaff 2009), and not necessarily where they would best cover the distributional ranges, nor where they would best contribute to the continued persistence of species and ecosystems (Margules and Pressey 2000; Jenkins and Joppa 2009). In addition, PAs often do not receive the resources necessary for effective management (Leverington *et al*. 2010; Dias, Cunha, and Silva 2016) which could affect the long-term survival of populations, persistence of habitats and the continued provision of ecosystem services (Newmark 1996; Durán *et al*. 2013; Márquez *et al*. 2017). Despite these issues, and in line with Aichi Biodiversity Target 11, global coverage of PAs has increased in recent years, with many countries meeting or exceeding the target to protect at least 17% of terrestrial ecosystems (UNEP-WCMC, IUCN, and NGS 2018). However, this target seems to be insufficient as anthropogenic pressures, mainly the expansion of agricultural areas and infrastructure development, are increasing in key areas (Pouzols *et al*. 2014; Vilela *et al.* 2020). In this scenario, the establishment of new PAs needs to be done in a way that minimizes the potential for conflict with local communities and agricultural production, including careful selection of the location for new PAs, truly participatory processes for their design and establishment, and integration with innovative public policies for conservation on community lands (Brandon *et al*. 2005; Dudley *et al*. 2018).

Systematic Conservation Planning (SCP) is a much used tool that can support more transparent and participatory decision-making processes that involves finding the best set of potential PAs (see Ardron, Possingham, and Klein 2010). In practice, SCP often involves setting quantitative objectives in relation to biodiversity features used as surrogates of overall biodiversity, taking into account the current system of PAs –when existing– to identify conservation gaps, and select a subset from the whole set of PAs to carry out conservation actions on the ground (Margules and Pressey 2000). In addition, the process is based on constraints (sometimes referred as costs) on where new PAs may be located, or where conservation actions may be implemented (Watson *et al*. 2011), such as economic factors, environmental impact, value for agriculture, or human density, among others (Brandon *et al.*

2005; Pinto and Grelle 2011; Lessmann, Muñoz, and Bonaccorso 2014; Lessmann *et al*. 2019; Quintana, Girardello, and Balslev 2019). In some specific cases, such constraints may be used as a surrogate for the socioeconomic context, with the aim of minimizing the chances of creating or fuelling conservation conflicts (Brandon *et al*. 2005; Pinto *et al*. 2007; Pinto and Grelle 2011; Quintana, Girardello, and Balslev 2019). The selection of the biodiversity features to be used as surrogates, and the setting of quantitative targets are key to a meaningful and useful SCP process. Sometimes, large sets of species are used as the biodiversity features (Lessmann, Muñoz, and Bonaccorso 2014; Lessmann *et al*. 2019), whereas in other cases, more limited groups of species are used representing a single taxonomic group, such as primates (Pinto and Grelle 2011; González 2015; Carretero-Pinzón 2016).

Primates are globally recognized as an important component of biodiversity, since they support ecosystem services such as seed dispersal (Chapman *et al.* 2013; Andresen, Arroyo-Rodríguez, and Ramos-Robles 2018). Their extirpation from ecosystems is related to loss of plant diversity, modification of plant recruitment patterns (Gardner *et al*. 2019) and may alter the carbon storage in the forest ecosystems (Peres *et al*. 2016). Local extinction of primates has been shown to have a higher negative effect on forest regeneration than loss of other animals such as ungulates and birds, especially on plants with large seeds (Gardner *et al*. 2019). Currently, 55% of primate species are globally threatened and the expansion of agriculture is one of the main threats (Estrada *et al*. 2017). In the Neotropical region, for example, more than 40 million hectares of soybean plantations displaced primate habitats (Estrada *et al*. 2017), and this area is likely to increase further, particularly across the Neotropical savannas, as global demand for soy and other commodities is also increasing (Lambin and Meyfroidt 2011). Primate diversity is also correlated with diversity of other mammals (Emmons 1999; Muldoon and Goodman 2015), and thus, primate local extinctions also potentially indicate larger impacts than those expected specifically by their loss.

The Savannas of Amapá, a complex of Amazonian savannas, are located in the Northeastern extreme of the Amazon, in the Brazilian state of Amapá. This complex is a mosaic of forest patches and open areas and is highly threatened by the rapid expansion of soybean plantations in the open areas (Hilário *et al*. 2017; Mustin *et al*. 2017). Only 9% of this biodiverse ecosystem is within PAs (Mustin *et al*. 2017). One nocturnal (*Aotus infulatus*) and seven diurnal primates occur there: the red-handed tamarin (*Saguinus midas*), the white-faced saki (*Pithecia*

pithecia), the squirrel monkey (*Saimiri sciureus*), the weeper capuchin (*Cebus olivaceus*), the brown capuchin (*Sapajus apella*), the Guiana red howler (*Alouatta macconnelli*), and the red-handed howler (*Alouatta belzebul*) (Sousa, Silva, and Kasecker 2008). One of these species (*A. belzebul*) is globally listed as threatened (vulnerable) according to the Red List of Threatened Species (Valença-Montenegro *et al*. 2019). Considering the accelerated transformation of this ecosystem and that anthropogenic cover in this landscape negatively affects primate occurrence and richness (Calle-Rendón *et al.* unpublished data), a conservation strategy for the biodiversity of the Savannas of Amapá, especially the primate community, is necessary. In fact, a greater proportion of this ecosystem has been identified as one of the regions of highest both biological importance and priority for environmental protection by the Brazilian government (Ministério do Meio Ambiente 2017).

In order to suggest a strategy for the conservation of this savanna complex, here we used the distributions of the seven diurnal primate species as conservation targets in a SCP approach to select a network of priority areas. As Neotropical primates are forest dwelling animals, we expect that a strategy which is expected to effectively conserve primates will also necessarily conserve forest patches, which are the primate habitat, as well as the ecosystem services they provide (e.g. vegetation regeneration, carbon storage). However, a conservation strategy for the savannas of Amapá would of course be incomplete if it did not consider the adjacent open areas, and as such we also set conservation targets for the four main vegetation types present in the savanna. The priority areas identified by this analysis represent a starting point to begin a participatory process that should bring together local communities, conservation practitioners, scientists and policy-makers, to design a holistic community conservation programme that might involve new PAs, as well as conservation on community lands, since such lands may contribute to positive outcomes for biodiversity conservation (Garnett *et al*. 2018; Leiper *et al.* 2018; Tran, Ban, and Bhattcharyya 2020).

2. Materials and methods

2.1. Study site

The Savannas of Amapá (here after SOA) are located in the Amazon region, in the far northeast of the Brazilian Amazon, in the state of Amapá. The SOA extends for ~10,000 km^2 and presents four main vegetation types: shrub savanna, woodland savanna, grass savanna and park savanna

(Figure 1). The vegetation composition and plant species richness are different among these vegetation types, varying especially in the density of trees and shrubs (Mustin *et al*. 2017), and all of them host patches of forest in the middle of open areas (i.e. a savanna matrix). Colonists and descendants of escaped African enslaved (traditional communities known as *Quilombolas*, who have legal land rights in Brazil) inhabit the SOA, and have lived there for centuries. Areas of the SOA have already been transformed for human use, including eucalyptus plantations, commercial plantations of maize and manioc, roads and human settlements (Hilário *et al*. 2017; Mustin *et al*. 2017). Rapid on-going transformation to soybean plantations is a particular current threat (Hilário *et al*. 2017; Mustin *et al*. 2017). Hunting is an additional pressure in the SOA (Silvestre *et al*. 2020), and primates are commonly hunted there (Calle-Rendón *et al.* unpublished data).

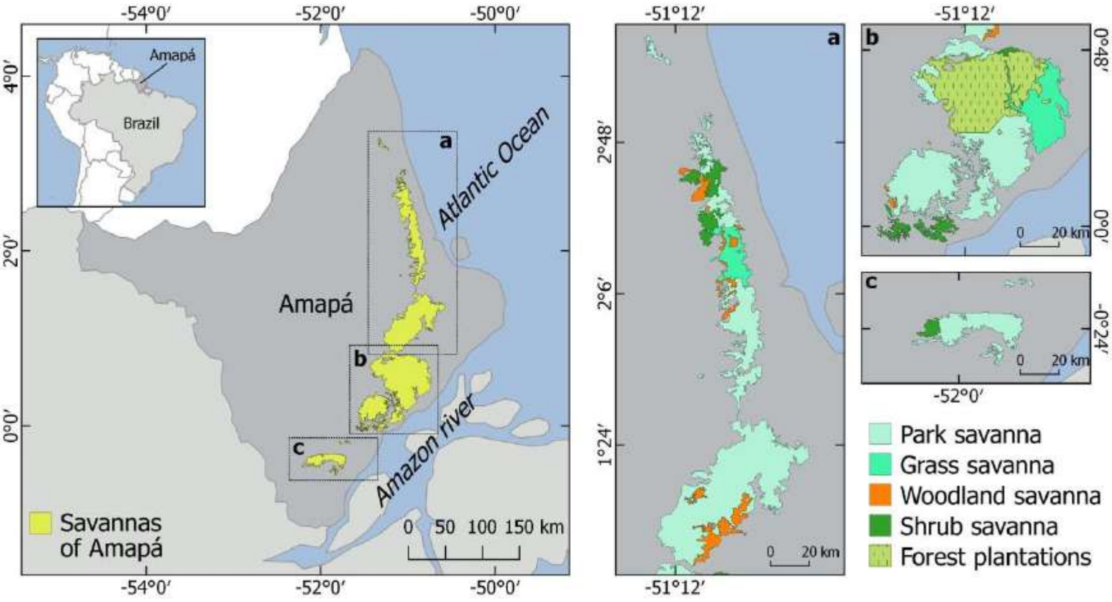

Figure 1. Location of the Savannas of Amapá in the state of Amapá, Northeastern extreme of the Brazilian Amazon.

2.2. Primate surveys

Between October 2017 and February 2018 (fieldwork-1), we carried out interviews with local inhabitants and gathered information about the occurrence of primate species in a region of approximately 3,000 km^2 in the center of the SOA (Figure 2). We conducted 77 interviews that provided information on primate presence in 59 locations representing 52 forest patches and 7 locations in continuous forest adjacent to the savanna ecosystem. In June 2019 (fieldwork-2), we visited an additional region in the northern part of the SOA of approximately 650 km^2 to carry out 20 additional interviews with local inhabitants, which provided information on primate presence in 17 forest patches (Figure 2). We used photographs of the primates from the region and asked the participants which species they had seen in a specific forest patch.

Previous studies have used interviews with local people to gather information about occurrence of several mammal species –including primates– in large areas (Urquiza-Haas, Peres, and Dolman *et al*. 2009; Martínez-Martí *et al*. 2016; Camino *et al*. 2020). Moreover, interviews have a higher detection probability than standard methods (e.g. transects and camera traps), represent a useful and cost-effective approach (Camino *et al*. 2020), and are useful to gather presence data for species distribution models (Luizza *et al*. 2016; Evangelista *et al*. 2018). Nevertheless, to validate the data on primate presence and absence obtained in the interviews, we performed playback sessions in 22 forest patches in the area of fieldwork-1 between July and December 2018. As *C. olivaceus* and *S. apella* were reported frequently by participants to be present in patches in which only one species was recorded during playback surveys, we joined the records of the presence of both species as presence of Capuchins. Both species are close ecospecies (i.e. classifications of platyrrhine primates according to functional traits of species that are ecologically equivalent, Peres and Janson 1999), and as such joining records of the species is not expected to affect our analyses. We calculated the Cohen's kappa coefficient to measure the concordance of presence-absence data between interviews and playbacks. We did not include *Aotus infulatus* in the analysis, as night monkeys are more difficult to detect. Published information about primate occurrence in the SOA is extremely scant and was not used here (e.g. Silva *et al*. 2013; Coelho, Juen, and Mendes-Oliveira 2014) (see details in the section Extended Methods in Appendix).

2.3. Species distribution models

We constructed species distribution models (SDMs) for all species using maximum-entropy models implemented in the software Maxent (version 3.4.1) (Phillips, Dudík; and Schapire 2019). The number of presence points used to develop the SDMs in the training area varied between species, depending on the total number of records gathered during the fieldwork (37 for *S. midas*, 35 for *S. sciureus*, 11 for *P. pithecia*, 35 for Capuchins, 17 for *A. macconnelli*, and 24 for *A. belzebul*). For all species (but *A. macconnelli*), we used the area of fieldwork-1 as a training area, and for *A. macconnelli*, we used the area of fieldwork-2 (Figure 2). We used images at a 1 km spatial resolution of four bioclimatic variables that represent annual trends (annual precipitation), seasonality (precipitation seasonality), and extreme or limiting environmental factors (precipitation of wettest quarter, and precipitation of driest quarter) from Worldclim 1.4 (Hijmans *et al*. 2005), height above the nearest drainage as a surrogate of topography (Rennó *et al*. 2008), and percentage tree cover (Hansen *et al*. 2003) as predictor variables. For each species, we gathered information on each predictor variable in the training area and conducted a pair-wise correlation test to exclude highly correlated variables ($r \geq |0.8|$) (Carvalho *et al.* 2017). We assessed the performance of each SDM through the area under the ROC (Receiver Operating Characteristic) curve (AUC), the difference between test and training AUC, and the test omission rate. We defined the background (i.e. the training area) and the projection area according to our knowledge about the species distribution in the SOA, hence some areas from the training and projection area were excluded for *Alouatta* spp. and *P. pithecia*. The SDMs were transformed into binary maps using the Minimum Training Presence as the threshold. Predictive models were projected to the northern and southern part of the SOA using the same predictors from the training models. Then we used an additional 7, 15, 1, 17 and 11 points outside the training area to test the projection for *S. midas*, *S. sciureus*, *P. pithecia*, Capuchins, and *A. macconnelli*, respectively. We calculated the percentage of correct classification by intersecting all presence data of each species with its binary map (Brito *et al*. 2009). Due to the resolution of the images used in the analysis, the identification of suitable areas took into account all savanna ecosystems, this means, SDMs will probably identify both forested and open areas as suitable. However, as some Neotropical primates from fragmented forests and savanna ecosystems (e.g. *Alouatta*, *Sapajus*, *Saimiri* and *Saguinus*) use open areas to travel between fragments (Boyle *et al.* 2013; Carretero-Pinzón 2013), we think this will not represent a problem in the use of our SDMs as potential areas of primate distribution in the SOA (see details in the section Extended Methods in Appendix).

2.4. Conservation goals

Persistence of a given species within a PA may depend on population size (Shaffer 1981), and consequently, conservation goals should be established according to individual criteria for each species such as minimum population size or population density (Shaffer 1981; Woodroffe and

Ginsberg 1998). However, due to the scarcity of information to establish those values for most species, other approximations have been used elsewhere to give priority to certain species in conservation schemes (e.g. Rodrigues *et al.* 2004b; Lessmann, Muñoz, and Bonaccorso 2014) according to traits that can predict vulnerability to extinction. Here we defined the conservation goals based on the proportion of the distribution of each of the six primate taxa (five species plus capuchins) to be included in the network of priority areas according to the SDMs. The proportion of each primate taxa range was set to be between 20% and 50% of the total distribution within the SOA, varying in accordance with species vulnerability to extinction based on four traits: body mass, home range, geographic extension within the SOA, and extinction risk. We assumed that larger-bodied species, those with larger home ranges, species with more restricted geographic extensions, and those listed by the IUCN as more threatened with extinction, would be more vulnerable (Table 1) (Woodroffe and Ginsberg 1998; Purvis *et al*. 2000; Lessmann, Muñoz, and Bonaccorso 2014). For body mass, home range and geographic extension a value between 1 and 3 was assigned for each species, with a value of 1 assigned to the least vulnerable of the six taxa (i.e. the smallest species, the species with the smallest home range, and the species with the largest geographic extension), a value of 3 assigned to the most vulnerable species (i.e. the largest species, the species with the largest home range, and the species with the smallest geographic extension), and linear interpolation was used to assign relative values to all other species. We used extinction risk based on the IUCN red list category, as a fourth characteristic of each species and we also assigned a score to that. However, all species were either Least Concern (LC) or Vulnerable (VU), and so we assigned scores of 1 to LC species (least vulnerable) and 3 to VU species (most vulnerable) (Table 1). These four values assigned to each trait and the extinction risk were then summed for each species to create a prioritization index with a minimum possible value of 4 (least vulnerable across all three traits and extinction risk) and a maximum value of 12 (most vulnerable across all three traits and extinction risk) (Table 1).

To set the target for proportional distribution in the SOA to be protected, we conducted a linear interpolation based on a goal of 20% where the prioritization index equals 4 (minimum), and 50% where the prioritization index equals 12 (maximum), leading to values between 20.7% for *S. midas* and 42.3% for *A.belzebul* (Table 1). Additionally, we defined that the proportion of savannas to be included within the network of priority areas would be 30% as recommended previously (Hilário *et al*. 2017), considering each type of vegetation (park savanna, woodland savanna, grass savannas and shrub savanna). We considered targets higher than the Aichi Biodiversity Target 11 (17%) as projections of agricultural expansion show that higher targets will be necessary to protect biodiversity (Pouzols *et al*. 2014) (see details in the section Extended Methods in Appendix).

