Universidade Federal de Goiás

Instituto de Ciências Biológicas

Programa de Pós-graduação em Ecologia e Evolução

Flávia de Figueiredo Machado

Conservação e risco de extinção em Primatas

Orientador: Prof. Dr. Daniel de Brito Candido da Silva

Goiânia - GO

Maio de 2018

sistema de bibliotecas ufg

PRPG
PRÓ-REITORIA DE PÓS-GRADUAÇÃO

UFG

TERMO DE CIÊNCIA E DE AUTORIZAÇÃO PARA DISPONIBILIZAR VERSÕES ELETRÔNICAS DE TESES E DISSERTAÇÕES NA BIBLIOTECA DIGITAL DA UFG

Na qualidade de titular dos direitos de autor, autorizo a Universidade Federal de Goiás (UFG) a disponibilizar, gratuitamente, por meio da Biblioteca Digital de Teses e Dissertações (BDTD/UFG), regulamentada pela Resolução CEPEC nº 832/2007, sem ressarcimento dos direitos autorais, de acordo com a Lei nº 9610/98, o documento conforme permissões assinaladas abaixo, para fins de leitura, impressão e/ou download, a título de divulgação da produção científica brasileira, a partir desta data.

1. Identificação do material bibliográfico: **[ ] Dissertação** **[x] Tese**

2. Identificação da Tese ou Dissertação:

Nome completo do autor: Flávia de Figueiredo Machado

Título do trabalho: Conservação e risco de extinção em primatas

3. Informações de acesso ao documento:

Concorda com a liberação total do documento [x] SIM [ ] NÃO[1]

Havendo concordância com a disponibilização eletrônica, torna-se imprescindível o envio do(s) arquivo(s) em formato digital PDF da tese ou dissertação.

Flávia de Figueiredo Machado
Assinatura do(a) autor(a)[2]

Ciente e de acordo:

Assinatura do(a) orientador(a)[2]

Data: 27 / 08 / 2018

[1] Neste caso o documento será embargado por até um ano a partir da data de defesa. A extensão deste prazo suscita justificativa junto à coordenação do curso. Os dados do documento não serão disponibilizados durante o período de embargo.
Casos de embargo:
- Solicitação de registro de patente;
- Submissão de artigo em revista científica;
- Publicação como capítulo de livro;
- Publicação da dissertação/tese em livro.

[2] A assinatura deve ser escaneada.

Flávia de Figueiredo Machado

Conservação e risco de extinção em Primatas

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Evolução do Departamento de Ecologia do Instituto de Ciências Biológicas da Universidade Federal de Goiás como requisito parcial para obtenção do título de doutora em Ecologia e Evolução.

Orientador: Prof. Dr. Daniel de Brito Candido da Silva

Goiânia-GO

Maio de 2018

Ficha de identificação da obra elaborada pelo autor, através do
Programa de Geração Automática do Sistema de Bibliotecas da UFG.

Machado, Flávia de Figueiredo
Conservação e risco de extinção em Primatas [manuscrito] / Flávia de Figueiredo Machado. - 2018.
CXIII, 113 f.: il.

Orientador: Prof. Dr. Daniel de Brito Candido da Silva.
Tese (Doutorado) - Universidade Federal de Goiás, Instituto de Ciências Biológicas (ICB), Programa de Pós-Graduação em Ecologia e Evolução, Goiânia, 2018.
Bibliografia. Apêndice.
Inclui mapas, gráfico, tabelas.

1. Primatas. 2. Risco de extinção. 3. Conservação. 4. Vulnerabilidade à extinção. 5. Cienciometria. I. de Brito Candido da Silva, Daniel , orient. II. Título.

CDU 574

SERVIÇO PÚBLICO FEDERAL
UNIVERSIDADE FEDERAL DE GOIÁS - UFG
INSTITUTO DE CIÊNCIAS BIOLÓGICAS - ICB
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO - PPGEE

ATA DA SESSÃO PÚBLICA DE DEFESA DE TESE Nº 68

Aos vinte e oito dias do mês de maio de 2018 (28/05/2018), às treze horas e trinta minutos horas (13h30min), no Auditório do ICB V, UFG, reuniram-se os componentes da banca examinadora**: Prof. Dr. Daniel de Brito Cândido Silva, ICB-UFG; Prof. Dr. Alessandro Ribeiro de Morais, IFGoiano/RioVerde; Prof. Dr. Matheus de Souza Lima Ribeiro, ICB-UFG/Jataí (via teleconferência); Profa. Dra. Levi Carina Terribile, ICB-UFG/Jataí (via teleconferência); Prof. Dr. Leonardo de Carvalho Oliveira, UERJ;** para, em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Conservação e risco de extinção em Primatas"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Flávia de Figueiredo Machado**, discente do Programa de Pós-Graduação em Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 30 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi APROVADA, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias

a contar da data da defesa. Cumpridas as formalidades de pauta, às 17 h e 00 min., encerrou-se a sessão de defesa e, para constar, eu, Suely Ana Ribeiro, secretária executiva da Universidade Federal de Goiás - UFG, lavrei a presente ata que, após lida e aprovada, será assinada pelos membros da banca examinadora em três vias de igual teor.

Prof. Dr. Daniel de Brito Cândido Silva
Presidente da banca
ICB-UFG

Prof. Dr. Alessandro Ribeiro de Morais
IFGoiano/RioVerde

Prof. Dr. Matheus de Souza Lima Ribeiro
ICB-UFG/Jataí
(via teleconferência)

Profa. Dra. Levi Carina Terribile
ICB-UFG/Jataí
(via teleconferência)

Prof. Dr. Leonardo de Carvalho Oliveira
UERJ

Dedico esta tese à minha mãe,

que sempre me apoiou e esteve presente.

AGRADECIMENTOS

Primeiramente, gostaria de agradecer à minha mãe, que sempre me incentivou e me apoiou em meus estudos.

Aos amigos que fiz na Ecoevol, que contribuíram para que esses quatro anos fossem muito mais fáceis, leves e felizes: Larissa, Lilian, Raísa, Fernando, Klein, Clô, André, Hauanny e Carol. Em especial, aos amigos do "Sábado maculelê", pela parceria constante: Barbba, Olivinha, Laritcha, Vini e Dani.

Ao pessoal do "Macroevolution & Macroecology Group", da "Australian National University", por terem me acolhido durante os seis meses que estive na Austrália e por terem contribuído com o meu segundo e terceiro capítulo. Em especial, ao Marcel Cardillo, pela supervisão, paciência, ideias e por estar sempre disponível para me auxiliar. Agradeço imensamente também o Russell, pela ajuda com as análises de parte do segundo capítulo e com as análises do terceiro capítulo.

Ao Lucas Jardim pela ajuda com os modelos do segundo capítulo. Ao Clô pelo auxílio com alguns dos meus primeiros *scripts*. À Thamires, Anne e Giovanna pela contribuição na compilação de dados para a minha cienciometria.

Aos amigos que fiz na Austrália, pelo companheirismo, amizade e pelas viagens incríveis: Thiago, Rodrigo, Milena, Weliton, Jéssica, Léo e Thaís.

Ao Daniel Brito, pela orientação durante esses quarto. Ao PPG em Ecologia e Evolução e todos os professores do programa que me proporcionaram profundo aprendizado.

Aos membros da banca examinadora: Levi Carina, Matheus Ribeiro, Leonardo Oliveira e Alessandro Morais, que se dispuseram a contribuir com a tese.

Por fim, agradeço à CAPES pela concessão da bolsa no Brasil e na Austrália, tornando possível a execução desta tese.