Table 1. Conservation goals of each target in a Brazilian Amazonian savanna in the state of Amapá.

Conservation target	ER	GE (km^2)	BM (kg)	HR (ha)	P	Conservation goal (%)
Saguinus midas	LC	7,910[a]	0.56[b]	35[c]		
	[1]	[1]	[1]	[1.18]	4.18	20.7
Saimiri sciureus	LC	6,167[a]	0.82[b]	153[d]		
	[1]	[1.51]	[1.09]	[2.01]	5.61	26.0
Pithecia pithecia	LC	1,120[a]	1.76[b]	9[e]		
	[1]	[3]	[1.41]	[1]	6.41	29.0
Capuchins*	LC	6,129[a]	2.95[b]	296[f g]		
	[1]	[1.52]	[1.82]	[3]	7.34	32.5
Alouatta belzebul	VU	1,378[a]	6.40[b]	11h[i]		
	[3]	[2.92]	[3]	[1.02]	9.94	42.3
Alouatta macconnelli	LC	4,346[a]	6.37[b]	18[j]		
	[1]	[2.05]	[2.99]	[1.07]	7.11	31.6
Savanna ecosystem	–	–	–	–	–	30

Note: Each conservation goal is the extent of each conservation target to be protected within the priority areas. For primate taxa it is based on the IUCN extinction risk (ER), the geographic extension within the SOA (GE), body mass (BM), and home range (HR). Numbers within brackets are the index values, being 3 for the most vulnerable species and 1 for the least. The P is the prioritization index, which ranges between 4 and 12 for each taxa. **Sapajus apella* and *Cebus olivaceus*. [a]This study [b]Galán-Acedo *et al*. (2019) [c]Day and Elwood (1999) [d]Defler (2010) [e]Oliveira *et al.* (1985) [f]Zhang (1995) [g]Miller (1996) [h]Bonvicino (1989) [i]Pinto, Azevedo-Ramos, and Carvalho (2003) [j]Boubli, DiFiore, and Mittermeier (2008)

2.5. Identifying priority areas for conservation

We used the software Marxan (version 2.4) (Ball, Possingham, and Watts 2009) to identify priority areas for the protection of the six primate taxa and the four vegetation types in the SOA. Marxan solves the *minimum set* system design problem, which aims to find the set of planning units (PUs) that will meet the conservation goals in terms of representing biodiversity characteristics, for the minimum possible cost. Planning units can be defined based on a regular grid across the landscape, or geographic or political boundaries, such as land parcels. Here we overlaid the landscape of the SOA with a grid of 4,203 hexagons of 3 km^2, a similar size to the largest home range among the target species (*S. apella*, ~3.2 km^2) (Zhang 1995). Using PUs of this size means that if a single PU was selected as a priority area, it could protect at least one group of *S.apella*, or indeed any of the other species which have smaller home range requirements. Priority areas may be made up of a single PU or several adjacent PUs.

The cost of each PU may be measured directly by a monetary value (Lessmann *et al.* 2019), or indirectly based on proxies, such as human population size (Pinto and Grelle 2011), the accessibility of land to humans (Drummond *et al.* 2010), or by an assessment of the threats to biodiversity (Lessmann, Muñoz, and Bonaccorso 2014). Here, we used two proxies for PU cost. The first was potential use of the land for agriculture, where the higher the potential, the higher the assumed land prices, but also higher potential for social conflict (Brandon *et al.* 2005; Quintana, Girardello, and Balslev 2019) and higher opportunity costs as a result of not using the land for agriculture (Naidoo *et al.* 2006). The second proxy was environmental risk –based on threat mapping– where the higher the risk, the higher the costs of conservation management because threats to biodiversity are higher and restoration and other management activities therefore more expensive in terms of resources required (Lessmann, Muñoz, and Bonaccorso 2014).

In terms of PU cost, we considered three possible scenarios. Firstly, we used six attributes related to agriculture (Nguyen *et al.* 2015), weighted according to a multi-criteria analysis (see Table A1 and Table A3 in the section Extended Methods in Appendix) to create a map of potential use of the land for agriculture across the SOA (scenario 1, see Figure A1 in the section Extended Methods in Appendix). The six attributes used were: 1) slope as an attribute of topography; 2) cation exchange capacity as an attribute of soil fertility; 3) percentage composition of the soil in terms of three components (sand, silt and clay) as an attribute of soil texture; 4) precipitation of the driest quarter as a bioclimatic attribute; and two measures of accessibility and ease of export of agricultural commodities, 5) distance to Santana city (where the fluvial port is located which is the main point of export for commodities such as soybean); and 6) distance to the nearest main road. Secondly, we mapped environmental risk (scenario 2, Figure A1) using six attributes that represent potential threats to biodiversity, weighted according to a multi-criteria analysis (see Table A2 and Table A4). The six attributes used were: 1) distance to main roads; 2) distance to secondary roads; 3) fire intensity; 4) distance to forest plantation; 5) distance to agricultural fields; and 6) distance to human settlements. Finally, we created a third map combining both the potential use of the land for agriculture and the environmental risk (scenario 3, Figure A1 - see details in the section Extended Methods in Appendix).

The Marxan algorithm includes a term for the Boundary Length Modifier (BLM) which essentially weights the importance of connectivity between selected PUs relative to the overall cost of the network of priority areas (Ball and Possingham 2000), helping to favor the selection of more connected networks. For the three scenarios, we tested BLMs of 0, 10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}, 10^{-1} and 1, and found that in all three cases the optimal BLM was 10^{-3} (see Figure S1). In all cases, we excluded PUs partially or fully overlapped with agriculture fields, forest plantations, and human settlements, and all PUs partially or fully overlapping with PAs were included, such that new priority areas would be selected to complement the existing reserve network in terms of reaching our conservation targets (Lessmann, Muñoz, and Bonaccorso 2014; Lessmann *et al.* 2019). The conservation goal for each target (i.e. the extension to be protected) was set according to the prioritization analysis carried out above (Table 1). In all cases, we executed Marxan applying the ‘annealing followed by the iterative improvement algorithm’ method, for 10^6 iterations, and 100 runs. We used the Marxan “best” solution (i.e. the run with the lowest cost from the 100 runs) as the best representation of the network of priority areas (see details in the section Extended Methods in Appendix).

2.6. Conservation feasibility

We evaluated the feasibility to establish each priority area. The feasibility of each area was assessed by using the size of each priority area divided by its total cost from the map of potential use of the land for agriculture, and the size of each priority area divided by its total cost from the map of environmental risk. Priority areas in sites of high potential use of the land for agriculture may indicate low feasibility as future conflicts between landowners and managers could happen, or because purchasing such sites require a higher economic effort. Additionally, areas in sites of high environmental risk may indicate low feasibility as a high effort for surveillance is needed. Thus, feasibility gives an idea about the future persistence of a priority area. We plotted the values of those variables (area/cost from the map of potential use of the land for agriculture in the abscise axis against area/cost from the map of environmental risk in the ordinate axis) (Figure S2) and then located each priority area in one of the following four categories: maximum feasibility, high feasibility, medium feasibility, and low feasibility (see details in the section Extended Methods in Appendix). In order to identify potential areas for conservation on community lands, we identified the priority areas with *Quilombos* communities inside their boundaries by overlapping the priority areas with a shape of *Quilombos* presence retrieved from the *Secretaria de Estado do Meio Ambiente* (SEMA 2016, Hilário *et al.* 2017).

2.7. Economic investment

Based on the current network of PAs in the state of Amapá, Dias, Cunha, and Silva (2016) made an estimation of the financial investment (in Brazilian reais – R$) that would be necessary to establish a new PA in the state. They took into account establishment costs related to infrastructure, equipment, planning and demarcation, as well as management costs related to staff, operation, maintenance and projects. All this represented an annual investment over five years of R\$1,196.8/km^2 (see details in Dias, Cunha, and Silva 2016). Based on this figure and our results, we used the size of the network of priority areas from Marxan to calculate the economic investment required to establish both the whole priority network and each subset of priority areas as PAs. We used an exchange rate of R$4.03 : US$1 according to the *Banco Central do Brasil* on 31 December 2019 (https://www.bcb.gov.br/conversao), this means an annual investment over five years of US\$297/km^2.

3. Results

3.1. Primate distribution in the Savannas of Amapá

For all species distribution models (SDMs), values of test AUC fell between 0.74 and 0.98 (Table S1). The percentage of correct classification of presences was high for all species (95.1% for *S. midas*, 94% for *S. sciureus*, 83.3% for *P. pithecia*, 90.1% for Capuchins and 85.7% for *A.*

macconnelli), indicating that projections were well supported. There was no common pattern in the SDMs, and depending on the species, either the northern or southern part of the savanna complex represented more suitable areas for the primates (Figure 2). However, most suitable areas for *P. pithecia* were found mainly in the center of the SOA (Figure 2). We found that the most important predictors in the SDMs of all species (but *A. belzebul*) were tree cover percent and a bioclimatic variable (annual precipitation or precipitation of driest quarter, Table S2), indicating higher probability to find primates in forested and more humid parts of the savanna complex. For *A. belzebul*, instead, the most important predictors were annual precipitation and height above nearest drainage (Table S2) indicating the preference of this species for forest patches along the water courses (which are the lowest parts of the relief). High precipitation and a forest cover in the landscape ranging between 0.2 and 0.3 km^2 (based on the resolution of the tree cover percent raster) might sustain a higher habitat suitability for *S. midas*, *S. sciureus*, *P. pithecia*, Capuchins and *A. macconnelli* (Figure S3). For *A. belzebul*, the higher the precipitation and the lower the distance to a drainage (i.e. lowland areas) the higher the habitat suitability (Figure S3).

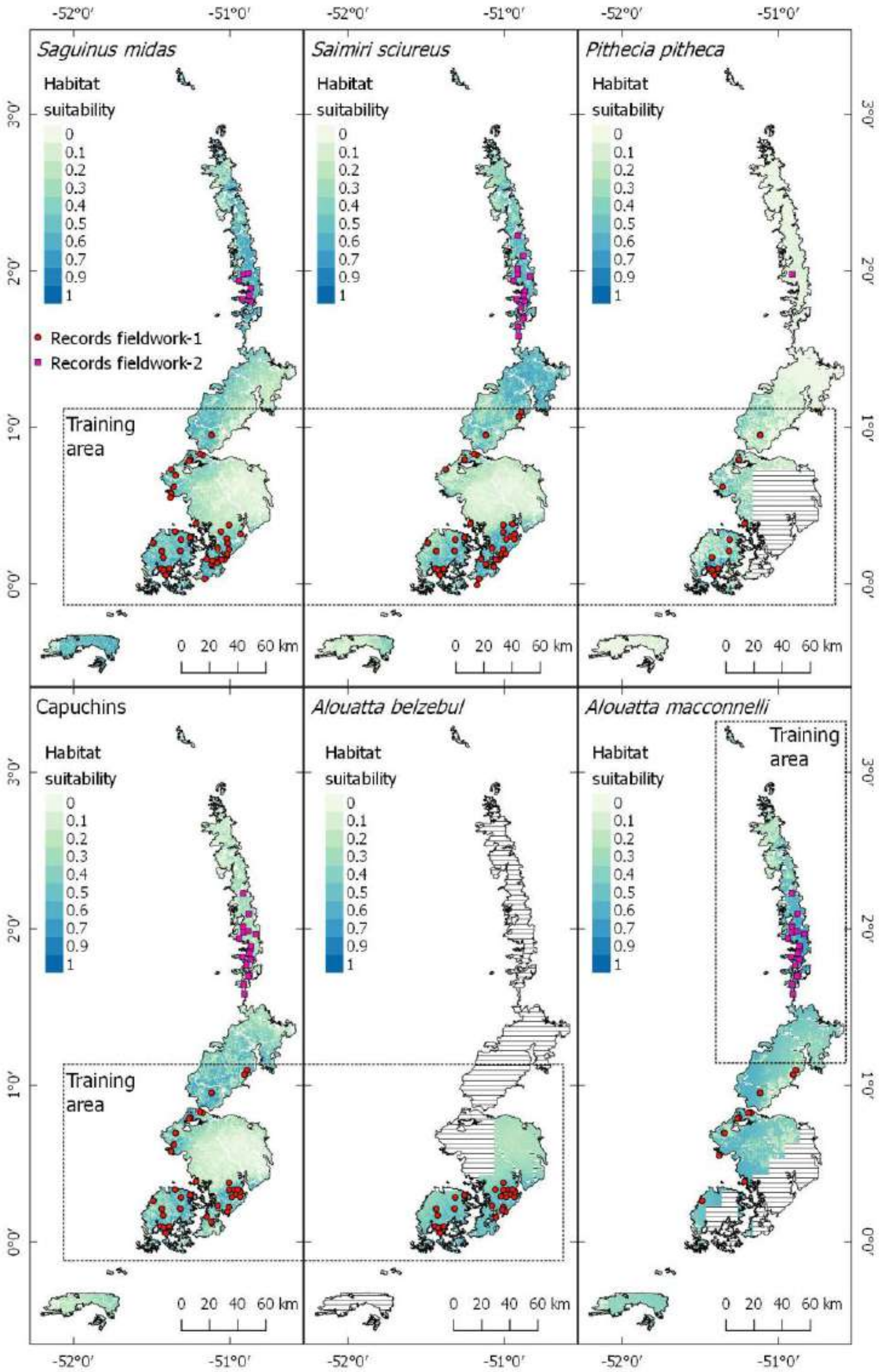

Figure 2. Habitat suitability for six primate taxa in a Brazilian Amazonian savanna in the state of Amapá, estimated by Maximum Entropy. Horizontal lines within the savannas are located where the species are not distributed.

3.2. Identifying priority areas for conservation

The “best” solutions chosen by Marxan in the three scenarios were spatially similar and showed the network of priority areas distributed along all parts of the SOA (Figure 3). In all three scenarios, conservation goals were reached (Table S3); however, the total cost and the extension protected in each network were different. Considering only the potential use of the land for agriculture (scenario 1), the network reached the protection of 3,183 km^2 within the SOA, with the selection of 20 priority areas and a total cost of 3,811 (Figure 3A). However, considering only the environmental risk (scenario 2), the network increased the protection by 3% (3,291 km^2) with the selection of 23 priority areas and a cost of 1,939 (Figure 3B). Considering both the environmental risk and the potential use of the land for agriculture (scenario 3), the network reached a size of 3,240 km^2 with a selection of 20 priority areas and a cost of 2,881 (Figure 3C).

3.3. Conservation feasibility of priority areas

The subset of maximum feasibility included four priority areas (including the biggest priority area, 807 km^2) that protected 1,611 km^2 (~16% of the SOA), located in the center of the SOA and had three *Quilombos* (Figure 3C). The subset of high feasibility had five priority areas and summed 273 km^2 (~3%), whose priority areas were located in the center of the SOA and had two *Quilombos* (Figure 3C). Two priority areas totaling 495 km^2 (~5%) were located in the northern part of the SOA and represented the subset of medium feasibility (Figure 3C). The subset of low feasibility had nine priority areas in the northern and southern part of the SOA, and protected 825 km^2 (~8%) (Figure 3C).

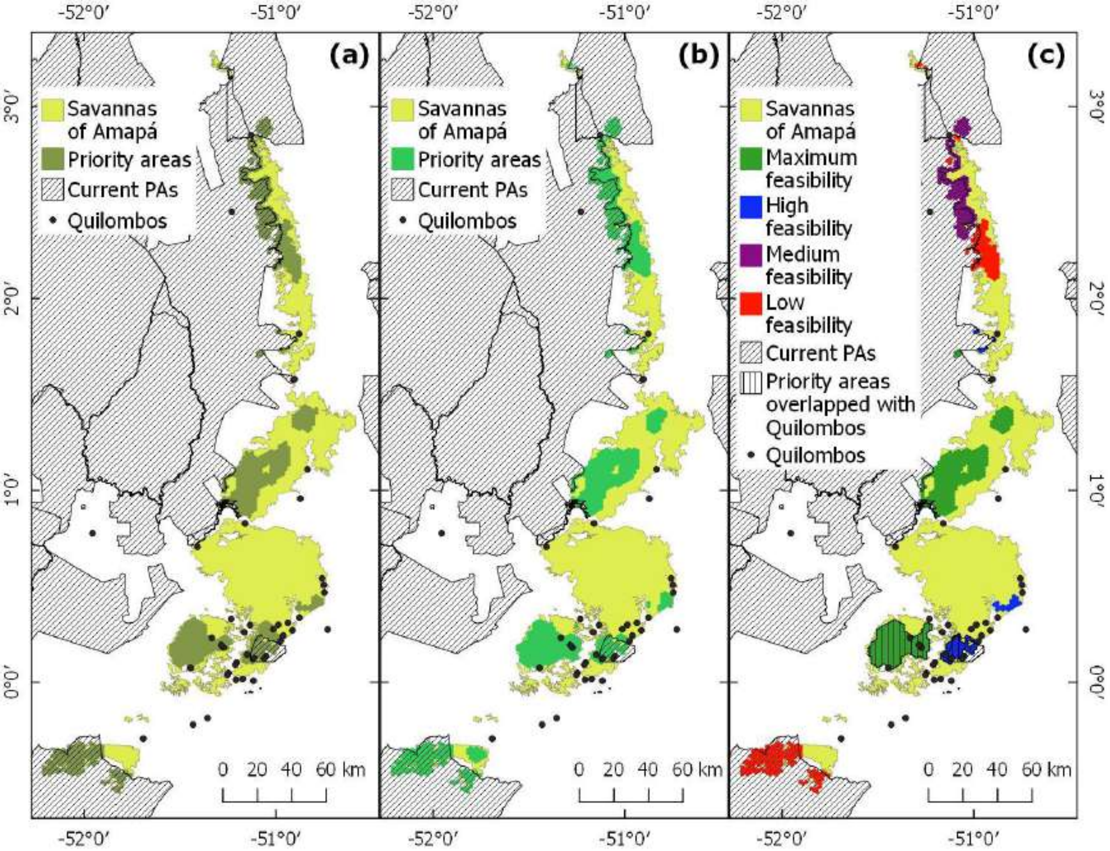

Figure 3. Priority areas defined using information of six primate taxa and four vegetation types in a Brazilian Amazonian savanna in the state of Amapá. The network of priority areas represent the Marxan "best" solution and were identified using three constraints: (a) potential use of the land for agriculture; (b) environmental risk; and (c) a combination of both potential use of the land for agriculture and environmental risk. In the last scenario, we identified four subsets of priority areas according to their feasibility and priority areas overlapped with *Quilombos*.

None of the four subsets of priority areas included all targets (Table 2). The four priority areas listed as maximum feasibility had the highest amount of targets held, and reached an average of 66.5% of the conservation targets. This was the only subset including all primate species, but they did not protect the shrub nor grass savanna (Table 2). The subset of priority areas listed as medium and low feasibility reached an average of 18.6% and 16% of its conservation targets, respectively. These were the only subsets including the four vegetation types, but both of them left *A. belzebul* and *P. pithecia* unprotected (Table 2). The subset listed as high feasibility reached an average of 7% of its conservation targets (Table 2).

Table 2. Amount in square kilometers (% within parenthesis) held for each target in four subsets of priority areas in a Brazilian Amazonian savanna in the state of Amapá.

Target	Maximum feasibility	High feasibility	Medium feasibility	Low feasibility
Saguinus midas	1,518 (92.7)	189 (11.6)	269 (16.4)	562 (34.3)
Saimiri sciureus	1,403 (87.5)	186 (11.6)	224 (14.0)	303 (18.9)
Pithecia pithecia	457 (140.6)	Not included	Not included	Not included
Capuchins*	1,462 (73.4)	165 (8.3)	68 (3.4)	334 (16.8)
Alouatta belzebul	412 (70.6)	171 (29.4)	Not included	Not included
Alouatta macconnelli	1,130 (82.3)	10 (0.7)	43 (3.1)	190 (13.9)
Woodland savanna	48 (35.6)	Not included	71 (52.5)	32 (23.9)
Shrub savanna	Not included	Not included	153 (92.7)	60 (36.5)
Park savanna	1,490 (82.1)	144 (7.9)	70 (3.9)	294 (16.2)
Grass savanna	Not included	61 (22.0)	5 (1.9)	213 (76.2)
Average (percentage)	66.5	7.0	18.6	16.0

Note: **Sapajus apella* and *Cebus olivaceus*

3.4. Economic investment

To establish PAs across the whole network of priority areas identified here, it would be necessary to invest approximately (considering the average of the three scenarios) US$958,122/year over five years. The subsets of maximum, high, medium and low feasibility had establishment costs of US$478,467/year over five years, US$81,081/year over five years, US$147,015/year over five years, and US$245,025/year over five years, respectively.

4. Discussion

We used the distribution of six primate taxa, four vegetation types, potential use of the land for agriculture, and environmental risk to identify a network of priority areas for the conservation of a threatened and largely unprotected savanna ecosystem in the Brazilian Amazon. Such a network would protect the ecosystem services provided by primates and the savannas themselves, such as seed dispersal, pollination, and fruit production, among others (Estrada *et al.* 2017; Hilário *et al.* 2017). However, the “best” solution presented here is not the only good solution in terms of priority areas, and as such represents a starting point to plan conservation action, rather than a plan in of itself. Indeed, in order to achieve positive outcomes for both biodiversity and local communities in the SOA, these priority areas should be used as part of a participatory process that should bring together local communities, conservation practitioners, scientists and policy-makers, to design a holistic community conservation programme. This programme might involve new PAs, public policies to support conservation on community lands, and other innovative partnerships to protect this culturally and environmentally important landscape (Haller *et al.* 2008). Such an approach should be implemented with collaborative management, being sure to identify resources important for locals, negotiate agreements among all stakeholders, and establish responsibilities to achieve the objectives related to conservation and livelihoods for local people (Barrow and Murphree 2001).

4.1. Priority areas as protected areas

Protected areas are one important tool that should form part of a conservation strategy for the savannas of Amapá. As a such, PAs have been shown to have higher species diversity of arthropods, birds, and mammals –including primates– inside than outside their boundaries (Fabricius, Burger, and Hockey 2003; Greve *et al*. 2011; Silva *et al*. 2018; Calle-Rendón, Hilário, and Toledo 2019). In the Neotropical region, protected forest patches conserve primate species of higher body mass than unprotected ones, with benefits for seed dispersal and for plant diversity (Calle-Rendón, Hilário, and Toledo 2019). Large primates such as *Alouatta* genus are important for the dispersal of large seeded fruits (Arroyo-Rodríguez *et al*. 2015). In consequence, these primates may support not only forest regeneration, but also carbon storage, since plants with larger seeds are expected to have life history traits associated to larger size, heavy wood density and long life-span and hence, store more carbon over a longer time period (Osuri and Sankaran 2016). Primates have been used as conservation targets in SCP (Pinto and Grelle 2011; González 2015; Carretero-Pinzón 2016), and have also been considered as flagship species because they are charismatic and may act as symbols of conservation movements (Dietz, Dietz, and Nagagata 1994; Savage *et al*. 2010; Supriatna *et al*. 2014). Thus, we propose *A. belzebul* as a flagship species in the SOA as it is charismatic and threatened. As a result, focusing conservation efforts on *A. belzebul* may also protect other species and ecosystem services. However, it is also important to guarantee a threshold of forest cover in the landscape (~30% in 1 km^2), as tree cover percent was the main predictor for the other primate species according to the species distribution models. This threshold, at the scale used in this study, suggests that heterogeneous environments (i.e. that contain both savanna areas and forest patches) could present higher habitat suitability for primates. Those areas may offer a higher length of borders and as such, this may result in an edge effect with benefit for primates (Lenz, Jack, and Spironello 2014). Globally, differences in land cover has shown to benefit both plant and animal diversity (Stein, Gerstner, and Kreft 2014), and in the SOA specifically, different environments have been shown to benefit mammal diversity (Piña *et al*. 2019). Concomitantly, it is imperative to give special attention to the forest in lowland areas for *A. belzebul*, as suitable areas for this species are related to lower values of height above nearest drainage. Such areas are important in terms of palm abundance, especially of *Euterpe oleracea* and *Mauritia* sp., and as such, those palm species are key for primates and other fauna species (Lees and Peres 2008; Hoek, Soas and Peñuela 2019; Silvestre *et al.* unpublished data).

Palms are also important for local communities, frequently being used as a source of non-timber forest products (FAO 2002), and indeed in the SOA, palm species produce fruits that represent an important aspect of livelihoods for rural families in the region (Lima 2003). These products, together with other services such as climate change mitigation, regulation of regional climate and hydrological cycles, and bushmeat, are provided by PAs (Naranjo and Bodmer 2007; Soares-Filho *et al*. 2010; Lima *et al*. 2014; Mukul *et al*. 2016). All these ecosystem services, in theory, should provide economic benefits for local residents and may contribute to poverty reduction through payments for environmental services (Lipper, McCarthy, and Zilberman 2009). Given that, the implementation of sustainable use PAs (i.e. categories III – VI from the IUCN protected areas categories system, Dudley 2008) in some of the priority areas identified here could help to protect biodiversity and local livelihoods. These areas could be co-managed by locals and environmental authorities, since such co-management is associated with higher levels of empowerment and monetary benefits for local communities, and in such circumstances, positive conservation outcomes are more frequently reported (Oldekop *et al*. 2016).

There are positive examples of conservation and sustainable management by local people in PAs in the state of Amapá, including in the Rio Cajari Extractive Reserve and Rio Iratapuru Sustainable Development Reserve where the Brazil nut (*Bertholletia excelsa*) and other non-timber forest products (oils of *andiroba*, *copaíba* and *pracaxi*, fibers, and fruit pulp of *açaí* palm) are extracted from the forest, processed and commercialized by local communities (Picanço 2009). These conservation experiences may be replicable for the SOA, given that many traditional communities are established there, using shifting cultivation system to produce manioc, pepper, pineapple and passion fruit and also extracting mangaba fruit (*Hancornia speciosa*) from natural savannas and açaí fruits (both for pulp production) from forest patches (Yokomizo and Costa 2016). Part of the production is consumed by the local families and the excess is commercialized in the local communities and in the city.

In our analysis of feasibility, we found that the selection of the most feasible priority areas would require the creation of three new PAs of approximately 1,548 km^2 in the center of the SOA. The establishment would have a cost of US$459,756/year over five years. Additionally, this could be supported by implementing the priority areas listed as high feasibility, which would involve protecting approximately 72 km^2 adjacent to current PAs, plus the creation of a new PA of 63 km^2, with an establishment cost of US$40,095/year over five years. The other subsets of priority areas correspond to areas of medium and low feasibility, and would be less likely to persist in the long term, due to high management cost in terms of surveillance as the environmental risk is high, and in some cases high potential for conflicts between conservation managers and farmers as potential use of the land for agriculture is also high. Hence, a possible route would be to present a plan to stakeholders involved in the SOA to choose among 1,683 km^2 (US$387,090/year over five years), including both the expansion of existing PAs and the creation of four new PAs of maximum and high feasibility. Considering that the budget from the Brazilian government in 2019 to manage 1,670,996 km^2 of federal PAs was ~US$219.3 million (SIGA Brasil 2020), the establishment of those 1,683 km^2 would represent just 0.18% of that total budget, and 4.9% of the budget for the state of Amapá (considering that US$7,894,800 are used to manage 60,156 km^2, as 3.6% from the federal PAs are located in the state of Amapá). An advantage is these priority areas consider both the expansion of a current PA and the creation of two areas potentially occupied by *A. belzebul*. Although caution with this network is necessary since a national road ranges through two priority areas of 648 km^2 and 807 km^2; however, it is expected that the negative effects can be compensated by the reserve size (Brashares, Arcese, and Sam 2001; Maiorano, Falcucci, and Boitani 2008) and by the fact that PAs mitigate the risk caused by roads (Barber *et al*. 2014).

Proposals to establish PAs are likely to meet with resistance from some sectors, particularly given the current political scenario of Brazil (Ferrante and Fearnside 2019). Moreover, Amapá has around 70% of its territory used for conservation and there are governmental plans to expand soybean production. In fact, despite complications related to land tenure, the plantations increased in the last years. Therefore, careful planning and an open and participatory process would be required to minimize the potential for conflicts between producers and environmental authorities (Brandon *et al*. 2005). Thus, in order to avoid conflicts, the potential use of the land for agriculture could guide conservation planning, as conversion of natural areas into agricultural fields is more likely in areas with suitable soils quality, access, etc., and as such, those areas have higher prices (Newburn *et al*. 2005). In addition, although in some cases it is not necessary to purchase lands, there are costs related to gains that could have been generated by using the land in another activity (i.e. the opportunity cost) (Naidoo *et al*. 2006). In fact, in the SOA many areas are public land (Lima 2003). However, some of this land has been occupied for generations by local people who do not have tenure security, and so demarcation of new PAs should proceed with caution to avoid the displacement of these people from their lands, as has commonly happened in top-down approaches to PA establishment around the world. Such enforced displacement is unethical, and can threaten culture and tradition, social structure, and the local economy (West, Igoe, and Brockington 2006). Instead, we advocate for recognition of the important role of communal use and titled lands within some of the priority areas identified here for both biodiversity conservation, by avoiding deforestation, and for local and traditional communities themselves, via increases in well-being (Blackman *et al*. 2017; Peña *et al*. 2017).

4.2. Other alternatives for the priority areas

It has globally been recognized that communal lands (e.g. indigenous lands) may significantly contribute to have a lower proportion of lands of high use intensity than other lands (Garnett *et al*. 2018), and even contain and conserve a high percentage of threatened species (Leiper *et al.* 2018). This highlights that indigenous peoples and local communities might contribute to biodiversity conservation, not necessarily with a PA, but through ‘other effective area-based conservation measures’ (OECMs) (Garnett *et al.* 2018). An OECM is a geographically defined area where actions related to management are carried out to achieve positive outcomes in terms of biodiversity conservation (IUCN 2019). However, such areas are not considered as PAs as the governance authority does not want such recognition, even if conservation is the primary objective (i.e. OECMs of primary conservation), the area is managed by the local communities in a way that they conduct a sustainable use of the territory themselves (i.e. OECM of secondary conservation), or the environment conservation is a by-product of other objectives, such as military lands for defense purposes (i.e. ancillary conservation) (IUCN 2019).

There are several examples of success in biodiversity protection through communal lands around the world (Tran, Ban, and Bhattcharyya 2020). However, positive outcomes broadly depend on the socioeconomic context (Robinson, Holland, and Naughton-Treves 2014) as in some cases the outcomes are negative (Buntaine, Hamilton, and Millones 2015). In that sense, the priority areas to be used as OECMs should ideally integrate the specific context of each territory. For example, we found five *Quilombos* inside two priority areas of maximum and high feasibility. Such territories could be considered as potential OECMs of either primary or secondary conservation. For the former approach, in such priority areas would be useful a partnership between locals and NGOs to create communal conservation areas (Shanee, Shanee, and Horwich 2015) and achieve collective decisions to stop the hunting of threatened species (Bennett *et al*. 2013). This is especially important since such areas may be potentially occupied by *A. belzebul*. For the second approach, it could work policies to support both sustainable small-scale family farming, by improving soil conditions, efficient use of water and pest control (Pretty, Morison, and Hine 2003), and land tenure, as many people are losing their lands because soybean farmers (which extirpates the savanna by setting large farms and using a mechanized production system) illegally use some governmental tools to own the land (Pereira 2017). In addition, collaborations between local communities, local NGOs and the government are necessary to include components related to sustainable use of natural resources into the education plans of local schools (Feilen *et al*. 2018). However, these alternatives must be part of a participatory process with local communities and as such, this reinforces the importance of bottom-up approaches in biodiversity conservation programmes (Garnett *et al.* 2018).

5. Conclusions

The SOA is an important provider of ecosystem services, not only for local communities through production of fruits, fish, bushmeat, among others, but also in terms of biodiversity protection and ecosystem processes such as carbon storage, climate regulation, water and nutrient cycling, pollination, seed dispersal and natural pest control (Hilário *et al*. 2017). Some of these ecosystem processes are supported by primates, so that it is also imperative to protect forest cover, but also the savannas, since the transition between forest patches and savanna represent a heterogeneous environment and such environments are suitable areas for primates and other biodiversity elements (Lenz, Jack, and Spironello 2014; Stein, Gerstner, and Kreft 2014). In addition, other key areas, such as lowland areas –which were found to be important for *A. belzebul*– also need to be protected. However, the conservation of the SOA must go beyond the biological aspects and needs to take as an opportunity the public support from inhabitants toward PAs in the state of Amapá (Cunha, Souza, and Silva 2019). Moreover, we think that an effective strategy for the conservation of the SOA must also consider OECMs. Thus, in order to be more integrative, a socio-ecological approach could be considered into the new network of priority areas (Palomo *et al*. 2014). This will help to avoid conflicts among stakeholders by incorporating their diverse views, value systems and knowledge through a participatory process on ground where they may interact (Palomo *et al*. 2014). This means highlighting both the intrinsic and instrumental values of biodiversity, working in partnership with local communities to share knowledge and experience to better design effective and long-lasting management actions, and seeking to integrate the landscape as a whole to turn it more resilient. Taking all these aspects into consideration will turn a network of priority areas in the SOA more representative of the overall biodiversity, it will persist in the long term, and will support the local communities through the sustainable use of the ecosystem services that nature provides.