SUMÁRIO

RESUMO

Nesta tese tive o objetivo de investigar os fatores relacionados ao risco de extinção em primatas, assim como as tendências e vieses nos esforços de pesquisas voltadas para a conservação do grupo. No primeiro capítulo, por meio de uma cienciometria, mostrei quais são os temas, abordagens e espécies mais estudadas, bem como as instituições e locais que mais realizam esses estudos. Demonstrei que os esforços de pesquisa com conservação de primatas não têm sido motivados pelo status de conservação das espécies e tamanho da sua distribuição, e sim pelo peso corporal e idade (tempo desde a sua descrição). No segundo capítulo, testei se a dieta de primatas pode predizer o risco de extinção das espécies, mensurando dieta de diferentes maneiras: amplitude de dieta, diversidade de dieta, tipo de dieta e disparidade de itens. Concluí que a dieta prediz o risco de extinção, mas apenas pela métrica de disparidade de itens, sendo que espécies capazes de consumir itens mais diferentes entre si estarão menos propensas à extinção. No terceiro e último capítulo, avaliei os padrões de risco de extinção em primatas. Incluí variáveis intrínsecas e extrínsecas em modelos que particionam a variância em componentes espaciais, filogenéticas e independentes. Mostrei que espécies próximas na filogenia e no espaço tendem a apresentar status de ameaça semelhantes. Além disso, encontrei que a região Madagascar é a pior para os primatas e que o tempo de desmame, tamanho da distribuição geográfica e fatores como "human footprint" e pobreza humana influenciam no risco de extinção das espécies. Por fim, demonstrei que o espaço possui grande influência no risco de extinção de primatas, não devendo ser ignorado nesse tipo de análise.

Palavras-chave: risco de extinção; primatas; cienciometria; dieta; esforços de pesquisa; sinal filogenético; sinal espacial.

INTRODUÇÃO GERAL

A extinção biológica é um processo natural [Purvis et al., 2000a]. Contudo, as taxas de extinção têm ocorrido a níveis muito altos, mais do que seria esperado por causas naturais [Pimm et al., 1995, 2014; Barnosky et al., 2011]. As ações humanas são as principais responsáveis por essa taxa elevada de perda de espécies [Dirzo et al., 2014; Pimm et al., 2014], que tem levado a uma sexta extinção em massa [Barnosky et al., 2011; Ceballos et al., 2015; De Vos et al., 2015].

Para se determinar o risco de uma espécie ser extinta existem algumas métricas, sendo uma delas as categorias da IUCN (International Union for Conservation of Nature and Natural Resources). Essas categorias predizem o declínio populacional ou extinção de uma espécie em um determinado período de tempo, apresentando maior risco de extinção aquelas com maior declínio [Fisher & Owens, 2004].

O risco de extinção está associado ao termo vulnerabilidade, que se refere ao grau em que um sistema, ou unidade do sistema é afetado com a exposição a algum perigo, perturbação ou estresse [Turner et al., 2003]. Dentre outros termos, vulnerabilidade tem sido usada também como sinônimo de suscetibilidade, exposição, sensibilidade e adaptabilidade [Füssel, 2007].

O termo vulnerabilidade é muito utilizado, dentre em outras áreas, na de mudanças climáticas. Williams e colaboradores [2008] a definem como o quanto uma espécie ou população está ameaçada ao declínio, à redução do valor adaptativo, à perda genética ou extinção, frente às mudanças climáticas. Nesse contexto, a vulnerabilidade possui três aspectos: exposição, sensibilidade e capacidade adaptativa [Williams et al., 2008; Dawson et al., 2011; Foden et al., 2013]. Considerando esses três aspectos da vulnerabilidade,

podemos perceber que ela depende de fatores intrínsecos e extrínsecos às espécies. Assim, o risco de extinção é dado pela interação entre os fatores intrínsecos (história de vida e ecologia) das espécies e fatores extrínsecos (ambiente e ameaças) a elas [Murray et al., 2014].

Os fatores extrínsecos são aqueles não relacionados à história de vida ou biologia das espécies, podendo ser variáveis ambientais ou geográficas (p. ex. temperatura, precipitação e latitude) ou ameaças diretas, tais como perda de habitat e densidade populacional humana [Murray et al., 2014]. As ameaças são importantes de serem consideradas em trabalhos de risco de extinção, pois elas podem influenciar o declínio populacional em diferentes escalas temporais e espaciais [Wilcove et al., 1998]. Além disso, trabalhos que desconsideram as ameaças podem perder informações práticas de interesse para implementação de ações de conservação [Murray et al., 2014].

A exposição às ameaças é a causa final das extinções, mas a biologia das espécies determinará o quão bem elas conseguirão lidar com as ameaças as quais estão expostas [Cardillo et al., 2004]. As espécies respondem às ameaças de diferentes formas, sendo mais suscetíveis ou não a elas por apresentarem diferentes traços biológicos, ecológicos e de história de vida [Bennett et al., 2005]. Assim, o risco de extinção também está relacionado à filogenia, não estando aleatoriamente distribuído entre os grupos taxonômicos [p. ex. Bennett and Owens, 1997; Purvis et al., 2000b; Purvis, 2008; Schwartz and Simberloff, 2001].

Existem vários trabalhos analisando a relação entre fatores intrínsecos e risco de extinção das espécies [p. ex. Brashares, 2003; Cardillo, 2003; Davidson et al., 2009; Davies et al., 2011; Harcourt et al., 2002; Matthews et al., 2011]. Contudo, o uso destes preditores explica somente parte da variação encontrada no risco de extinção das espécies [Cardillo et

al., 2008]. O restante desta variação seria explicado pelos fatores extrínsecos e pela interação destes com os fatores intrínsecos [Fisher et al., 2003; Cardillo et al., 2005; Price & Gittleman, 2007].

Alguns dos fatores intrínsecos mais relacionados ao status de ameaça são: tamanho corporal, história de vida, tamanho da distribuição geográfica, nível trófico, uso do habitat, especializações ecológicas e sociais [Cardillo et al., 2005, 2004; Cardillo et al., 2008; Fisher et al., 2003; Purvis et al., 2000a, 2000b]. Apesar disso, predizer quais traços estão relacionados à vulnerabilidade depende de qual ameaça está afetando a espécie [González-Suárez et al., 2013].

Os primeiros trabalhos de risco de extinção com mamíferos estavam interessados em compreender quais eram os fatores intrínsecos que tornam as espécies mais vulneráveis [p. ex. Bodmer et al., 1997; Jernvall & Wright, 1998]. Esses não consideravam a relação de parentesco entre as espécies, não utilizando métodos para controlar o sinal filogenético. Purvis et al. [2000b] foram os primeiros a investigar a relação entre características biológicas e ecológicas em mamíferos com o seu risco de extinção controlando esse sinal. Posteriormente, começou-se a incluir fatores extrínsecos nas análises, tais como ameaças [p. ex. Isaac & Cowlishaw, 2004; Yackulic et al., 2011]. Contudo, percebeu-se que os fatores intrínsecos e extrínsecos em si prediziam somente parte do risco de extinção, sendo necessário incluir a interação entre eles [Cardillo et al., 2008]. Além da autocorrelação filogenética, as espécies também estão sujeitas à autocorrelação espacial, já que muitas das características das espécies são processos adaptativos com influência do espaço [Gaston et al., 2008]. Assim, surgiram trabalhos integrando a autocorrelação espacial e filogenética nas análises de risco de extinção, mas essa ainda é uma abordagem incipiente, com poucos

trabalhos considerando o sinal filogenético e espacial [p. ex. Safi & Pettorelli, 2010; Jetz & Freckleton, 2015].

Nesta tese investiguei os fatores relacionados ao risco de extinção em primatas, buscando avaliar os fatores intrínsecos, extrínsecos e ameaças, incorporando o sinal filogenético e espacial. Além disso, pesquisei as tendências e vieses nos esforços de pesquisas voltadas para conservação de primatas.