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APPENDIX

Priority areas for conservation of primates in a threatened Amazonian savanna

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1. EXTENDED METHODS

1.1. Primate survey

We selected 70 forest patches in the central part of the SOA by using images from Google Earth Pro (version 7.3.2.5776). Between October 2017 and February 2018 (fieldwork-1), we visited the surroundings of these forest patches to carry out 77 interviews with local inhabitants and gathered information about the occurrence of primate species in a region of approximately 3,000 km^2 and obtained information on primate presence in 59 locations (52 forest patches and 7 locations in continuous forest adjacent to the savanna). In June 2019 (fieldwork-2), we visited another region in the northern part of the SOA of approximately 650 km^2 to carry out 20 additional interviews with local inhabitants and obtained information on primate presence in 17 forest patches. Both in the fieldwork-1 and the fieldwork-2, we showed photographs of the 10 primate species known to be present in the state of Amapá (*Alouatta belzebul*, *Alouatta macconnelli*, *Ateles paniscus*, *Chiropotes sagulatus*, *Pithecia pithecia*, *Cebus olivaceus*, *Sapajus apella*, *Saimiri sciureus*, *Aotus infulatus*, and *Saguinus midas*) to the participants (Silva *et al*. 2013), plus one Neotropical primate species absent in the study region (*Callithrix jacchus*) (Bezerra *et al*. 2018). Participants were asked to identify which species they had seen in forest patches.

To validate the data on primate presence and absence obtained in the interviews, we performed playback sessions in 22 forest patches in the area of fieldwork-1 between July and December 2018. We established transects of 800 m in length in each forest patch using Google Earth Pro to conduct the playback sessions, and standardized the sampling effort according to the patch area: area < 25 ha (2 transects), 25 < area < 50 ha (3 transects), 50 < area < 100 ha (4 transects) and area > 100 ha (5 transects). Along each transect, we established five playback stations at intervals of 200 m. We broadcasted a playback session from each station, consisting of a sequence of vocalizations of seven diurnal primates in the following order: *A. belzebul*, *S. midas*, *P. pithecia*, *A. macconnelli*, *S. sciureus*, *S. apella* and *C. olivaceus*. Each vocalization was broadcasted for 3-minutes, except for *Alouatta* spp., which were broadcasted for 7-minutes, since the vocalizations of these species are longer than those of other species (Drubbel and Gautier 1993). Each vocalization was followed by a 7-minute interval without playback which was used to listen for any response (except for *Alouatta*, whose interval was 8-minutes). Playback sessions began at 07:00, 09:00, 10:30, 15:10, and 16:40. Vocalizations of *Alouatta* spp. were only broadcasted at the first and the last playback station of each transect (07:00 and 16:40). Between playback sessions, we walked slowly for 40 minutes, either following our own transect in a GPS or using human and cattle paths to detect any primate and to check the forest floor for primate fecal matter. In eight of the 43 forest patches it was not possible to establish transects of 800 m in length due to patch size and shape, and in these cases we performed just two or three playback sessions per day (i.e. transects of 200 m and 600 m in length respectively).

We used the data from the playback sessions to correct the interview data in two cases: 1) where species identified as absent in the interviews were recorded as present using playback; and 2) where species presence was recorded as unknown during the interview (because the interviewee was unsure), in whose case presence/absence was established by the playback data. We used three opportunistic confirmations of presence made outside of playbacks to evaluate the veracity of the interview data: two presences of *A. belzebul* (a vocalization and a sighting) and a sighting of *S. sciureus*. *Cebus olivaceus* and *S. apella* were reported frequently by participants to be present in patches in which only one species was recorded during playback, then records of the presence of both species were joined as presence of Capuchins. Thus, Capuchins absences were only recorded in those patches in which participants reported both species as absent, and where neither species was recorded during playback. Since both species are close ecospecies (Peres and Janson 1999), this junction is not a problem in our analyses.

We calculated the Cohen's kappa coefficient to measure the concordance of presence-absence data between interviews and playbacks, by using the ‘irr’ package (Gamer *et al*. 2012) in R software (version 3.5.1) (R Core Team 2018). Concordance was high for *A. belzebul* (Kappa = 0.83) and *P. pithecia* (Kappa = 1), moderate for *S. midas* (Kappa = 0.529), and low for *S. sciureus* (Kappa = 0.188) and Capuchins (Kappa = 0.253). There was only one false positive (i.e. an interview participant reporting an absence when a playback reported a presence) and was regarding to *S. midas*. Low concordance coefficients must be due to a poor detection of some primate species during the playback sessions, instead of an erroneous indication of presence by locals during the interviews. Once a species is detected, its presence is assured, conversely, it may take a number of several surveys (e.g. playback) without detection to be sure about the absence of a primate species. Therefore, it is more common to have false absences (i.e. false negatives) than false presences (i.e. false positives). Thus, while playback sessions may have missed some species, such species may have been detected by locals, as they have spent far more time within the forest patches. Moreover, no participant reported the presence of *C. jacchus* (the species used as a control). As in the playback session *A. macconnelli* was present in only one forest patch, we did not calculate the Cohen's kappa coefficient for this species, however, since the interviews were reliable for the other species, we assumed that information about the occurrence of this species was also reliable.

Vocalizations for playback sessions were obtained from Emmons, Whitney, and Ross (1997). Only for *A. macconnelli*, the vocalization used was of *A. seniculus*, a closely related species (Boubli, DiFiore, and Mittermeier 2008). Vocalizations were edited to standardize the total playback time and reduce the background noise. We broadcasted the vocalizations using a Max Print 601205-3 speaker (frequency range: 50 to 20,000 Hz, output power: 100 RMS). The speaker was tested before carrying out the playback sessions and we established that the maximum distance at which we could still hear the vocalizations was ~100 m. The same person carried out all of the playback sessions to avoid biases in species detection.

1.2. Species distribution models

We carried out species distribution models (SDMs) using maximum-entropy models in MaxEnt software (version 3.4.1) (Phillips, Dudík, and Schapire 2019). We used 159 presence data (37 for *S. midas*, 35 for *S. sciureus*, 11 for *P. pithecia*, 35 for Capuchins, 17 for *A. macconnelli*, and 24 for *A. belzebul*) to train the models. For all species (but *A. macconnelli*), we used the area of fieldwork-1 as training area, and for *A. macconnelli*, we used the area of fieldwork-2. As predictor variables, we used four bioclimatic variables (annual precipitation, precipitation seasonality, precipitation of wettest quarter, and precipitation of driest quarter) from Worldclim 1.4 (Hijmans *et al*. 2005), height above nearest drainage from the Shuttle Radar Topography Mission as a surrogate of topography (Rennó *et al*. 2008), and tree cover percent (Hansen *et al*. 2003). All predictors were downloaded from the *Divisão de Processamento de Imagens* from the *Instituto Nacional de Pesquisas Espaciais* (INPE 2019a). All predictors were at a 1 km spatial resolution. For each species we gathered information of each predictor variable in the training area with the ‘sampling tool’ in QGIS (version 2.14.9-Essen) and then we did a pair-wise correlation test to exclude those highly correlated variables (r ≥ |0.8|) (Carvalho *et al*. 2017).

Maximum-entropy models use only presence data and have a good performance even with low sample sizes (Pearson *et al*. 2007; Shcheglovitova and Anderson 2013). We acknowledge that our presence data did not encompass the whole range of environmental space where the species could be present; however, we set the models taking into account attributes that might maximize the models performance. For example, we choose the 'hinge' feature to carry out the SDMs, as previous works that modeled the habitat suitability of a Neotropical primate from the Amazon region (Rabelo *et al*. 2018), used a low sample size (Shcheglovitova and Anderson 2013), and used presence data that did not full all the environment space of a mammal species (Shcheglovitova and Anderson 2013) showed a well performance using such feature.

Some approaches in SCP use species occurrences (Pinto and Grelle 2011) or geographic ranges (Rodrigues *et al*. 2004; Brandon *et al*. 2005; Pinto *et al*. 2007), however, this may led to omission (i.e. not considering all suitable areas for a species) and commission (i.e. consider as suitable areas where the species is not present) errors. In order to avoid such errors, other approaches in SCP have used SDMs (e.g. Lessmann, Muñoz, and Bonaccorso 2014; Lessmann *et al*. 2019), but the model performance has been evaluated by using only the area under the ROC curve (AUC). Model performance based only on the AUC does not consider overfitting, which "occurs when a model fits the calibration data too closely (in environmental space) and, therefore, fails to predict independent evaluation data accurately" (Radosavljevic and Anderson 2014). In order to build models with adequate support, we evaluated the models performance not only by using the AUC, but also by evaluating the overfitting.

As recommended by Merow, Smith, and Silander (2013), we explored a range of regularization multipliers (β) for each species. Then we ran five models for each species by giving different values of β (0.5, 1, 2, 3, and 4) and chose the best models according to three criteria in the following order: 1) reduced test omission rate (Shcheglovitova and Anderson 2013; Radosavljevic and Anderson 2014); 2) low differences between test and training AUC (Radosavljevic and Anderson 2014); and 3) a high value of test AUC (Shcheglovitova and Anderson 2013; Radosavljevic and Anderson 2014). With the two former criteria we expect to reduce the overfitting in the models, and with the last criteria we expect to choose a model with a high performance by considering an AUC near or higher than 0.75 (Elith 2000; Phillips and Dudík 2008). We did not test β values above 4 since we used only nine predictor variables, and a higher β would need a higher number of predictors (Phillips and Dudík 2008) as this value may penalize the predictors by turned them zero (Elith *et al*. 2011).

We ran the models by using 10,000 (*S. midas*, *S. sciureus* and capuchins), 9,000 (*A. macconnelli*), 7,000 (*P. pithecia*) and 5,000 (*A. belzebul*) back-ground points according to the size of the training area, a random test percentage of 20 by using cross-validation technique, and 500 maximum iterations. We reclassified the SDMs into binary maps using as threshold the Minimum Training Presence. This threshold is the pixel with the lowest value of an environmental attribute where the species is present (Pearson *et al*. 2007). Since in conservation strategies it is necessary to be less restrictive, and as such, to include some less suitable areas (Liu *et al*. 2005), we chose this threshold (Phillips, Anderson, and Schapire 2006).

We projected the models to the northern and southern part of the SOA (for *A. macconnelli* only the southern part) by applying them to another set of environmental factors with the same predictors from the training models. We used 51 presence data (7 for *S. midas*, 15 for *S. sciureus*, 1 for *P. pithecia*, and 17 for Capuchins from the fieldwork-2, and 11 for *A. macconnelli* from the fieldwork-1) outside the training area to test the projection of the models (i.e. calculate the percentage of correct classification of presences for each species in the projection area). Then, we intersected all 210 presence data (159 presences from the training area and 51 presence from projection area) of each species with its binary map (Brito *et al*. 2009). The percentage of correct classification was high for all species: 95.1% for *S. midas*, 94% for *S. sciureus*, 83.3% for *P. pithecia*, 90.1% for Capuchins and 85.7% for *A. macconnelli*.

Additionally, we analyzed the spatial distribution of the training data for each species by assessing the 'nearest neighbor index' in QGIS. We found that *P. pithecia* and *A. macconnelli* had a dispersed pattern (index = 1.21 and 1.43, respectively) and the other species were clustered (index = 0.77, 0.70, 0.65 and 0.91 for *S. midas*, *S.sciureus*, capuchins and *A. macconnelli*, respectively). Only *A. belzebul* and *P. pithecia* presented random distributions, however, as we did not have duplicates in the pixels, we expect that the possible spatial autocorrelation in the presence data of those species without a random distribution does not result in spatial biased models. Moreover, we used as background for each species the same area of presence data and such approach avoids spatial biased models (Phillips *et al*. 2009).

1.3. Conservation goals

Usually, conservation targets are decided by giving a higher priority for more threatened species or areas with higher probability of transformation (Smith, Goodman, and Matthews 2006; Lessmann, Muñoz, and Bonaccorso 2014). Following those assumptions, we established conservation goals between 20% and 50% of the species distribution within the SOA according to a prioritization (P) based on four traits, and giving higher prioritization for species that could be more vulnerable:

$$P = ER + GE + BM + HR$$

where ER is the extinction risk according to the classification of the IUCN Red List of Threatened Species, GE is the geographic extension of each species within the SOA, BM is the body mass, and HR is the home range. Each trait ranged between 1 and 3, and therefore P varied between 4 and 12.

Because information about the population structure of each primate species is unknown for the SOA, we used the ER of each species as a proxy of extinction proneness (Lessmann, Muñoz, and Bonaccorso 2014; Calle-Rendón, Moreno, and Hilário 2018), since ER is related to a quantitative measure of reduction in population size (IUCN 2012). We used BM since this trait is also related to the extinction proneness, with larger species being more vulnerable than smaller ones (Purvis *et al*. 2000). Additionally, we used GE, considering that the smaller the GE, the higher the extinction proneness (Purvis *et al*. 2000). Finally, HR has also been related to extinction proneness (Woodroffe and Ginsberg 1998), then we established that the higher the HR, the higher the extinction proneness.

For each category of ER we assigned values as follow: Least Concern (LC) = 1; Near Threatened (NT) = 2; and Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) = 3 (Lessmann, Muñoz, and Bonaccorso 2014). For GE, BM, and HR, a value of 1 was given for the least vulnerable species (i.e. a species with the smallest body mass, smallest home range, and largest geographic extension), and a value of 3 was assigned to the most vulnerable species (i.e. the species with the highest body mass, largest home range, and smallest geographic extension). Then we used the extreme values of each trait to do a linear interpolation among the other species. We also used the extreme values of P to perform a linear interpolation and calculate the conservation goal for each primate species, leading P = 4 to be equivalent to a conservation goal = 20% of the distribution of a species, and a P = 12 to be equivalent to a conservation goal = 50% of the distribution of a species. For the savannas, we defined that the proportion within the network of protected areas would be 30% as recommended previously (Hilário *et al.* 2017), considering each type of vegetation separately (park savanna, woodland savanna, grass savannas and shrub savanna).

1.4. Identifying priority areas for conservation

We used the Marxan software (version 2.4) (Ball, Possingham, and Watts 2009) to select the areas that represent the better protection of the six primate taxa and the four vegetation types in the savanna ecosystem. This software use planning units (PUs) that have an associated cost and may contain the conservation targets. The Marxan objective is to find a group of PUs that maximizes the protection of the conservation targets while minimizing the total cost, allowing define as a new priority area a single PU or a set of PUs adjacent to each other. We used three cost scenarios: 1) a map of potential use of the land for agriculture; 2) a map of environmental risk; and 3) a map averaging the information of the first two scenarios. We used QMarxan Toolbox plugin (version 0.3.4) from QGIS as support to create the input files in the selection of the network of priority areas. We did seven runs for each scenario with different values (0, 10^{-5}, 10^{-4}, 10^{-3}, 10^{-2}, 10^{-1} and 1) of Boundary Length Modifier (BLM) and selected as the best run, the network in which an increase of the BLM increased the total cost but did not reduce the boundary (BLM = 10^{-3}, Fig. S1).

1.4.1. Attributes of potential use of the land for agriculture

For the first scenario, we used six attributes important for agriculture to create the map of potential use of the land for agriculture used as proxy of land cost: 1) slope as an attribute of topography; 2) cation exchange capacity (CEC) as an attribute of soil fertility; 3) percentage composition of the soil in terms of three components (sand, silt and clay) as an attribute of soil texture; 4) precipitation of driest quarter as a bioclimatic attribute; and 5) distance to Santana city (where the fluvial port is located) and; 6) distance to the nearest main road as attributes of accessibility (Nguyen *et al.* 2015). We used raster images at a ~30 m spatial resolution from the Shuttle Radar Topography Mission (SRTM) retrieved from the *Instituto Nacional de Pesquisas Espaciais* (INPE 2019b) to obtain values of slope. Additionally, raster images at a ~230 m spatial resolution of CEC, content of sand, content of silt and content of clay at 60 cm in deep were downloaded from the SoilGrids database (Hengl *et al.* 2017). The raster at a 1 km spatial resolution of the precipitation of driest quarter was retrieved from Worldclim 1.4 (Hijmans *et al.* 2005).We used the ‘raster distance’ algorithm from GDAL (Geospatial Data Abstraction Library) in QGIS to create the two raster of accessibility (distance to the nearest main road and distance to Santana) at a 100 m spatial resolution.

All raster were re-projected at a 100 m spatial resolution. With the raster calculator from QGIS, we transformed all raster into standardized values between 1 and 5 that represented the cost of the area: very high-cost = 5, high-cost = 4, middle-cost = 3, low-cost = 2, and optimal-cost = 1 (Table A1). For the slope, we defined a slope between 0% and 8% as the better to establish an agriculture field, and slopes above to 30% as the worse (Nguyen *et al*. 2015). Then we used these slope values to do a linear interpolation and give a cost to each slope class (Table A1). A soil with a CEC higher than 20 cmol/kg is considered as a soil with high fertility, conversely, a soil with a value lower than 5 cmol/kg is considered as a soil with a low fertility (Bertsch 1987). Consequently, we did an interpolation between these extreme values of CEC to assign land cost values (Table A1). The raster of precipitation of the driest quarter was reclassified according to the upper and lower limits in the study site, and areas of higher precipitation had a higher cost (Table A1). The two raster of accessibility were reclassified according with the knowledge about the study site, assigning higher land cost to those areas closer to Santana city and a main road (Nguyen *et al*. 2015) (Table A1).

We combined in the raster calculator the three raster of soil components (sand, silt, and clay) to identify sites with loam soils (i.e. soils in which no component dominant), since such soils can offer a better support for plants (Jaramillo 2002). Thus, we reclassified each raster according to following criteria: the sand raster to identify sites with a proportion of sand ranging between 3% and 52%, the silt raster to identify sites with a proportion of silt between 32% and 50%, and the clay raster to identify sites with a proportion of clay ranging between 7% and 27% (Jaramillo 2002). Then the three reclassified raster were overlapped to create a map of soil texture and identify: 1) regions with soils that meet the three criteria to be classified as loam soils (Jaramillo 2002); 2) regions with soils that meet at least two criteria; 3) regions that meet at least one criteria; and 4) regions that does not meet any criteria (Table A1). We assigned a cost of 5 to soils that meet three criteria, 4 to at least two criteria, 3 to at least one criteria, and 2 to no criteria (Table A1).

Table A1. Cost and class of each attribute of potential use of the land for agriculture. The cost ranges between 1 and 5 and is classified as very high-cost = 5, high-cost = 4, middle-cost = 3, low-cost = 2, and optimal-cost = 1.

Attribute	Cost				
	5	4	3	2	1
Slope (%)	slope < 8	8 ≤ slope < 15	15 ≤ slope < 22	22 ≤ slope < 30	slope ≥ 30
Cation Exchange Capacity (cmol/kg)	CEC > 20	20 ≥ CEC > 15	15 ≥ CEC > 10	10 ≥ CEC ≥ 5	CEC < 5
Soil texture (% of sand, silt, and clay)	3 criteria (loam soil)	2 criteria	1 criteria	No criteria	–
Precipitation of driest quarter (mm)	prec ≥ 175	175 > prec ≥ 150	150 > prec ≥ 125	125 > prec ≥ 100	prec < 100
Distance to Santana (km)	dist ≤ 50	50 < dist ≤ 130	130 < dist ≤ 210	210 < dist ≤ 290	dist > 290
Distance to the nearest main road (km)	dist ≤ 1	1 < dist ≤ 5	5 < dist ≤ 10	10 < dist ≤ 20	dist > 20

1.4.2. Attributes of environmental risk

For the second scenario, we used six attributes that represent potential threats for biodiversity to create a map of environmental risk used as map of cost: 1) distance to main roads; 2) distance to secondary roads; 3) fire intensity; 4) distance to forest plantation; 5) distance to agricultural fields; and 6) distance to human settlements (Lessmann, Muñoz, and Bonaccorso 2014). For each attribute but fire intensity, we obtained shape-files from the *Secretaria de Estado do Meio Ambiente* (Secretary of State for the Environment) (SEMA 2018). Each shape-file was transformed into a raster at a 100 m spatial resolution using QGIS, then we created a raster of distance using the 'raster distance' algorithm from GDAL in QGIS. For fire intensity, we used the dataset from Fire Information for Resource Management System (version M6 stands for MODIS Collection 6) (NASA 2019). We downloaded a shape-file with the daily information of fire occurrence along three years (between January 2016 and December 2018). Each occurrence point has associated a value of fire strength called Fire Radiative Power (FRP) measured in Megawatts. The higher the FRP, the higher the energy released by burning vegetation (Wooster, Roberts, and Perry 2005). Then, we created a fire raster at a 100 m spatial resolution for each year using the 'Heatmap' plugin (version 0.2) in QGIS, which uses the Kernel density estimation. For each fire raster we used a 3,000 m search radius as this is the distance in which the fire in a landscape has a negative effect within a forest fragment in the Amazon region (Cochrane and Laurance 2002), the shape Kernel 'quartic-biweight', and the values of FRP as field weight. After this processes, we filled the pixels without information using the 'Fill nodata' algorithm from GDAL in QGIS with a 1,000 m search distance. Finally, we created a fire raster by averaging the raster of each year in the raster calculator.

We used the raster calculator to transform all raster distances and the fire raster into standardized values, ranging between 1 and 5, which represent the environmental cost: very high-cost = 5, high-cost = 4, middle-cost = 3, low-cost = 2, and optimal-cost = 1 (Table A2). Those distances were based in the negative effect that each attribute has on the biodiversity. A distance of 5,000 m is a distance in which both main roads and human settlements have a negative effect on mammal abundance and biodiversity within protected areas (Benítez-López, Alkemade, and Verweij 2010; Lessmann, Muñoz, and Bonaccorso 2014). Additionally, the scale of effect (i.e. the distance in which a landscape attribute has the strongest effect on a biological response, such as species richness or species occurrence) (Jackson and Fahrig 2012) of anthropogenic cover (including main roads and human settlements) on primate occurrence in the SOA is 400 m (Calle-Rendón, unpublished data). Consequently, we used these distances to do a linear interpolation and assign a cost to each distance class for distance to main roads and distance to human settlements (Table A2). The distance in which the secondary roads affect the biodiversity within protected areas is 1,000 m (Lessmann, Muñoz, and Bonaccorso 2014), then we used this distance and the scale of effect (400 m) of anthropogenic cover (including secondary roads) in the SOA (Calle-Rendón, unpublished data) to do a linear interpolation and give a cost to each distance class (Table A2). In the SOA, forest plantations have shown having a positive effect on mammal species richness (Piña *et al*. 2019); however, plantations may have a negative effect when harvest activities are being conducted (Brockerhoff *et al*. 2008). Thus, we defined that the distance in which the forest plantations affect the biodiversity within protected areas would be 1,000 m (Lessmann, Muñoz, and Bonaccorso 2014), but due to the mild effect of such plantations on biodiversity in the SOA, we determined 100 m as the minimum distance in which could have a negative effect. Then, we did a linear interpolation between 100 m and 1,000 m to assign costs to each distance class (Table A2). Agriculture fields have a negative effect on biodiversity up to maximum distance of 2,000 m (Lessmann, Muñoz, and Bonaccorso 2014). Then this distance and the scale of effect (400 m) of anthropogenic cover (including agriculture fields) in the SOA (Calle-Rendón, unpublished data) were used to do a linear interpolation (Table A2). Finally, we divided into categories the values of FRP (Table A2) according to the intensity of the fire (Armenteras, González, and Retana 2013).

Table A2. Cost and class of each attribute of environmental risk. The cost ranges between 1 and 5 and is classified as very high-cost = 5, high-cost = 4, middle-cost = 3, low-cost = 2, and optimal-cost = 1.

Attribute	Cost				
	5	4	3	2	1
Distance to main roads (m)	dist ≤ 400	400 < dist ≤ 1933	1933 < dist ≤ 3466	3466 < dist ≤ 5000	dist > 5000
Distance to secondary roads (m)	dist ≤ 400	400 < dist ≤ 600	600 < dist ≤ 800	800 < dist ≤ 1000	dist > 1000
Fire intensity (MW)	FRP > 200	200 ≥ FRP > 100	100 ≥ FRP > 50	50 ≥ FRP ≥ 1	FRP < 1
Distance to forest plantations (m)	dist ≤ 100	100 < dist ≤ 400	400 < dist ≤ 700	700 < dist ≤ 1000	dist > 1000
Distance to agriculture fields (m)	dist ≤ 400	400 < dist ≤ 933	933 < dist ≤ 1466	1466 < dist ≤ 2000	dist > 2000
Distance to human settlements (m)	dist ≤ 400	400 < dist ≤ 1933	1933 < dist ≤ 3466	3466 < dist ≤ 5000	dist > 5000

1.4.3. Multi-criteria Analysis

We carried out an Analytic Hierarchy Process to define the weight of each attribute in the map of potential use of the land for agriculture and environmental risk. This tool is useful for multi-criteria decisions (Saaty 2005) and has been used to support decision-making in nature conservation and land-use planning (Moffett, Dyer, and Sarkar 2006; Chowdary *et al*. 2013). In this method, pairwise comparison among attributes are made, using numerical values between 1 and 9 to measure the degree of importance of one attribute on another one, scaling the degree of importance as: equal (value = 1), low (value = 3), strong (value = 5), very strong (value = 7), and extreme (value = 9) (Saaty 2005). We then defined through this method the weight (*w*) of each attribute by analyzing separately the attributes of potential use of the land for agriculture and the attributes of environmental risk. This analysis showed that for attributes of potential use of the land for agriculture, slope has the highest weight (*w* = 37%) and distance to Santana the lowest (*w* = 3%) (Table A3), and for attributes of environmental risk, distance to human settlements was the attribute with the highest weight (*w* = 36%) and distance to forest plantation the attribute with the lowest weight (*w* = 2%) (Table A4).

Table A3. Attributes of potential use of the land for agriculture in an Analytic Hierarchy Process. The parameter *w* is the weight of each attribute. Numerical values between 1 and 9 are used to measure the degree of importance of one attribute on another one, scaling the effect as: equal (value = 1), slow (value = 3), strong (value = 5), very strong (value = 7), and extreme (value = 9).

Attribute	Slope	Cation Exchange Capacity	Soil texture	Precipitation of driest quarter	Distance to Santana	Distance to the nearest main road	*w* (%)
Slope	1/1	5/1	7/1	3/1	5/1	5/1	37
Cation Exchange Capacity	1/5	1/1	5/1	1/3	5/1	5/1	16
Soil texture	1/7	1/5	1/1	5/1	7/1	7/1	20
Precipitation of driest quarter	1/3	3/1	1/5	1/1	7/1	7/1	18
Distance to Santana	1/5	1/5	1/7	1/7	1/1	1/5	3
Distance to the nearest main road	1/5	1/5	1/7	1/7	5/1	1/1	6

Table A4. Attributes of environmental risk in an Analytic Hierarchy Process. The parameter *w* is the weight of each attribute. Numerical values between 1 and 9 are used to measure the degree of importance of one attribute on another one, scaling the effect as: equal (value = 1), slow (value = 3), strong (value = 5), very strong (value = 7), and extreme (value = 9).

Attribute	Distance to main roads	Distance to secondary roads	Fire intensity	Distance to forest plantations	Distance to agriculture fields	Distance to human settlements	*w* (%)
Distance to main roads	1/1	5/1	5/1	9/1	5/1	1/3	25
Distance to secondary roads	1/5	1/1	3/1	5/1	3/1	1/7	11
Fire intensity	1/5	1/3	1/1	9/1	9/1	1/3	20
Distance to forest plantations	1/9	1/5	1/9	1/1	1/5	1/9	2
Distance to agriculture fields	1/5	1/3	1/9	5/1	1/1	1/7	5
Distance to human settlements	3/1	7/1	3/1	9/1	7/1	1/1	37

1.4.4. Maps of environmental risk and potential use of the land for agriculture

We used the raster calculator to create the three maps used as maps of cost in the Marxan analysis: potential use of the land for agriculture, environmental risk, and environmental risk plus potential use of the land for agriculture. We created the maps of environmental risk and potential use of the land for agriculture through a weighted overlay, by summing the raster of the six attributes from each map and multiplying each attribute for its *w*. The map of the combination of both potential use of the land for agriculture and environmental risk (third scenario of cost) was created with the average pixel between the two maps. For the three maps, pixel values (i.e. the cost) ranged between 1 and 5. These maps showed that the northern and the southern parts of the SOA had sites with high potential use of the land for agriculture (Fig. A1). Additionally, such sites represent higher environmental risk (Fig. A1). When the three scenarios are compared, the potential use of the land for agriculture (scenario 1) had the highest cost (3.5 ± 1.5, considering the pixels as sampling units) and the environmental risk (scenario 2) the lowest (2.0 ± 0.7). The combination of both scenarios presented intermediate cost (2.8 ± 0.4).

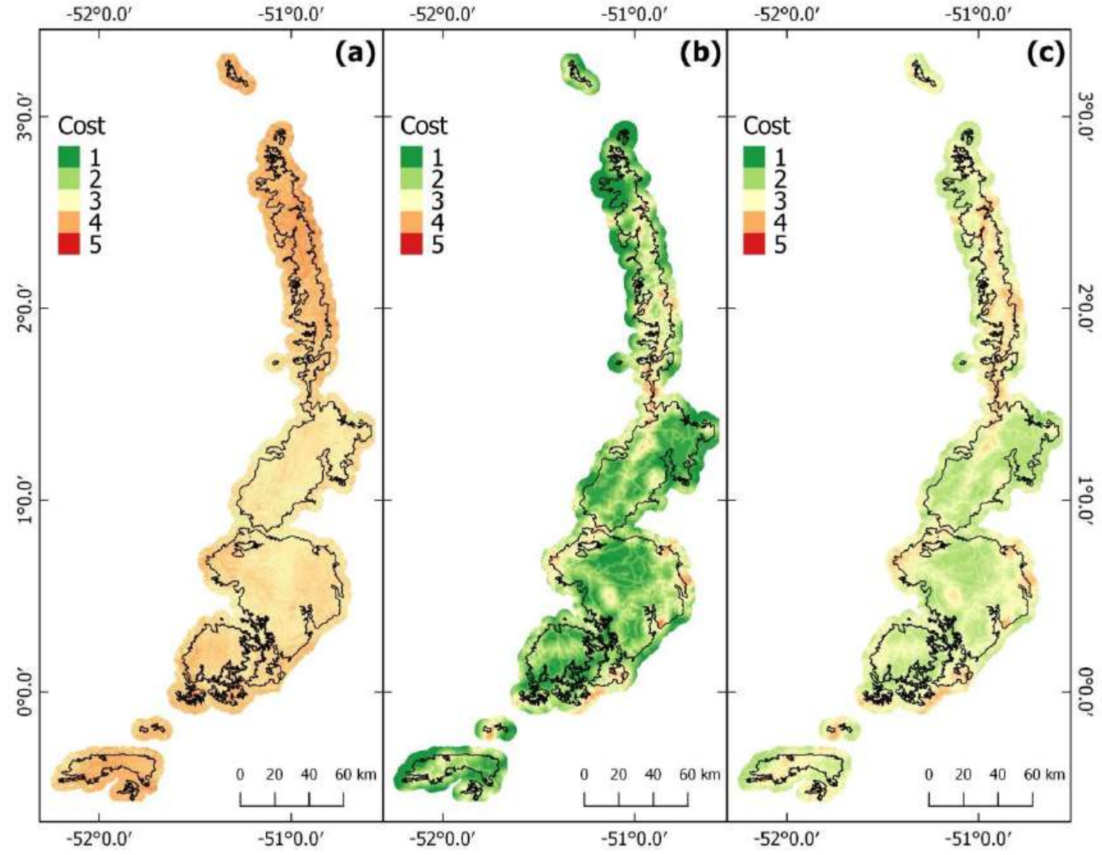

Figure A1. Maps representing the three scenarios of cost used by Marxan. (a) potential use of the land for agriculture; (b) environmental risk; and (c) a combination of both potential use of the land for agriculture and environmental risk in a Brazilian Amazonian savanna in the state of Amapá. Cost values range between 1 (optimal-cost) and 5 (very high-cost).

1.5. Conservation feasibility

We evaluated the feasibility of each priority area from the Marxan "best" solution in the third scenario (i.e. using as cost the combination of both potential use of the land for agriculture and environmental risk), which is an indicator of the success of implementing a priority area in a site (Lessmann, Muñoz, and Bonaccorso 2014). We evaluated the feasibility of each priority area by using the size of each area divided by the total cost of each area from the map of potential use of the land for agriculture, and the size of each area divided by the total cost from the map of environmental risk. We plotted these variables (area/cost from the map of potential use of the land for agriculture in the abscise axis against area/cost from the map of environmental risk in the ordinate axis) and according to the quadrant where each priority area was located, we classified each area as maximum feasibility (upper right side), high feasibility (lower right side), medium feasibility (upper left side), or low feasibility (lower left side) (Fig. S3). We used the Jenks natural breaks in QGIS to divide each axis in the graphics.

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Table S1. Summary of quantitative evaluation metrics of Maximum Entropy models of six primate taxa in a Brazilian Amazonian savanna in the state of Amapá. AUC is the area under the ROC (Receiver Operating Characteristic) curve, OR is the omission rate, and β is the regularization multiplier.

	Saguinus midas	*Saimiri sciureus*	*Pithecia pithecia*	Capuchins*	*Alouatta belzebul*	*Alouatta macconnelli*
Training AUC	0.861	0.842	0.940	0.829	0.793	0.939
Test AUC	0.863	0.851	0.986	0.816	0.742	0.806
Test OR	0	0	0	0	0	0.333
β	2	1	0.5	1	4	4

**Sapajus apella* and *Cebus olivaceus*

Table S2. Relative contribution of each predictor variable to the Maxent models for six primate taxa in a Brazilian Amazonian savanna in the state of Amapá. Predictors are annual precipitation (Bio12), precipitation seasonality (Bio15), precipitation of wettest quarter (Bio16), precipitation of driest quarter (Bio17), height above nearest drainage (HAND) and tree cover percent (TCP).