Os primatas compreendem um grande grupo de mamíferos, com 440 espécies [IUCN, 2018]. São carismáticos, a ecologia e a história natural da maior parte das espécies estão bem descritas, além de ter muitas espécies abundantes e com ampla distribuição [Purvis et al., 2000b]. Assim, é um bom grupo para se testar modelos de risco de extinção, além de ser de grande interesse para a biologia da conservação, pois aproximadamente 61% de todas as espécies são ameaçadas de extinção [IUCN, 2018].

A tese está organizada em três capítulos, estando eles estruturados em formato de artigo científico, em inglês.

No primeiro capítulo, investiguei as tendências e vieses nos esforços de pesquisa com conservação de primatas. Eu revisei a literatura na área para identificar as espécies, temas e abordagens mais estudadas, bem como os países onde essas pesquisas ocorrem e de onde são os pesquisadores que as lideram. Além disso, avaliei o que motiva as pesquisas com primatas voltadas para a conservação. Para isso, relacionei o número de artigos publicados por espécie com o seu peso corporal, tamanho da distribuição geográfica, tempo de descrição da espécie e status de ameaça.

No segundo capítulo, pesquisei se o risco de extinção em primatas pode ser predito pela dieta da espécie. Para isso, utilizei uma extensa base de dados, com informações para todas as regiões e habitats e incluí o peso corporal e o tamanho da distribuição geográfica

como covariáveis. Avaliei a dieta utilizando diferentes métricas: amplitude de dieta, diversidade de dieta, tipo de dieta e disparidade de itens.

No terceiro e último capítulo, investiguei os padrões de risco de extinção em primatas. Considerei fatores intrínsecos e extrínsecos, incluindo características biológicas e ecológicas das espécies, variáveis ambientais e ameaças as quais elas estão submetidas. De forma a controlar o sinal filogenético e espacial, usei um modelo que particiona a variância em componente espacial, filogenético e independente.

REFERÊNCIAS

Barnosky AD, Matzke N, Tomiya S, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature [Internet] 471:51–57. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21368823

Bennett PM, Owens IPF. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society B: Biological Sciences 264:401–408.

Bodmer RE, Eisenberg JF, Redford KH. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology 11:460–466.

Brashares JS. 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. Conservation Biology 17:733–743.

Cardillo M. 2003. Biological determinants of extinction risk: why are smaller species less vulnerable? Animal Conservation [Internet] 6:63–69. Available from: http://dx.doi.org/10.1017/S1367943003003093

Cardillo M, Mace GM, Gittleman JL, et al. 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proceedings. Biological sciences / The Royal Society 275:1441–1448.

Cardillo M, Mace GM, Jones KE, et al. 2005. Multiple causes of high extinction risk in large mammal species. Science (New York, N.Y.) 309:1239–1241.

Cardillo M, Purvis A, Sechrest W, et al. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology 2:909–914.

Ceballos G, Ehrlich PR, Barnosky AD, et al. 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. Sciences Advances 1:1–5.

Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G. 2009. Multiple ecological pathways to extinction in mammals. Proceedings of the National Academy of Sciences of the United States of America 106:10702–10705.

Davies TJ, Smith GF, Bellstedt DU, et al. 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. PLoS biology [Internet] 9:e1000620. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3101198&tool=pmcentrez&rendertype=abstract

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science (New York, N.Y.) 332:53–58.

Dirzo R, Young HS, Galetti M, et al. 2014. Defaunation in the Anthropocene. Science [Internet] 345:401–406. Available from: http://www.sciencemag.org/cgi/doi/10.1126/science.1251817%5Cnhttp://www.sciencemag.org/content/345/6195/401.short

Fisher DO, Blomberg SP, Owens IPF. 2003. Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. Proceedings. Biological sciences / The Royal Society 270:1801–1808.

Fisher DO, Owens IPF. 2004. The comparative method in conservation biology. Trends in Ecology and Evolution 19:391–398.

Foden WB, Butchart SHM, Stuart SN, et al. 2013. Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. PLoS ONE 8:1–13.

Füssel HM. 2007. Vulnerability: A generally applicable conceptual framework for climate change research. Global Environmental Change 17:155–167.

Gaston KJ, Chown SL, Evans KL. 2008. Ecogeographical rules: Elements of a synthesis. Journal of Biogeography 35:483–500.

González-Suárez M, Gómez A, Revilla E. 2013. Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. Ecosphere [Internet] 4:art76. Available from: http://dx.doi.org/10.1890/ES12-00380.1%5Cnhttp://www.esajournals.org/doi/pdf/10.1890/ES12-00380.1

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization and extinction in primates. Journal of Biogeography 29:445–456.

Isaac NJB, Cowlishaw G. 2004. How species respond to multiple extinction threats. Proceedings. Biological sciences / The Royal Society 271:1135–1141.

IUCN. 2018. Available from: http://www.iucnredlist.org/

Jernvall J, Wright PC. 1998. Diversity components of impending primate extinctions. Proceedings of the National Academy of Sciences [Internet] 95:11279–11283. Available from: http://www.pnas.org/cgi/doi/10.1073/pnas.95.19.11279

Jetz W, Freckleton RP. 2015. Towards a general framework for predicting threat status of data-deficient species from phylogenetic, spatial and environmental information. Philosophical Transactions of the Royal Society B: Biological Sciences [Internet] 370:20140016–20140016. Available from: http://rstb.royalsocietypublishing.org/cgi/doi/10.1098/rstb.2014.0016

Matthews LJ, Arnold C, Machanda Z, Nunn CL. 2011. Primate extinction risk and historical patterns of speciation and extinction in relation to body mass. Proceedings of the Royal Society B: Biological Sciences [Internet] 278:1256–1263. Available from: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2010.1489

Murray KA, Verde Arregoitia LD, Davidson A, Di Marco M, Di Fonzo MMI. 2014. Threat to the point: improving the value of comparative extinction risk analysis for conservation action. Global Change Biology [Internet] 20:483–494. Available from: http://doi.wiley.com/10.1111/gcb.12366

Pimm SL, Jenkins CN, Abell R, et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science (New York, N.Y.) [Internet] 344:1246752. Available from: http://www.ncbi.nlm.nih.gov/pubmed/24876501

Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The Future of Biodiversity. Science [Internet] 269:347–350. Available from: http://www.ncbi.nlm.nih.gov/pubmed/17841251

Price SA, Gittleman JL. 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. Proceedings. Biological sciences / The Royal Society [Internet] 274:1845–1851. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2270938&tool=pmcentrez&rendertype=abstract

Purvis A. 2008. Phylogenetic Approaches to the Study of Extinction. The Annual Review of Ecology, Evolution, and Systematics [Internet] 39:301–319. Available from: http://geology.gsapubs.org/content/43/8/751.full?etoc

Purvis A, Jones KE, Mace GM. 2000a. Extinction. Bioessay 22:1123–1133.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000b. Predicting extinction risk in declining species. Proceedings. Biological Sciences / The Royal Society 267:1947–1952.

Safi K, Pettorelli N. 2010. Phylogenetic, spatial and environmental components of extinction risk in carnivores. Global Ecology and Biogeography 19:352–362.

Schwartz MW, Simberloff. 2001. Taxon size predicts rates of rarity in vascular plants. Ecology Letters 4:464–469.

Turner BL, Kasperson RE, Matson PA, et al. 2003. A framework for vulnerability analysis in sustainability science. Proceedings of the National Academy of Sciences of the United States of America 100:8074–8079.

De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL. 2015. Estimating the normal background rate of species extinction. Conservation Biology [Internet] 29:452–462. Available from: http://doi.wiley.com/10.1111/cobi.12380

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G. 2008. Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. PLoS Biol [Internet] 6:e325. Available from: http://dx.doi.org/10.1371/journal.pbio.0060325

Yackulic CB, Sanderson EW, Uriarte M. 2011. Anthropogenic and environmental drivers of modern range loss in large mammals. Proceedings of the National Academy of Sciences [Internet] 108:4024–4029.

Capítulo 1

Twenty years of primate conservation research

Flávia de Figueiredo Machado[1,2]

Daniel de Brito Candido da Silva[1]

Authors' affiliations:

[1]Laboratório de Ecologia Aplicada e Conservação, Departamento de Ecologia, Universidade Federal de Goiás, Brazil.

[2]Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás, Brazil.

ABSTRACT

The species extinction rate has been occurring at levels more accelerated than would be expected without impacts on biodiversity, so that scientists are concerned with identifying priority species and areas for conservation. Species better studied receive more conservation attention, been necessary optimize our research efforts. However, some factors contribute that some species are more studied than others. Our aim was investigate the biases and trends in allocation of research efforts on primate conservation, across species, themes and countries. We reviewed the literature from 20 years (1994 – 2014) on six conservation journals and four primatology journals, selecting papers with determined tags related with primate conservation. We found 550 articles about primate conservation, and this theme has increased in the primatology area, but not in the conservation area. Fragmentation was the most addressed theme. Most of the authors are from universities and the studies were conducted mostly in protected and unprotected areas. Most of the studies used empiric approach and was conducted by 49 different countries, been United States and United Kingdom which published most of them. These studies were made in 55 different countries and Madagascar and Indonesia were those that more receive these researches. The articles are related to 388 species, from all 16 primate families, been *Pan troglodytes* the species with more number of articles. Allocation of research effort was motivated by time since description and species body size, but not by threat status and size of distribution. Ours results showed that the studies not always reflect conservation needs. To improve the primate conservation efforts, primatologists need to rethink their priorities, focusing in conservation need, such as threatened species and important threats.

Keywords: research efforts; primates; trends; biases; scientometrics.

INTRODUCTION

The current species extinction rate is between 1.000 to 10.000 times higher than natural background rates [Pimm et al., 1995], leading to a sixth mass extinction event [Barnosky et al., 2011; Ceballos et al., 2015], mainly driven by anthropogenic causes [Ceballos et al., 2015]. Vertebrates have depicted dramatic declines [Baillie et al., 2011; McCallum, 2015]. Among the seriously threatened mammals [Schipper et al., 2008], primates' conservation status is particularly worrysome, with a high proportion of threatened species and severe population declines [Estrada et al., 2017].

Primates play key ecological roles within ecosystems, are models to study the evolution of social behavior, and are key to comprehend human evolution [Marshall & Wich, 2016]. They are also important when discussing human welfare, both as sources of diseases and as models to prevent them [Marshall & Wich, 2016]. Therefore, the protection of primate diversity may be advocated using both a biocentric and an anthropocentric standpoint.

The conservation literature dedicated to primates increased significantly in the last decades [Marshall & Wich, 2016]. The question is if all this increase in research effort is representative both of primate diversity and conservation priorities. Biases in allocation of research effort might compromise the conservation efforts to preserve primate species. Conservation practices should be based on good science [Verde Arregoitia et al., 2015], but sometimes there is a gap between published conservation planning and on-the-ground conservation actions [Sutherland et al., 2004; Meijaard & Sheil, 2007], and also between how researchers choose their study sites and species. In order to optimize research effort, we should consider both conservation practices already set in place and current scientific

knowledge [Sitas et al., 2009]. In doing so, we should be able to identify species-specific knowledge biases and gaps [e.g. Amori & Gippoliti, 2000; Bonnet et al., 2002; Trimble & Van Aarde, 2010].

In human-dominated landscapes, a species that is threatened by extinction, that provides an ecosystem service, or that has economic importance, receives more attention from the scientific community [Trimble & van Aarde, 2012]. Such biases may also occur due to conscious or unconscious preferences of researchers by some biological aspects of species [Lawler et al., 2006; Trimble & van Aarde, 2010]. This results in an uneven knowledge of the natural world [e.g. Amori & Gippoliti, 2000; Clark & May, 2002]. There is evidence for a bias knowledge towards large-bodied [Ward et al., 1998; Brodie, 2009; Johnson et al., 2010], wide-ranged [Harris & Pimm, 2008] animals. Large-bodied animals are easier to spot, facilitating their use as target-species by researchers. Species with large geographic distributions potentially overlap their range with the fieldwork areas of many researchers, increasing their chances to be picked up by a researcher as a focus for their study. The same rationale may be applied to "older" species. Species described a long time ago, have had more time to be picked up by researchers, and are more likely to have accumulated more studies than recently described species. Threatened species should be conservation priorities and receive attention from the scientific community, but that is not always the case [Brito, 2008].

Here we will test if body size, geographic range size, species age (time since description), phylogeny and threat status influence the current scientific knowledge of primate species (measured as the number of published articles for each species).

METHODS

Trends in primate conservation research effort

We selected the major primatological journals (American Journal of Primatology, Folia Primatologica, International Journal of Primatology and Primates) and the major conservation science journals (Animal Conservation, Biodiversity and Conservation, Biological Conservation, Conservation Biology, Journal for Nature Conservation and Oryx), that are representative of the research published in the scientific literature on primate conservation. We compiled all articles and reviews published on primate conservation between 1994 and 2014. Article search was conducted in web of science using species, genus and family, scientific names and species common names (for conservation journals), and conservation actions, threats and/or methods (for primatological journals) as keywords (see Supporting Text for more details).

The scope of primate conservation research themes we considered in our search were: (i) habitat loss and fragmentation, (ii) hunting, (iii) road kill, (iv) wildlife management, (v) conservation medicine, (vi) habitat use, (vii) conservation genetics, (viii) environmental disasters, (ix) population/species status, (x) extinction, (xi) human-primate conflicts and interactions, (xii) environmental education, (xiii) conservation policies, (xiv) tourism, (xv) animal trade, (xvi) invasive exotic species, (xvii) life in captivity, (xviii) pesticide use and (xix) umbrella species (see Table S1 for definitions).

For each published article or review, we extracted the title, the year of publication, the species studied, the authors (first and last), author affiliation (both country and type of affiliation: university, zoo or theme park, NGO, private institution, governmental agency, research center, research society, sanctuary/rehabilitation center, museum, medical center, protected area staff or autonomous), the approach used in the research (empiric,

experimental, theoretical and review), the research theme (e.g. habitat fragmentation, hunting, conservation medicine, animal trade, captivity life) (see Table S1 for all themes and for definitions), and the nature of the research locality (zoo/captivity, protected area, sanctuary, non-protected area, agricultural/agroforestry, urban/rural, natural area with undefined status, laboratory/clinical, and theoretical) (Table S1).

Research effort is the number of articles/reviews published for each species. If an author reported more than one affiliation, we considered the first listed institution for the as its main affiliation. We followed the taxonomy currently accepted for all primate species and subspecies [Mittermeier et al., 2013]. To investigate temporal trends primate conservation research efforts, we divided the number of articles selected per year by the total number of articles published in the chosen primatology and conservation journals published in the same year. We related the proportion of articles across the years using a generalized linear model (GLM), considering a binomial distribution, in R [R Development Core Team, 2016].

Allocation of research effort in primate conservation

To investigate spatial allocation of research effort we counted the number of authors and studies by country, that realized empiric studies. In order to evaluate if research effort is influenced by species body size [Mittermeier et al., 2013], threat status [IUCN, 2016], range size [IUCN, 2016] and species age (time since description) [Mittermeier et al., 2013], we used a generalized linear model (GLM). The GLM model was specified using a negative binomial error distribution and a log link, in R [R Development Core Team, 2016]. We transformed threat status categories in numbers varying from 0 (Least Concern) to 5 (Extinct in the Wild or Extinct) [Purvis et al., 2000].