Species		Predictors				
Saguinus midas		TCP	Bio17	Bio12	HAND	
	Percent contribution	56.4	20.8	20.4	2.4	
	Permutation importance	57.5	24.7	15.1	2.8	
Saimiri sciureus		TCP	Bio12	HAND	Bio16	Bio15
	Percent contribution	36.6	32.3	25.3	4	2
	Permutation importance	19.9	48.4	25.9	1.1	4.7
Pithecia pithecia		TCP	Bio17	Bio16	Bio12	Bio15
	Percent contribution	74.4	17.2	5.1	3.1	0.2
	Permutation importance	67.5	25.7	3.8	0.9	2.1
Capuchins*		TCP	Bio12	Bio15	HAND	
	Percent contribution	52.6	42.8	2.4	2.2	
	Permutation importance	37.7	55	3.1	4.3	
Alouatta belzebul		Bio12	HAND	Bio16	Bio17	TCP
	Percent contribution	53.3	27.7	11.6	7.4	0
	Permutation importance	22.5	14.9	36.6	26	0
Alouatta macconnelli		TCP	Bio17	Bio15	HAND	
	Percent contribution	72.9	26.8	0.3	0	
	Permutation importance	49	51	0	0	

**Sapajus apella* and *Cebus olivaceus*

Table S3. Summary of the Marxan "best" solution. We present the three scenarios of cost to prioritize areas for conservation of ten targets (six primate taxa and four vegetation types) in a Brazilian Amazonian savanna in the state of Amapá.

Scenario	Total cost	Area (km^2)	Number of priority areas	Conservation target	Conservation goal (km^2)	Amount held (km^2)	Percentage held
Using the potential use of the land for agriculture as cost	3,811.8	3,183	20	*S. midas*	1,637	2,512	153
				S. sciureus	1,603	2,112	132
				P. pithecia	325	353	109
				Capuchins*	1,992	2,007	101
				A. belzebul	583	583	100
				A. macconnelli	1,373	1,373	100
				Woodland savanna	135	138	102
				Shrub savanna	165	213	129
				Park savanna	1,815	1,983	109
				Grass savanna	279	280	100
Using the environmental risk as cost	1,939.5	3,291	23	*S. midas*	1,637	2,578	157
				S. sciureus	1,603	2,154	134
				P. pithecia	325	431	133
				Capuchins*	1,992	2,037	102
				A. belzebul	583	583	100
				A. macconnelli	1,373	1,374	100
				Woodland savanna	135	157	116
				Shrub savanna	165	244	148
				Park savanna	1,815	2,030	112
				Grass savanna	279	280	100
Using both the environmental risk and the potential use of the land for agriculture as cost	2,881	3,204	20	*S. midas*	1,637	2,547	156
				S. sciureus	1,603	2,112	132
				P. pithecia	325	416	128
				Capuchins*	1,992	2,039	102
				A. belzebul	583	583	100
				A. macconnelli	1,373	1,374	100
				Woodland savanna	135	147	108
				Shrub savanna	165	212	129
				Park savanna	1,815	2,022	111
				Grass savanna	279	279	100

**Sapajus apella* and *Cebus olivaceus*

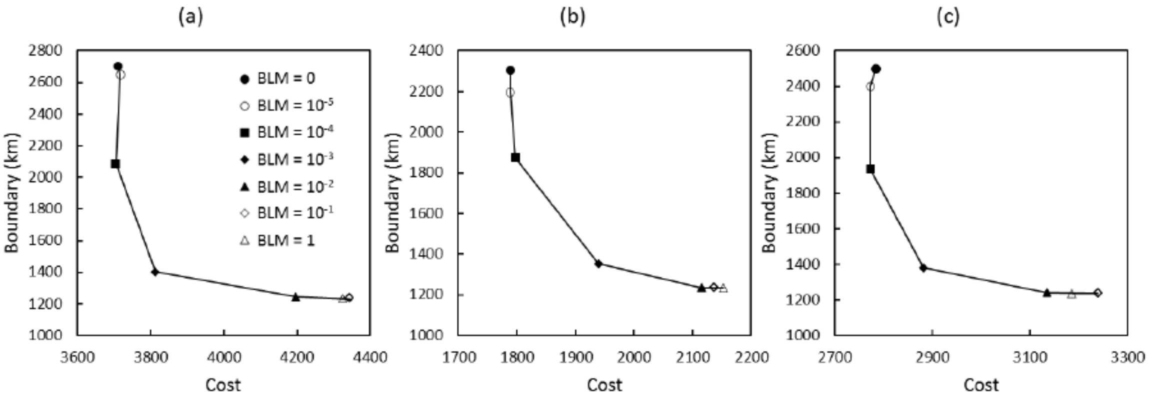

Figure S1. Boundary length and total cost of the network of priority areas from the Marxan "best" solution in a Brazilian Amazonian savanna in the state of Amapá. The three scenarios of cost are: (a) potential use of the land for agriculture; (b) environmental risk; and (c) a combination of both potential use of the land for agriculture and environmental risk. Each observation in the graphics represents a run of Marxan with a different value of the Boundary Length Modifier (BLM). Note that in the three scenarios, the best solution is given with a BLM = 10^{-3}, where an increase of the BLM increased the total cost but did not reduce the boundary.

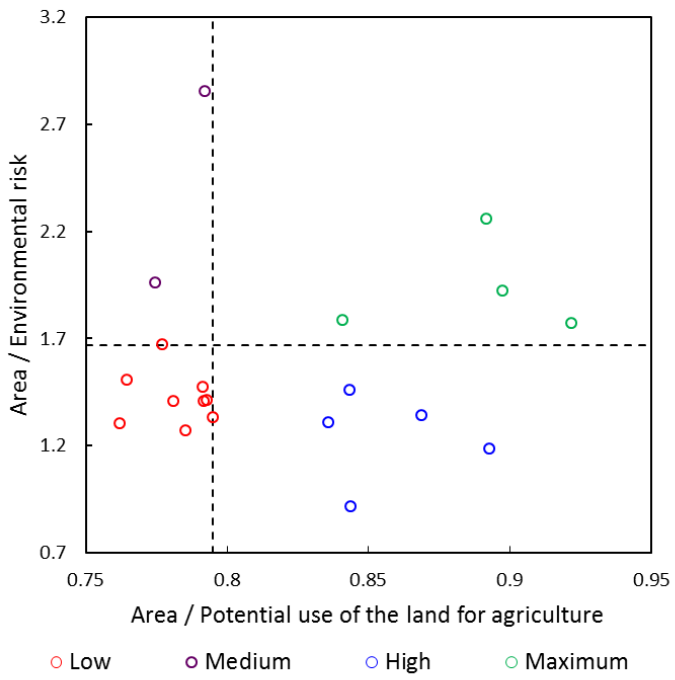

Figure S2. Evaluation of the conservation feasibility of priority areas in a Brazilian Amazonian savanna in the state of Amapá. Each observation in the graphics represents a priority area from the Marxan “best" solution using the third scenario (i.e. a combination of both potential use of the land for agriculture and environmental risk). Priority areas in the upper right side are considered as maximum feasibility, upper left side are medium feasibility, lower right side are high feasibility, and lower left side are low feasibility. Dotted lines are the Jenks natural breaks.

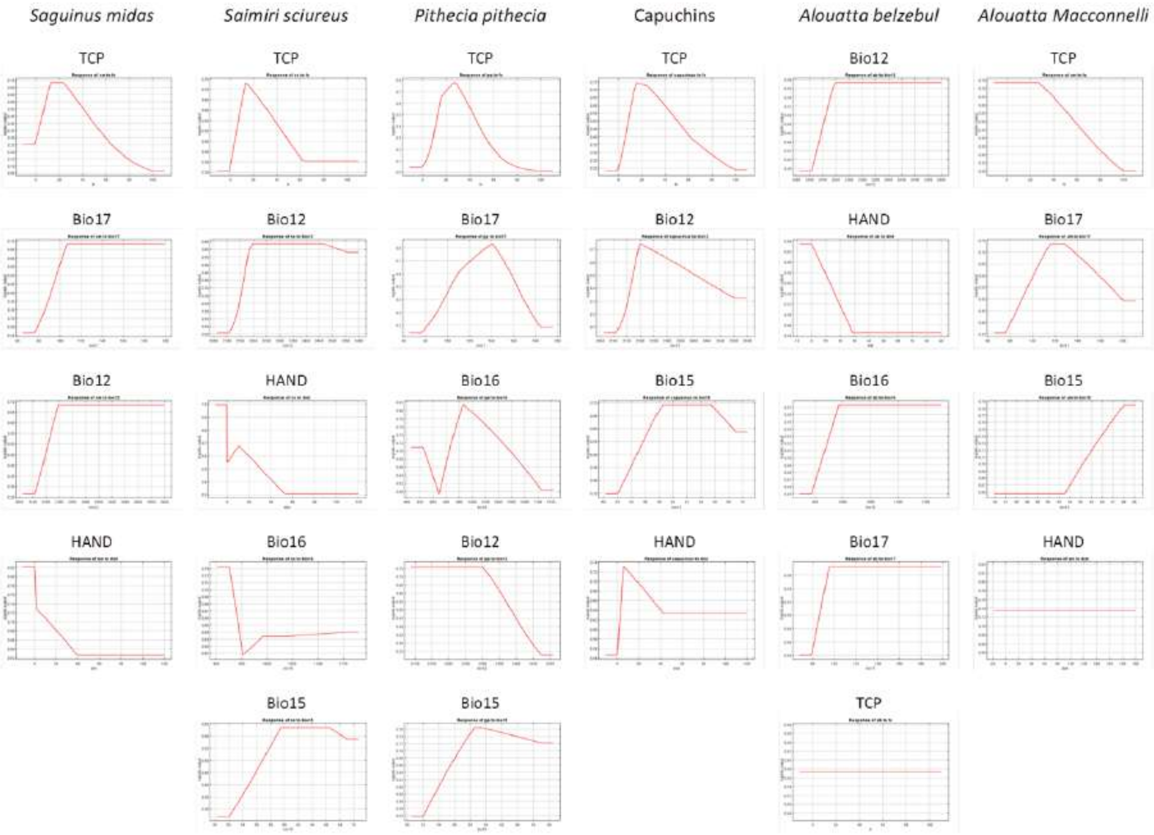

Figure. S3. Response curves for predictors of six primate taxa in a Brazilian Amazonian savanna in the state of Amapá. The curves show how the predicted probability of presence of each taxa changes as each predictor variable is varied, keeping all other predictors at their average sample value (i.e. marginal response). Predictors are annual precipitation (Bio12), precipitation seasonality (Bio15), precipitation of wettest quarter (Bio16), precipitation of driest quarter (Bio17), height above nearest drainage (HAND) and tree cover percent (TCP). Capuchins consider both *Sapajus apella* and *Cebus olivaceus*.

ARTIGO CIENTÍFICO 4

Vulnerability of mammals to land-use changes in Colombia’s post-conflict era

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RESEARCH ARTICLE

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Vulnerability of mammals to land-use changes in Colombia's post-conflict era

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Abstract

Colombia, one of the most biodiverse countries in the world, is entering a peaceful period after more than fifty years of armed conflict. Due to land use changes resulting from this new situation, negative effects on biodiversity, including mammals are expected. We think that mammal populations will be more sensitive in municipalities where activities related to post-conflict will be carried out. In that order, we aim to: 1) identify which mammal species would be more sensitive and 2) identify the critical regions where there is higher richness of sensitive mammals. We used the distributions of 95 mammal taxa and calculated a sensitivity index by combining four factors: 1) the proportion of each species distribution within protected areas in relation to their proposed extinction thresholds, 2) the proportion within post-conflict municipalities, 3) the proportion of five types of potential land use in post-conflict municipalities and 4) the threat status of each species. Using this index, we drew a map of species richness for mammals classified at high-risk and very high-risk categories. Primates were the most sensitive group to post-conflict changes. Urabá and the region near to the Serranía de San Lucas were the areas with the highest richness of sensitive species. We suggest using primates as flagship species to carry out conservation schemes in the post-conflict era in programmes led by local farmers and former fighters who have been reintegrated into civilian life.

Keywords

Armed conflict, biodiversity loss, flagship species, primates, protected areas

Introduction

After more than 50 years of armed conflict in Colombia, the Government and FARC (Revolutionary Armed Forces of Colombia), the oldest guerrilla army from Latin America, signed a peace agreement in 2016. One of the central points in such agreement is rural reform (Gobierno Nacional and FARC-EP 2016). As a consequence, it is expected that many people who suffered forced displacement will return to rural areas. This immigration process could represent a risk for biodiversity due to expansion of the agricultural frontier in formerly abandoned lands (Negret et al. 2017).

Colombia is a megadiverse country (Andrade 2011) that encompasses two biodiversity hotspots (Myers et al. 2000) and holds 518 mammal species (Ramírez-Chaves et al. 2016). Mammals are important due to their economic importance and ecological value (Ceballos and Brown 1994), but their populations around the world are threatened by several anthropogenic factors, including those related to armed conflicts (Ceballos and Ehrlich 2002, Dudley et al. 2002, Daskin and Pringle 2018). Notwithstanding, there are no specific studies analysing the relationship between warfare and mammals population in Colombia.

War in Colombia has had both negative and positive effects on biodiversity. Forests from many areas were cleared for illicit crop plantations, mining and land grabbing for cattle ranching. In addition, terrorist attacks spilled oil causing pollution over vast areas (Dávalos et al. 2011, Sánchez-Cuervo and Mitchell 2013, Asociación Colombiana del Petróleo 2014). On the other hand, due to the violence, vegetation regrowth and absence of human disturbance in many abandoned areas may have preserved biodiversity (Sánchez-Cuervo and Mitchell 2013).

In the current post-conflict era, many social and environmental changes are expected in Colombia (Baptiste et al. 2017, Negret et al. 2017). Experiences from other countries have shown that some activities related to post-conflict, such as resettlement and rural reforms, can have negative effects on biodiversity (Suarez et al. 2018). These effects may be exacerbated in Colombia by the low representation of threatened areas and endemic species within protected areas (Forero-Medina and Joppa 2010). In the Colombian case, we expect biodiversity –and specifically mammal species– will be affected mainly in those areas where post-conflict activities will be carried out. As many mammal species are sensitive to human activities, it is important to identify which areas and species would need more attention in that new scenario. With the premise that environmental changes will follow in municipalities where peace agreements are to be implemented, we aim to: 1) identify which mammal species are most sensitive and, 2) identify critical regions where negative effects on mammals are most likely.

Methods

Study Polygons selection

We selected mammals from six orders (Artiodactyla, Carnivora, Cingulata, Perissodactyla, Pilosa and Primates) with known distributions in Colombia. Species distributions were downloaded from the IUCN Red List of Threatened Species (IUCN 2017) and the digital tool BioModelos (Instituto Humboldt 2017).

We considered as post-conflict areas, the polygons retrieved from the Departamento Administrativo Nacional de Estadístca (DANE 2017) of the 170 municipalities, where activities related to rural reform will be carried out to develop the rural economy, according to Decree 893 of 2017 (Ministerio de Agricultura y Desarrollo Rural 2017). Additionally, we used polygons of national protected areas retrieved from the Colombian National Parks (Parques Nacionales Naturales de Colombia 2017) and polygons of the types of potential land use retrieved from the Instituto Geográfico Agustín Codazi (IGAC 2018).

Risk evaluation

To identify the sensitivity of mammal species to post-conflict land use change, we calculated the proportion of its distribution that overlaps with post-conflict areas and protected areas. Additionally, we calculated the proportion of species distribution that overlaps with five main types of potential land use for Colombia, only within municipalities of post-conflict in QGIS software (2.14.8-Essen). Then, we developed a sensitivity index (*S*) for each species considering four factors:

$$S = TS + PAET + Post + PLU$$

where *TS* is the threat status according to the classification of the IUCN Red List of Threatened Species (IUCN 2017). *PAET* is an index that relates the proportion of the distribution of each species within national protected areas and its proposed extinction threshold. *Post* is the proportion of the distribution of each species within post-conflict areas and *PLU* is the proportion of the distribution of each species within a type of potential land use in post-conflict municipalities. *TS*, *PAET*, *Post* and *PLU* ranged between 0 and 5 each. Thus *S* varied from 0 to 20 and was classified into five categories: non-risk ($S = 0$), low-risk ($0 < S < 5$), middle-risk ($5 \leq S < 10$), high-risk ($10 \leq S < 15$) and very high-risk ($S \geq 15$).