To investigate the phylogenetic pattern in the allocation of research effort, we checked if there is phylogenetic signal in the number of articles per species, contributing for close species be more studied than others. We used the Springer et al. [2012] primate's tree and for all primates species which were not in the tree, we inserted them randomly in the node clade, 1.000 times.

RESULTS

Trends in primate conservation research effort

In the time period studied, the ten journals published a total of 17,234 articles/reviews, 550 of which on primate conservation. Analyzing separately, we found that primatology journals increased the number of conservation articles published (estimate = 0.08; $z = 6.98$; $p < 0.01$), but the number of articles dedicated to primates in conservation journals remained stable (estimate = 0.001; $z = 0.13$, $p = 0.89$) (Figure 1).

a **b**

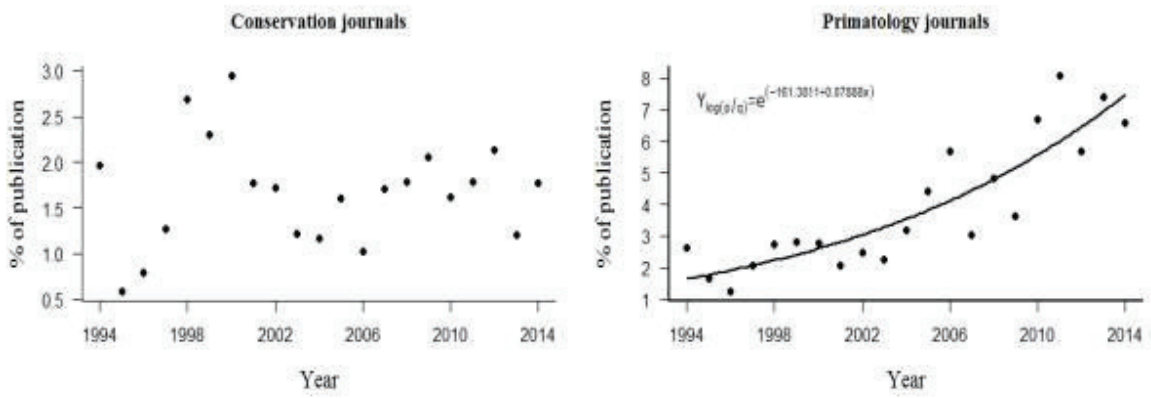

Figure 1. Temporal trends in the publication of primate conservation articles/reviews published in (a) conservation journals (Animal Conservation, Biodiversity and Conservation, Biological Conservation, Conservation Biology, Journal for Nature Conservation and Oryx) and (b) primatology journals (American Journal of Primatology, Folia Primatologica, International Journal of Primatology and Primates) between 1994 and 2014. The number of articles on primate conservation has increased in primatology journals (estimate = 0.08; $z = 6.98$; $p < 0.01$), but stayed stable in conservation journals (estimate = 0.001; $z = 0.13$, $p = 0.89$).

Habitat fragmentation was the most studied research subject (n=149) whereas roadkill was the least studied one (n=1) (Figure 2). Most of primate research is carried out in the field (n=391, 73.2%), followed by theoretical approaches (n=103, 19.3%) and reviews (n=40, 7.5%). We found no experimental research on primate conservation. The bulk of primate conservation research is carried out by authors affiliated to universities (n=728; 60%) (Figure 3). Researches are conducted mainly in protected areas (n=270, 39.53%) and unprotected natural areas (n=221, 32.35%) (Figure 4).

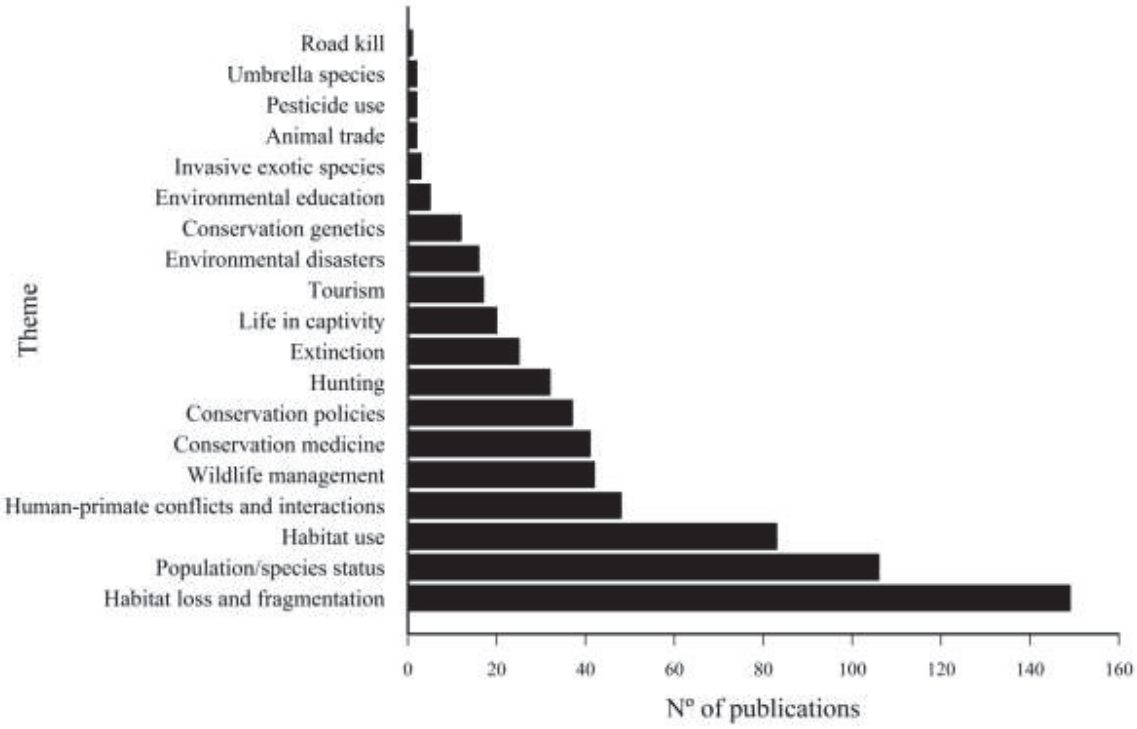

Figure 2. The total number of articles/reviews published between 1994 and 2014 in each conservation theme considered in this study (see Table S1 for details).