As detailed information about population structure of each species across all the country is unknown, we therefore used the threat status (*TS*) of the species as a proxy of extinction proneness since it is related to a quantitative measure of reduction in population size in a temporal scale and geographic range (IUCN 2012). We assigned *TS* values for each species according to the following: Least Concern (LC) = 0; Data Deficient (DD) or Not Evaluated (NE) = 1; Near Threatened (NT) = 2; Vulnerable (VU) = 3; Endangered (EN) = 4; Critically Endangered (CR) = 5.

Considering that any place outside protected areas will be more vulnerable to changes in land use in the post-conflict era, it is expected that species with a higher proportion of their distribution within protected areas will be less vulnerable. Then, we considered each protected area as a 'patch of habitat' and that each species would need an amount of habitat (i.e. proportion of its distribution overlapped with protected areas) equivalent to its extinction threshold to maintain a population in equilibrium (Fahrig 2001). Previous simulations highlight that the four main factors determining extinction threshold are (from least to most important): habitat pattern, matrix quality, dispersal rate and reproductive rate (Fahrig 2001). As body weight of mammals is negatively related to reproductive rate (Western 1979), we expect that the greater the body size, the higher the extinction threshold. Thus, we used body mass of each species (or the average mass of the genus) (Jones et al. 2009) to classify them into four categories: small (< 1 kg), medium (1–5 kg), large (5–15 kg) and very large (> 15 kg). We defined the extinction threshold for each species knowing *a priori* that a species like *Panthera onca* (a very large species) need at least 50% of its distribution within protected areas to maintain its subpopulations in lower risk (de la Torre et al. 2018). Then, we used species body weight to classify the extinction threshold for our species as 50% of remaining habitat for very-large, 40% for large, 30% for medium and 20% for small species. We used each threshold as the amount of habitat needed within protected areas to guarantee adequate protection for each species, and calculated the relationship between the proportion of the distribution of each species within national protected areas and its proposed extinction threshold (*PAET*) as:

$$PAET = \frac{5}{\left(\frac{pa * 4}{et}\right) + 1}$$

where *pa* is the proportion of the distribution of each species within national protected areas and *et* is the extinction threshold applied for the species considering its body weight.

We assumed that the greater the post-conflict area overlapped with species distribution, the greater the negative effect on the species. However, the effects will be more negative in municipalities where more people will return in the post-conflict era since this immigration process is a driver of environmental impacts in the post-conflict era (Suarez et al. 2018). Consequently, we used the number of displaced people in each municipality between 1993 and 2013 (Consejería Presidencial para los Derechos Humanos 2015, Unidad para las Víctimas 2018) as the surrogate number of people that might return to each municipality. Then we calculated the proportion of the distribution of each species within post-conflict areas (*Post*) as:

$$Post = 5 * \left(\sum_{i=1}^{n} A_i * disp\right)$$

where A_j is the proportion of a species distribution within the municipality *i* and *disp* is a factor associated with each municipality according to the number of displaced people (dp): *disp* = 0.7 (dp < 10,000), *disp* = 0.8 (10,000 ≤ dp < 25,000), *disd* = 0.9 (25,000 ≤ dp < 50,000) and *disp* = 1 (dp ≥ 50,000).

Peace agreements between the Colombian Government and FARC have a special focus on rural reform to carry out agricultural activities according to the potential land use (Gobierno Nacional FARC-EP 2016). Negative effects on biodiversity depend of the land use, being most negative on croplands and least negative on uses that maintain natural vegetation to some extent (i.e. extractivism) (see Newbold et al. 2015). We selected five main types of potential land use proposed for Colombia: conservation, forestry, agroforestry, cattle ranch and agriculture. These potential uses are based on the natural capacity of the land to support a given activity under sustainable conditions (IGAC 2012). We calculated the proportion of the distribution of each species within a type of potential land use in post-conflict municipalities (PLU) as:

$$PLU = 5 * \left(\sum_{j=1}^{n} A_j * lu\right)$$

where A_j is the proportion of a species within a type of potential land use j and lu is a factor associated with each land use according to the intensity of use: $lu = 0.2$ (conservation), $lu = 0.4$ (forestry), $lu = 0.6$ (agroforestry), $lu = 0.8$ (cattle ranch) and $lu = 1$ (agriculture).

Finally, we created a grid on a map of Colombia using squared cells of 0.1° (approximately 10.6 km). Then the species richness was calculated in each cell by overlapping all species distributions and considering that a given species was present if the cell occupancy was greater than 50%. We created two maps: one considering all present species and another considering only species classified at high-risk and very high-risk according to our sensitivity index to identify critical regions where negative effects on mammals are most likely. Both maps were designed using the SAM Software Version 4.0 (Rangel et al. 2010).

Results

We obtained spatial distributions of 95 taxa: 44 primates, 26 Carnivora, nine Artiodactyla, seven Pilosa, six Cingulata, and three Perissodactyla (see Suppl. material 1: Table S1: mammal species used in the analysis). A total of 36.84% of all species were classified as low-risk, 48.42% as middle-risk, 13.68% as high-risk and 1.05% as very high-risk (represented only by the primate species *Plecturocebus caquetensis*). No species was classified as non-risk (Figure 1). With 12 out of 44 species classified as high-risk and very high-risk, primates are the mammal group that is most sensitive to post-conflict changes in Colombia. *Tapirus bairdii* (Perissodactyla) and *Mazama temama* (Artiodactyla) were also classified as high-risk (Figure 2).

Amazon and some points from the Orinoco region (including the eastern side of the Cordillera Oriental) were the areas with greatest overall species richness, followed by the Serranía de San Lucas and the transition zone between the Caribbean and the Pacific region near to the Urabá Gulf (Figure 3a). The areas with highest richness of sensitive species were those near to Urabá Gulf (municipalities of Turbo, Chigorodó

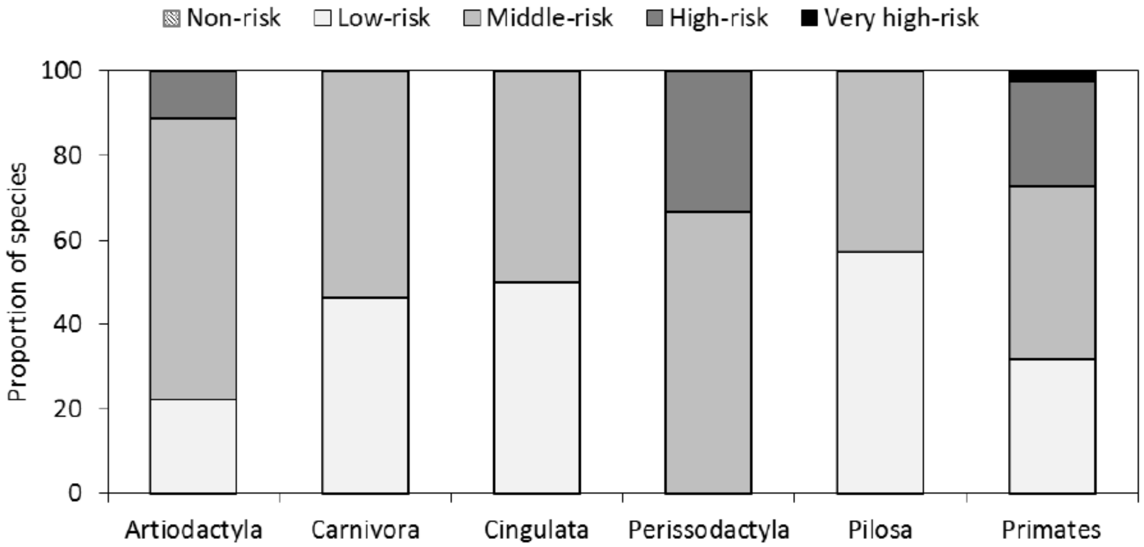

Figure 1. Proportion of mammal species amongst six orders within each category of sensitivity in the Colombian post-conflict era. Non-risk ($S = 0$), low-risk ($0 < S < 5$), middle-risk ($5 \le S < 10$), high-risk ($10 \le S < 15$) and very high-risk ($S \ge 15$).

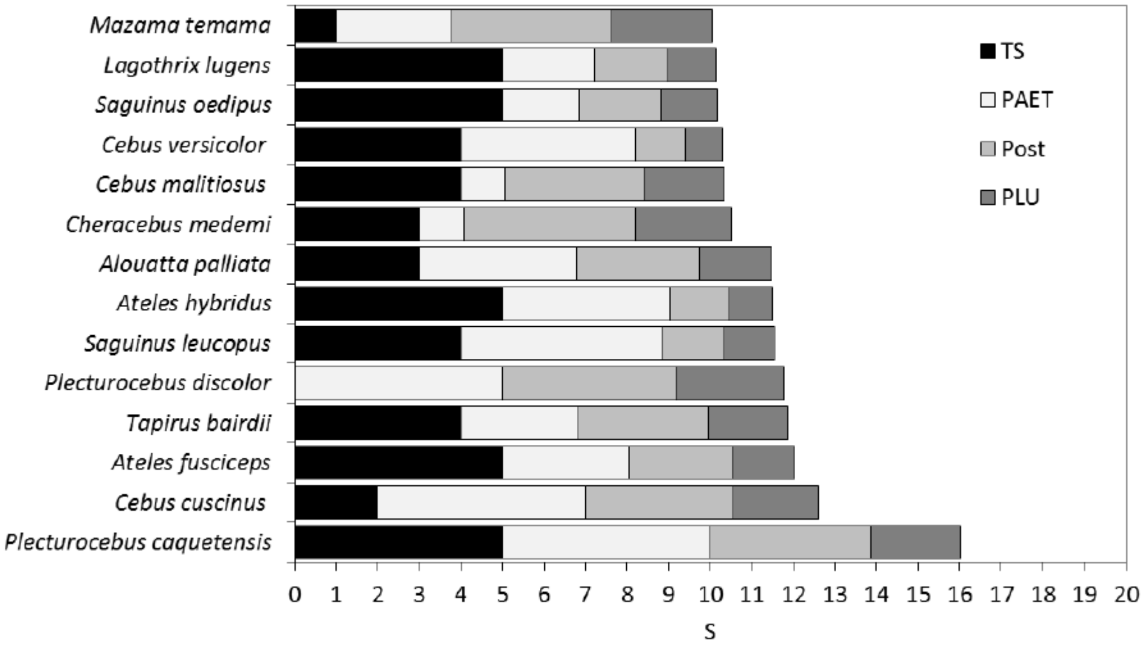

Figure 2. Most sensitive ($S \ge 10$) mammal species in Colombian postconflict areas and the contribution of each of the four factors to the sensitivity index (S). ***TS***: threat status; ***PAET***: relationship between the proportion of the distribution of each species within national protected areas and its proposed extinction threshold; ***Post***: proportion of the distribution of each species within post-conflict areas; ***PLU***: proportion of the distribution of each species within a type of potential land use in post-conflict municipalities.

and Mutatá in Antioquia, Tierralta in Cordoba and Riosucio in Chocó) and the region near to the Serranía de San Lucas (municipalities of Yondó, Segovia, El Bagre and Remedios in Antioquia and Arenal, Cantagallo, Morales, San Pablo, Santa Rosa del Sur and Simití in Bolivar) (Figure 3b).

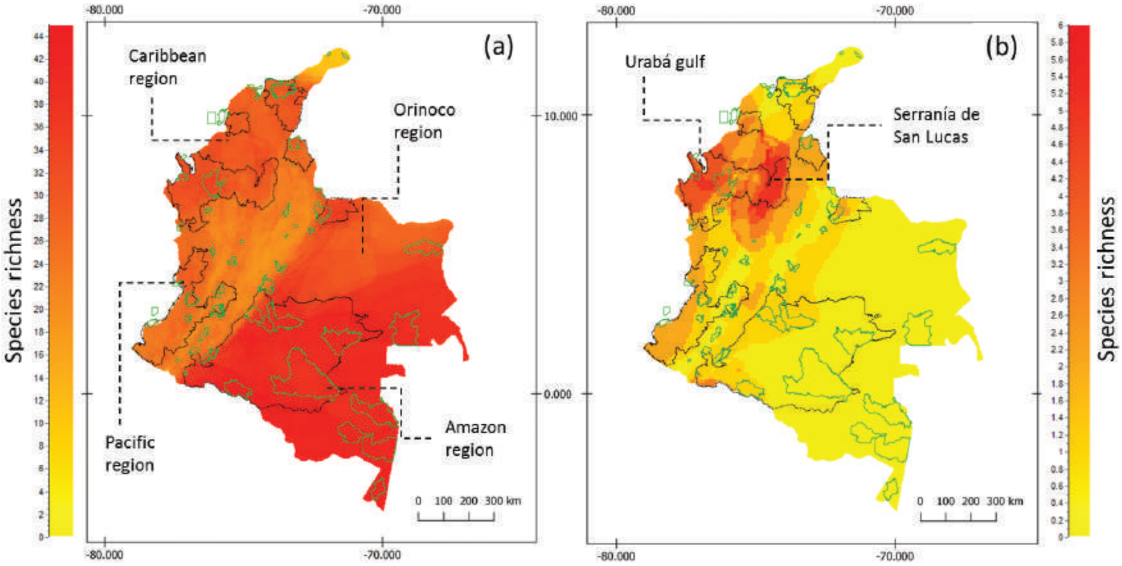

Figure 3. a Mammal species richness in Colombia considering the distribution of 95 taxa of six orders. **b** Critical regions (Urabá and Serranía de San Lucas) where negative effects on mammals are most likely considering only those species classified as high-risk and very high-risk in post-conflict era ($S \geq 10$). Black polygons correspond to the 170 municipalities used as post-conflict areas and green polygons to protected areas.

Discussion

Increased attention has been given to the effects of warfare on biodiversity in the last two decades and Colombia is one of the areas of special attention (Dudley et al. 2002, Hanson et al. 2009, Lawrence et al. 2015, Daskin and Pringle 2018, Hanson 2018, Suarez et al. 2018). Colombia not only holds the Tropical Andes and the Tumbes-Chocó-Magdalena as biodiversity hotspots, but is also part of the Amazon region, the greatest extension of tropical forest on the earth (Myers et al. 2000, FAO ITTO 2011). Preserving these areas is not only of national concern, but also of global interest due to their contribution of these regions to global biodiversity, high endemism of plants and fauna and regulation of global climate (Myers et al. 2000, Werth and Avissar 2002, Malhi et al. 2008).

We found that post-conflict alterations in Colombia represent a threat to many mammal species and that primates are the most vulnerable group to such alterations. As forest dwelling animals, primates are highly sensitive to deforestation, as well as other animals such as the Baird's Tapir, that also depends on closed canopy forests (Matola et al. 1997). Other international examples support the fact that many species might be highly impacted by forest loss during the post-conflict era in Colombia. When civil war ended in Nicaragua, deforestation increased because many people returned to rural areas (Stevens et al. 2011). In addition, rapid forest loss was also documented in post-conflict periods in Bosnia, Liberia, Rwanda and Sierra Leone (Suarez et al. 2018).

Other human activities, such as hunting, may increase the threats to some primate species. For example, four Atelids and the Central American Red Brocket, which are classified as high-risk species in our study, face known hunting pressure (Weber and Gonzalez 2003, de Thoisy et al. 2005, Aquino et al. 2009) concomitant with post-conflict land-use change. Previous studies demonstrated that in the Rwanda Republic and the Democratic Republic of Congo for example, bushmeat hunting increased after peace negotiation, affecting ungulates and the emblematic flagship species *Gorilla* spp. (Plumptre et al. 1997, Glew and Hudson 2007). Increased hunting also caused wildlife decline in Cambodia during its post-conflict era (Loucks et al. 2009).

We found that areas near to the Serranía de San Lucas and Urabá gulf are the most critical regions since they host the largest numbers of mammals considered at risk according to our sensitivity index. Historically, some guerrillas in San Lucas imposed environmental restrictions for locals to preserve the area, such as prohibition of hunting and logging and they planted landmines to avoid mining and logging by foreign people (Dávalos 2001). Nevertheless, after the peace agreement, FARC abandoned this area, ending this protective measure. The National Liberation Army (ELN) is another armed group that still occupies some areas in Colombia and has similar environmental policies (Dávalos 2001). However, ELN and the Colombian Government have been under negotiations since 2017 and a similar effect on biodiversity could arise should such negotiations succeed, not only due to the absence of environmental control imposed by guerrillas, but also due to the changes related to land use inherent in the new peace agreement. On the other hand, armed conflict displaced more than 10,000 people in some municipalities from Urabá (see database in Consejería Presidencial para los Derechos Humanos 2015 and Unidad para las Víctimas 2018). As a consequence, we expect the return of a large number of people to this region, leading to deforestation, increased hunting and raising the risk of local extinctions.