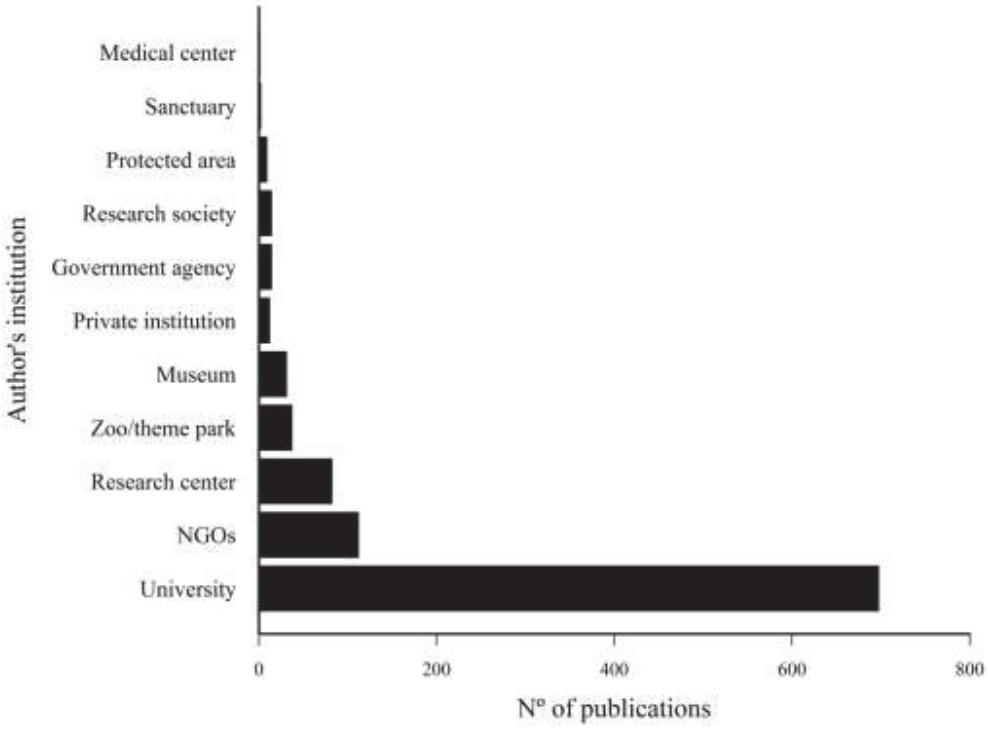

Figure 3. Types of institutional affiliation of authors (first and last) on primate conservation articles/reviews published between 1994 and 2014 (n=1,170).

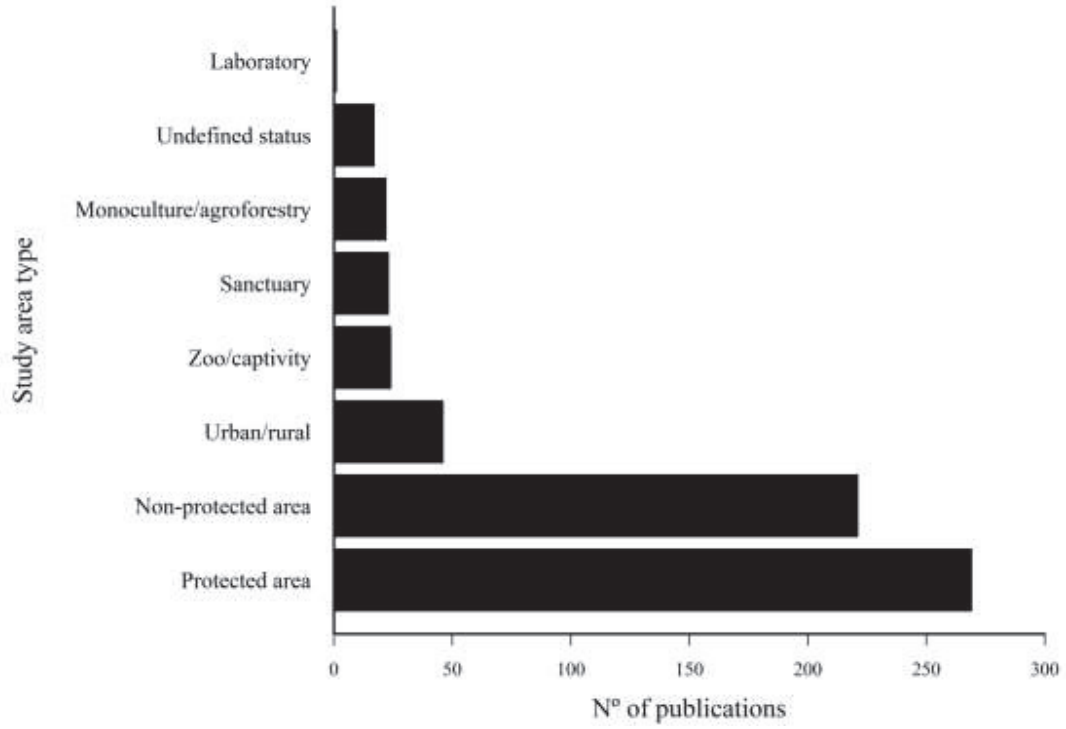

Figure 4. The total number of published articles (n=623) according to the nature of the locality of the study area (considering empiric and experimental studies).

Allocation of research effort in primate conservation

Researchers from 49 countries published empiric studies about primate conservation. Authors based in the United States and in the United Kingdom were the most prolific publishing on primate conservation (114 articles and 52 articles, respectively) (Figure 5a). Field research on primate conservation was carried out in 55 countries, with Madagascar (n=53) and Indonesia (n=46) leading the rank as countries of choice for work (Figure 5b). There is a phylogenetic signal in the published primate conservation literature, with close-related species sharing similar degrees of attention (number of articles published) ($\lambda = 0.54$, $p < 0.05$) (Figure 6).

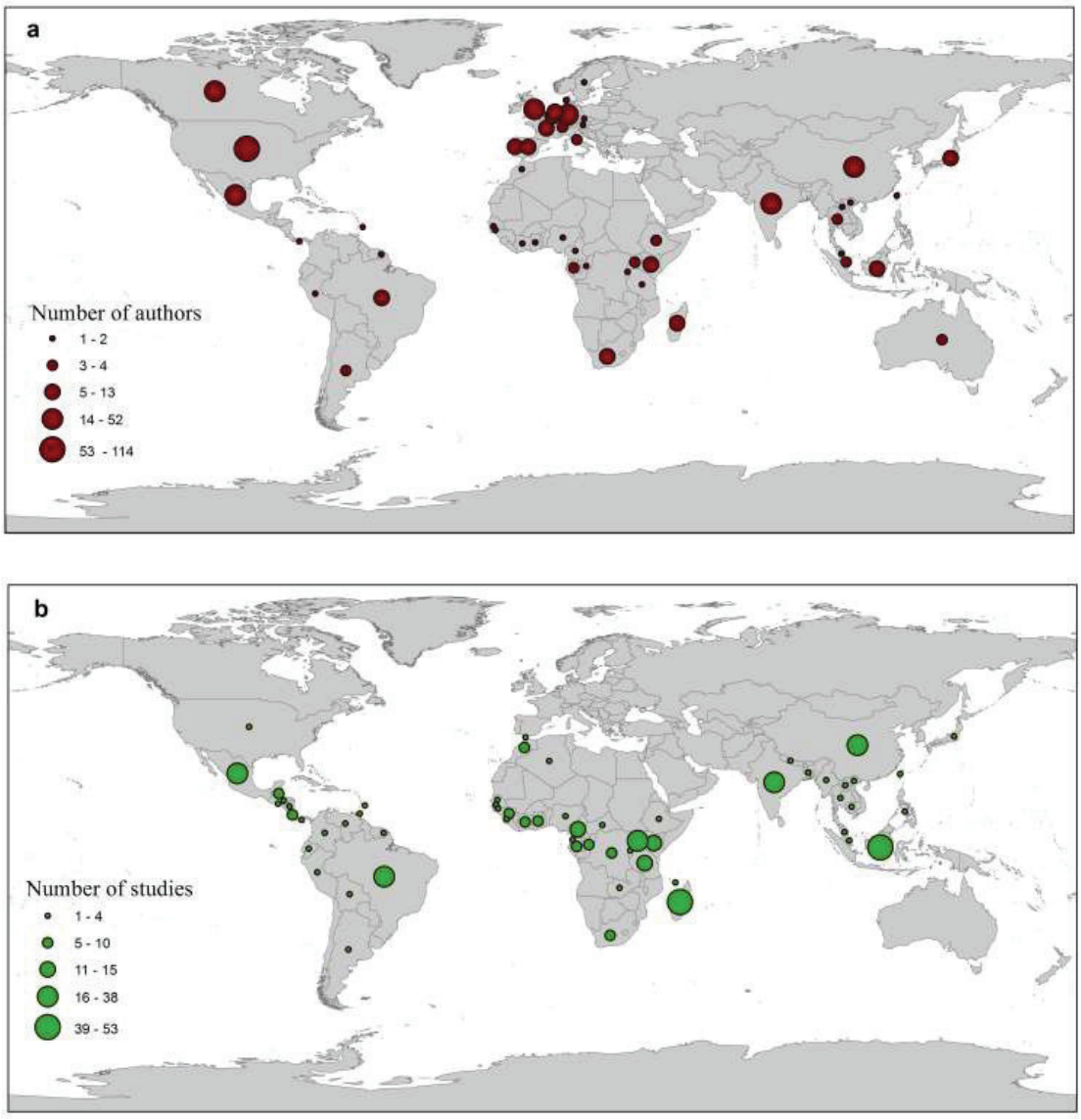

Figure 5. Global patterns of research effort on primate conservation. (a) Number of authors based on countries that produced scientific literature on primate conservation. (b) Number of empiric studies on primate conservations carried out within each country.

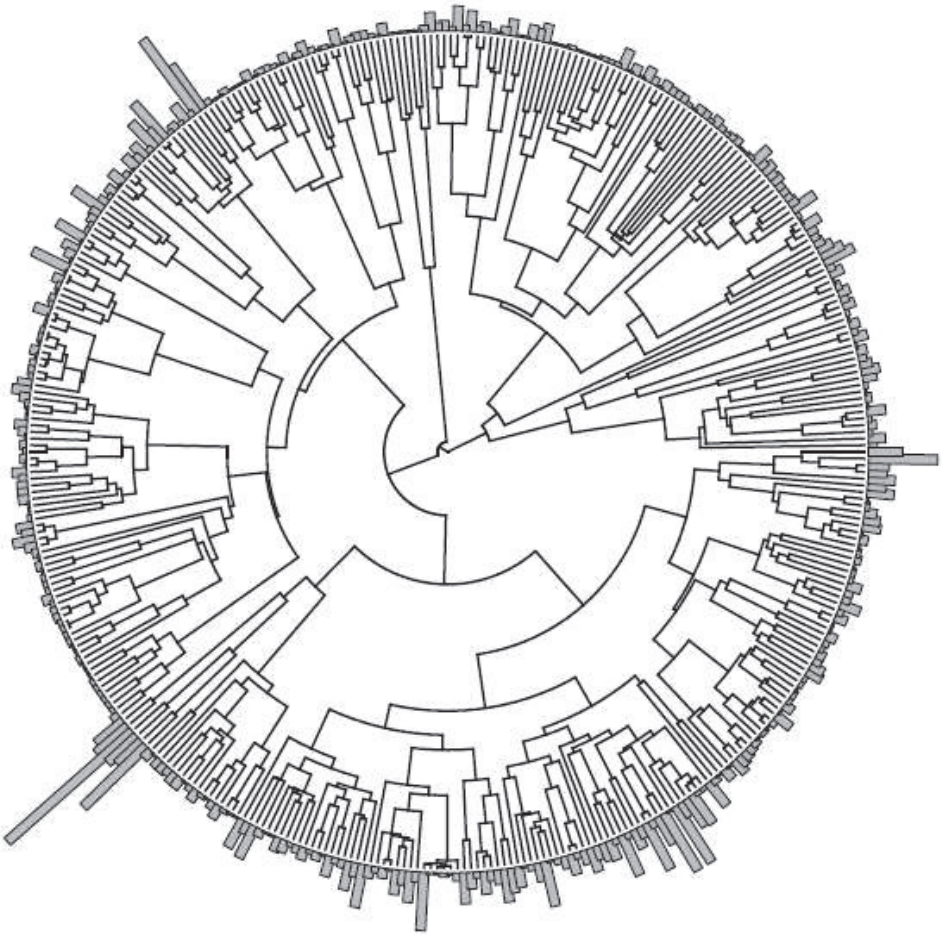

Figure 6. Phylogenetic bias in the pattern of published research on primate conservation shows that closely related species tend to receive similar attention from the scientific community (measured as the number of published articles/reviews).

A total of 388 primate species were the focus of the published scientific literature analyzed, from all 16 primate families. The species with the largest number of articles/reviews dedicated to it was *Pan troglodytes* (n=80; 14%) (Figure 7). The unexpected result was that 102 (27% of the currently valid species, presented in Mittermeier et al., 2013) (Table S2) were not the focus of a single study, a higher proportion than we expected for a charismatic mammal order. Of these, 66 are listed as

threatened [IUCN, 2016] (Figure 7). There were only three species with more than 40 studies, *Pan troglodytes* (n=80) (Critically Endangered), *Alouatta palliata* (n=44) (Least Concern) and *Gorilla gorilla* (n=40) (Critically Endangered).

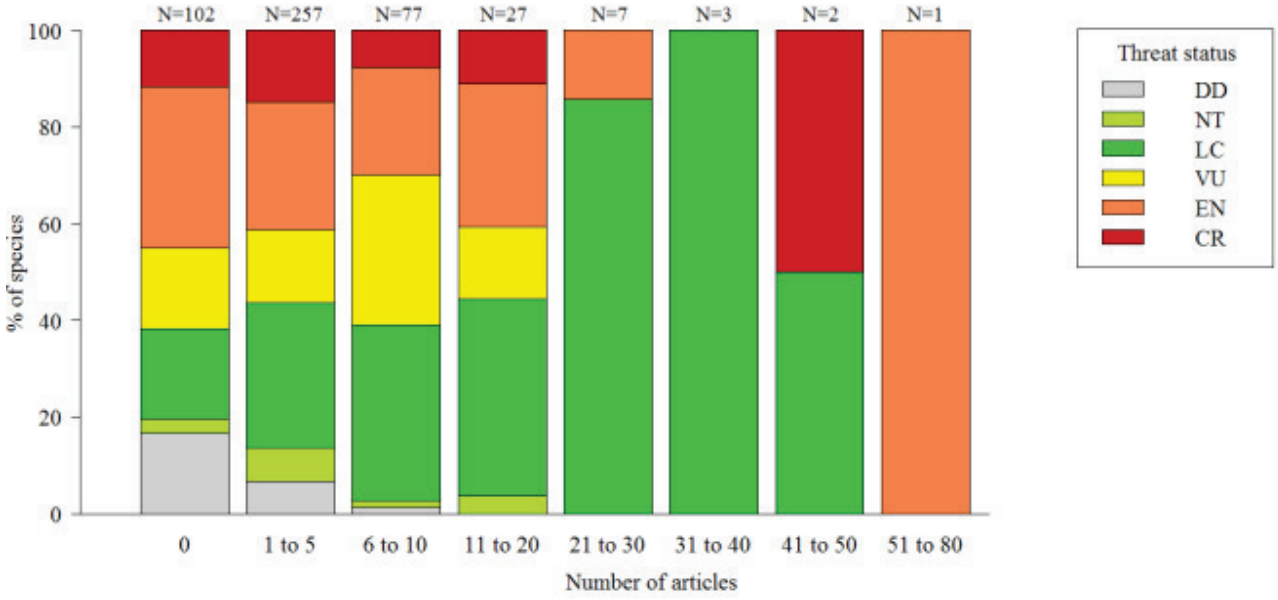

Figure 7. The number of articles/reviews published for each primate species, according to threat status [IUCN, 2016].

We also found that large-sized and "older" (time since description) species have more articles dedicated to them, whereas threat status and geographic range size had no influence whatsoever on the number of articles a species has (Table 1).

Table 1. Variables' predictive power to describe the allocation of research effort about primate conservation. The allocation effort was significantly related only with body size and species age.