The relationship between biodiversity and warfare can be separated in three stages: 1) preparations, 2) war and, 3) post-war activities (Machlis and Hanson 2008). As the Colombian conflict is old (more than 50 years), it is difficult to gather information related to biodiversity in the former stage (i.e. pre-war). However, current geopolitical and social scenarios provide an opportunity to guide the Colombian government in thinking about the last two stages. Concerning the second stage, there are other armed groups in Colombia disputing territories in a few regions of the country and they have dominion or take advantage of the gap left by the former armed groups. In this case, the government can carry out actions to reduce the negative effects of this regionalised war on biodiversity and environment. Such actions may include (1) increasing research, (2) applying the resolutions of the United Nations against pollution in war time and the environmental protection in conflicts areas and (3) taking into account the "International Day for Preventing the Exploitation of the Environment in War and Armed Conflict" (Hanson 2018). Concerning the third stage, primates, similar to birds (Ocampo-Peñuela and Scott 2017), could be targeted by touristic activities in the post-conflict era or became flagship species in a "green economy based on low-emissions land/resource use systems" (Baptiste et al. 2017).

Increasing the protected areas should be a government strategy associated with the rural reform to prevent biodiversity losses during the post-conflict period. The critical regions for the implementation of such protected areas would be areas near to Urabá Gulf and Serranía de San Lucas, since they harbour most of the high-risk species from this study. Most of the species classified as high-risk or very high-risk in our analysis have less than 10% of their distribution under legal protection. The most critical case was *Plecturocebus caquetensis*, the single very high-risk species in our analysis that occurs outside of the most critical areas in post-conflict: its distribution does not overlap any protected area, its entire distribution is within post-conflict area and it was recently classified amongst the world's 25 most endangered primates (Defler et al. 2017). This species, similar to others, demands urgent conservation schemes, such as economic incentives for the establishment of private protected areas and agro-silvoforestry plots (Baptiste et al. 2017) in programmes led by local farmers and former fighters who have been reintegrated into civilian life. This option is highly feasible taking into account the forestry vocation of Colombia (IGAC 2012). For this reason, the government needs to consider the current types of potential land use of Colombia in the post-conflict era to avoid biodiversity loss, as evidence around the world has shown that some environmental drivers of change in post-conflict countries are "ineffective land use planning" and "unsustainable agricultural practices" (Suarez et al. 2018).

Conclusions

Around the world, in the last half of the past century, more than 80% of armed conflicts took place within biodiversity hotspots (Hanson et al. 2009). Therefore, mitigating warfare impacts is imperative for biodiversity conservation, as many conflicts of state-based violence and non-state violence have been increasing in the last century throughout the globe, including countries such as Mexico, Somalia, Syria and Myanmar (UCDP 2018), which host biodiversity hotspots (Myers et al. 2000, Mittermeier et al. 2004). As other conflicts are certain to occur in the future, approaches such as ours may aid other conflict areas to promote biodiversity conservation when these conflicts are over.

When the environmental context is not cohesive with peace agreements, several drivers of environmental change can emerge (Suarez et al. 2018). In that order, conservation planning is vital for peace building in regions of high biodiversity (Lujala and Rustad 2012). Some countries reached a peace agreements in the last 30 years, for example: El Salvador (1992), Rwanda (1993), Bosnia and Herzegovina (1995), Sierra Leone (2000), Liberia (2003) and Burundi (2008) (Suarez et al. 2018). These six countries and Colombia have a common denominator and can prospectively induce positive changes within their territories if peace is ongoing, because high biodiversity make people more resilient when war has devastated their society (Hanson 2018). Since biodiversity can be seen as an opportunity for peace building, it is important to work together with locals, researchers and former fighters with financial support to bring welfare to the people without threatening the biodiversity (Hanson 2018).

This first evaluation of the possible consequences of the peace agreement between Colombian government and FARC on mammals can help to improve the current scenario of peace in Colombia. Fourteen species classified at high-risk or very high-risk categories need to be included in schemes for conservation based in local initiatives led by former fighters and victims of armed conflict. Experiences from Asia, Africa and Central America have shown how the lack of planning can have negative effects on biodiversity, since impacts on the environment increase after cessation of conflict or peace treaties (Loucks et al. 2005, Glew and Hudson 2007, Suarez et al. 2018). In the current scenario of political division in Colombia after the negative result of a plebiscite for peace in October 2016, there is a challenge for the new government that started on August 2018, independent of its political ideology, to include in its environmental strategies the creation of protected areas in the biodiversity hotspot Tumbes-Chocó-Magdalena, specifically in Urabá and Serranía de San Lucas regions. As well as the sustainable use of the biodiversity (e.g. ecotourism approaches with locals and former fighters), using mammals as flagships species, especially primates, to prevent the biodiversity loss and its consequences. Additionally, we think the same analysis with other biological groups would be extremely useful for the design of conservation schemes, land use policies and rural reform programmes in order to prevent extinctions and to decrease threats to the species in Colombia, one of the most biodiverse countries in the world.

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Supplementary material 1

Table S1

Authors: Bayron R. Calle-Rendón, Flavio Moreno, Renato R. Hilário

Data type: species data

Explanation note: Mammal species used in the analysis and value of each factor to calculate the sensitivity index of each species (*S*) is available for this article online.

Link: https://doi.org/10.3897/natureconservation.29.28943.suppl1

5. CONCLUSÕES

À respeito de como a comunidade de primatas, através da riqueza de espécies e dos traços funcionais, responde aos componentes da matriz, às características do fragmento e aos fatores ambientais na região Neotropical e nas sub-regiões, foi encontrado que:

- Na região Neotropical, a área do fragmento influencia a maior retenção total de espécies, retenção de espécies de maior massa e retenção de dietas baseadas em partes reprodutivas e vegetativas das plantas. Tais relações podem ser devidas ao fato que fragmentos maiores mantem uma melhor estrutura da floresta, maior quantidade de recursos e podem manter populações viáveis.
- Fragmentos em áreas protegidas podem reter maior massa de primatas do que fragmentos desprotegidos, provavelmente devido a que áreas protegidas oferecem resistência contra a caça e degradação ambiental.
- Primatas com dietas baseadas em presas são mais retidos em fragmentos com matrizes com menos presença humana e menor quantidade de corpos de água, o que pode ser explicado pelos efeitos negativos da agricultura e empreendimentos hidrelétricos sobre as populações de artrópodes.
- Primatas de maior tamanho e com dietas mais folívoras são perdidos majoritariamente na Mata Atlântica e mais retidos na Mesoamérica, indicando que processos biogeográficos podem agir sobre como os primatas percebem o ambiente. Assim, em avaliações de grande escala (e.g. continentais), é necessário considerar as diferenças entre sub-regiões.

Com referência a como opera a escala do efeito na relação entre a paisagem e os primatas, e como os atributos da paisagem, características das manchas e fatores humanos estão relacionados com a comunidade de primatas em uma paisagem de savana amazônica, é possível concluir que:

- As características das espécies, como área de vida, não explicam como os primatas percebem a paisagem. Porém, o grau de alteração na paisagem é importante para entender a relação entre a riqueza de espécies e a quantidade de hábitat devido à diferença na escala do efeito em regiões com diferente grau de perturbação.
- Os atributos da paisagem foram mais importantes para explicar a ocorrência de espécies, e os fatores humanos mais importantes para explicar a riqueza de espécies.
- À respeito dos atributos da paisagem, de forma geral, houve maior probabilidade de ocorrência de espécies em paisagens com maior cobertura de floresta. Além disso, houve menor probabilidade de ocorrência em paisagens com maior cobertura antrópica e menos quantidade de savana e corpos de água. Desta forma, manter uma maior quantidade de hábitat e matrizes menos perturbadas e mais permeáveis na paisagem pode assegurar a ocorrência de populações de primatas nas savanas.
- Em referência às características das manchas, em termos gerais, houve maior probabilidade de ocorrência de espécies em manchas com maior altura das árvores, o que pode ser explicado por uma maior segregação de nicho. Porém, não foi o caso para *A. belzebul*. De fato, esta espécie teve maior probabilidade de ocorrência em

manchas de formas mais irregulares, o qual pode estar associado ao efeito de borda combinado com a alta proporção de folhas na dieta desta espécie.

- Fatores humanos como número de pessoas no entorno das manchas de floresta teve um efeito negativo na riqueza de primatas. Além disso, a distância da mancha de floresta até a cidade teve um efeito negativo sobre a probabilidade de ocorrência de primatas de grande (*A. belzebul*) e médio porte (*S. apela* e *C. olivaceus*), o que pode estar associado, para ambos os fatores, a processos relacionados com a caça.

O uso de primatas como objetos de conservação em um processo de Planejamento Sistemático para a Conservação para identificar áreas prioritárias para a conservação das Savanas do Amapá, pode ser uma ferramenta que pode atingir a conservação não só dos primatas, mas também dos serviços ecossistêmicos que eles desenvolvem e das áreas chaves que eles habitam. Porém, é necessário ir além de aspectos meramente biológicos e considerar uma aproximação sócio-ecológica para incluir os atores que têm relação com as Savanas do Amapá. Ali, tanto primatas humanos como primatas não humanos são beneficiados pelos bens e serviços que esta região, ameaçada palas mudanças no nível da paisagem, oferece.

Por fim, foi encontrado que das 95 espécies de mamíferos analisadas, os primatas representaram o grupo que poderá ser mais afetado no pós-conflito na Colômbia. Além disso, as regiões onde poderá acontecer a maior parte dos efeitos negativos sobre as populações de mamíferos são a região de Urabá e a Serra de San Lucas, ambas as regiões no *Hotspot* de biodiversidade Tumbes-Chocó-Magdalena (ou também chamado de Chocó-Darién). Assim, é imperativo incluir as espécies mais sensíveis em esquemas de conservação através do fomento de economias locais baseadas no uso sustentável dos recursos naturais e no uso do ecoturismo usando os mamíferos, especialmente os primatas, como espécies bandeira.

ANEXOS

1. Guariba-de-mãos-ruivas (*Alouatta belzebul*)
© Angélica Martínez Alfonso
Site do Projeto Guariba AP https://labecoap.wixsite.com/projetoguariba-ap
Instagram https://www.instagram.com/projetoguariba.ap/
Facebook https://www.facebook.com/projeto.guariba.ap/

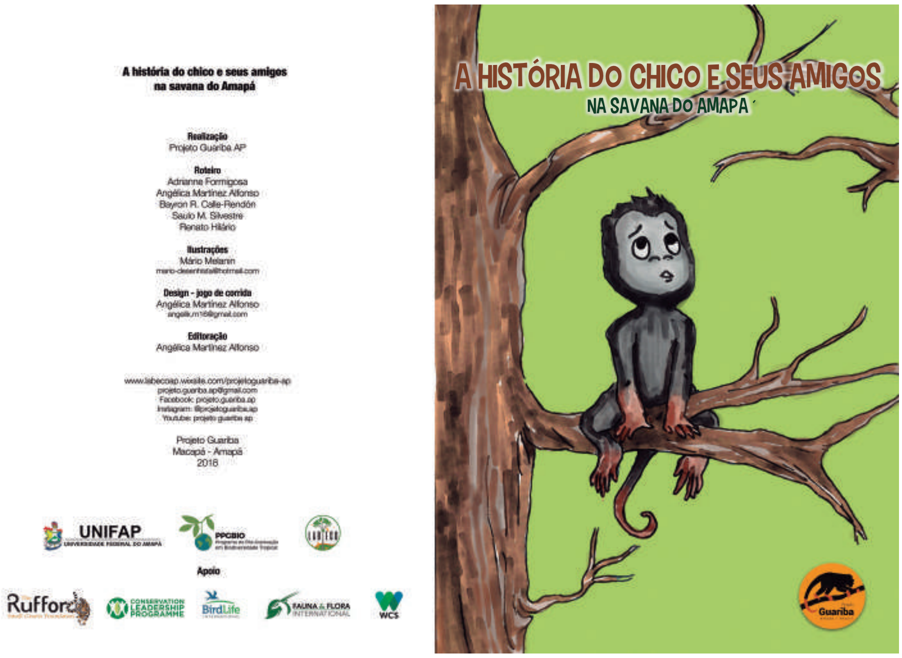
2. Documentário Savanas do Amapá 2019 © Projeto Guariba AP
https://www.youtube.com/watch?v=xJJfhmUpNT4

3. Oficina Amigos da Natureza © Projeto Guariba AP
4º série, Escola Estadual José Bonifácio, Quilombo do Curiaú, Macapá

4. Oficina Amigos da Natureza © Projeto Guariba AP
3º e 4º serie, Escola Municipal de Igarapé do Lago, Santana

5. Oficina Amigos da Natureza © Projeto Guariba AP
Entrega da cartilha na Escola Estadual Teixeira de Freitas
Comunidade São Pedro dos Bois, Macapá

6. Savanas do Amapá © Bayron R. Calle-Rendón



A história do chico e seus amigos
na savana do Amapá

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Projeto Guariba
Macapá - Amapá
2018

Apoio

7. Cartilha A História do Chico e seus Amigos © Projeto Guariba AP
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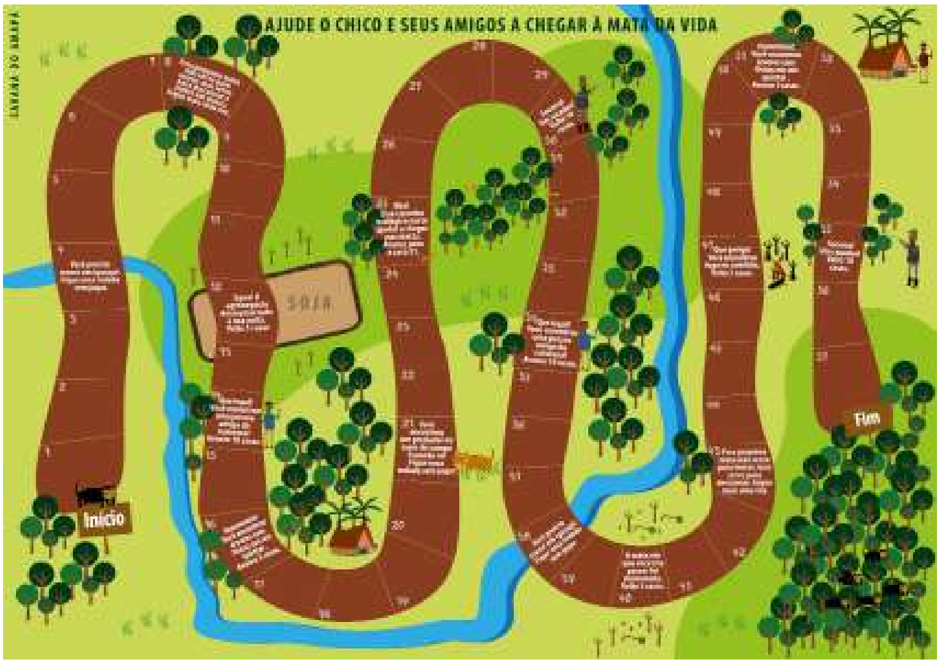

8. Jogo de tabuleiro © Projeto Guariba AP
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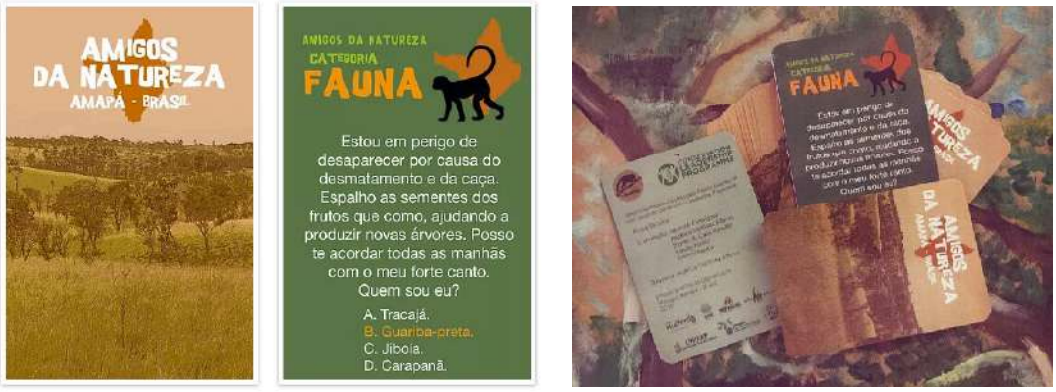
9. Jogo de baralho Amigos da Natureza Amapá - © Projeto Guariba AP
5º serie, Escola Municipal José Bonifácio, Quilombo do Curaiú, Macapá



AMIGOS DA NATUREZA
CATEGORIA
FAUNA

Estou em perigo de desaparecer por causa do desmatamento e da caça. Espalho as sementes dos frutos que como, ajudando a produzir novas árvores. Posso te acordar todas as manhãs com o meu forte canto. Quem sou eu?

A. Tracajá.
B. Guariba-preta.
C. Jiboia.
D. Carapanã.

10. Jogo de baralho Amigos da Natureza Amapá - © Projeto Guariba AP
41 cartas com perguntas sobre a biodiversidade das savanas do Amapá
Download https://labecoap.wixsite.com/projetoguariba-ap/amigos-da-natureza