Effect	Estimate	Z
Threat status	-0.066	-1.720
Species age	0.004	6.237*
Range size	0.014	0.553
Body size	0.226	7.014*

*$p < 0.05$

DISCUSSION

Trends in primate conservation research effort

Primates ranks third among the most studies mammal orders [Amori & Gippoliti, 2000]. The attention conservation biologists dedicate to primates stayed stable in the last two decades, whereas primatologists increased the conservation approach among them. The increase of conservation as a research focus among primatologists may be related both to the rapid increase in the number of primate species listed as threatened, and the increase in the threat status of primate species [IUCN, 2016].

Primate conservation research is fieldwork-centered. The positive side of this is that primary data for research is readily available. Theoretical primate conservation is on the rise, fueled by the availability of primary data on primate biology [e.g. Harcourt & Schreier, 2009]. However, there is a lack of experimental studies. Even though logistically more complicated, we expected some researches taking advantage of these unexplored paths of primate research. These researches, if they do exist, have not been published.

Habitat fragmentation was the most studied primate conservation theme. This is expected since habitat loss and fragmentation are the main threats to biodiversity [Foley et

al., 2014] in general and to primates in particular [IUCN, 2016]. Hunting is an important threat for primates, affecting 289 species (59% of primate species) [IUCN, 2016], and is poorly studied (32 articles). Animal trade is another serious threat to primate species [Schwitzer et al., 2015]. Despite being listed either in Appendix I (precluding all commercial trade) or Appendix II (regulating all commercial trade) in the Convention on International Trade in the Endangered Species of Wild Flora and Fauna (CITES), illegal trade is widespread [CITES, 2016]. The study of this threat poses difficulties due to the nature of the activity, and only 19 species were the target of such studies (out of 261 threatened by illegal trade). Despite being severely affected by illegal trade and by habitat loss and fragmentation, conservation policies towards primate conservation is also an understudied theme. There is a gap between scientific knowledge on threats and how species/populations are affected by them, and the implementation of on-the-ground conservation practices [e.g. Pullin et al., 2004; Sutherland, 2006]. Conservation practices should always be guided by scientific knowledge [Sutherland et al., 2004; Cardillo & Meijaard, 2012].

It is no surprise that most of the scientific knowledge published on primate conservation originates in universities. Despite being collection-based institutions in their origin, zoos and natural history museums have recently adopted a conservation agenda [Miller et al., 2004]. However, since this is a recent trend, and not the main goal of such institutions, these conservation departments are usually small and with a small budget, limiting their actions [Miller et al., 2004].

Allocation of research effort in primate conservation

Most conservation primatologists are based in low-primate diversity countries (e.g. United States and England), whereas most of the fieldwork on primate conservation is carried on within high-primate diversity countries (e.g. Madagascar and Indonesia). Interestingly, the countries with higher concentration of conservation primatologists (United States, United Kingdom, Canada, Germany and France), do not have native non-human primates within their borders. The cause of concern is the relatively low numbers of conservation primatologists in high-primate diversity countries (e.g. Colombia). Global primate distribution covers 88 countries, and research on primate conservation was conducted on 55 countries. However, the number of studies per country was skewed towards countries with both high-primate diversity and higher proportion of primates listed as threatened (e.g. Madagascar, Indonesia and Brazil). Studies from countries with high proportion of threatened species have higher impact [Meijaard et al., 2015], and this may also contribute to a knowledge bias.

We found a preference among conservation primatologists towards large-bodied and "older" (time since description) species. There is evidence for a correlation between large body size and charisma in animals, and charisma draws more attention from people (scientists included according to our results) than threat status [Colléony et al., 2017]. Conservation primatologists also seem to prefer already known, stable species, than newly described species. Like the new kid at school, they have a hard time to fit in the existing scenario. Conservation primatologists are consciously or unconsciously biased in their research decisions. The choice of a species to be the focus of a study is driven more by charisma and safety (choosing an "old" species) than by real conservation priorities and needs. In order to be more effective in safeguarding global primate diversity this behavior must change.

REFERENCES

Amori G, Gippoliti S. 2000. What do mammalogists want to save? Ten years of mammalian conservation biology. Biodiversity and Conservation 9:785–793.

Baillie JEM, Griffiths J, Turvey ST, Loh J, Collen B. 2011. Evolution lost: status and trends of the world's vertebrates. London: Zoological Society of London.

Barnosky AD, Matzke N, Tomiya S, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature [Internet] 471:51–57. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21368823

Bonnet X, Shine R, Lourdais O. 2002. Axonomic Chauvinism. Trends in Ecology & Evolution 17:2000–2002.

Brito D. 2008. Amphibian conservation: Are we on the right track? Biological Conservation [Internet] 141:2912–2917. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0006320708003108

Brodie JF. 2009. Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodiversity and Conservation [Internet] 18:2927–2939. Available from: http://link.springer.com/10.1007/s10531-009-9617-3

Cardillo M, Meijaard E. 2012. Are comparative studies of extinction risk useful for conservation? Trends in Ecology and Evolution [Internet] 27:167–171. Available from: http://dx.doi.org/10.1016/j.tree.2011.09.013

Ceballos G, Ehrlich PR, Barnosky AD, et al. 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. Sciences Advances 1:1–5.

CITES. 2016. Convention on international trade in endangered species of wild fauna and flora.

Clark JA, May RM. 2002. Taxonomic Bias in Conservation Research. Science 297:191–192.

Colléony A, Clayton S, Couvet D, Saint Jalme M, Prévot AC. 2017. Human preferences for species conservation: Animal charisma trumps endangered status. Biological Conservation [Internet] 206:263–269. Available from: http://dx.doi.org/10.1016/j.biocon.2016.11.035

Estrada A, Garber PA, Rylands AB, et al. 2017. Impending extinction crisis of the world's

primates: Why primates matter. Science Advances 3.

Foley JA, Foley JA, Defries R, et al. 2014. Global Consequences of Land Use. 570.

Harcourt AH, Schreier BM. 2009. Diversity, body mass, and latitudinal gradients in primates. International Journal of Primatology 30:283–300.

Harris G, Pimm SL. 2008. Range size and extinction risk in forest birds. Conservation Biology 22:163–171.

IUCN. 2016. Available from: http://www.iucnredlist.org/

Johnson PJ, Kansky R, Loveridge AJ, Macdonald DW. 2010. Size, Rarity and Charisma: Valuing African Wildlife Trophies. PLoS ONE [Internet] 5:e12866. Available from: http://dx.plos.org/10.1371/journal.pone.0012866

Lawler JJ, Aukema JE, Grant JB, et al. 2006. Conservation science : a 20-year report card In a nutshell : Front Ecol Environ 4:473–480.

Marshall AJ, Wich SA. 2016. Why conserve primates? In: Wich SA, Marshall AJ, editors. An introduction to primate conservation. Oxford: Oxford University Press.

McCallum ML. 2015. Vertebrate biodiversity losses point to a sixth mass extinction. Biodiversity & Conservation 24:2497–2519.

Meijaard E, Cardillo M, Meijaard EM, Possingham HP. 2015. Geographic bias in citation rates of conservation research. Conservation Biology 29:920–925.

Meijaard E, Sheil D. 2007. Is wildlife research useful for wildlife conservation in the tropics? A review for Borneo with global implications. Biodiversity and Conservation [Internet] 16:3053–3065. Available from: http://link.springer.com/10.1007/s10531-007-9161-y

Miller B, Conway W, Reading RP, et al. 2004. Evaluating the Conservation Mission of Zoos, Aquariums, Botanical Gardens, and Natural History Museums. Conservation Biology 18:86–93.

Mittermeier R, Rylands A, DE W, editors. 2013. Handbook of the Mammals of the World - Volume 3. Barcelona: Lynx Edicions. 950 p.

Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The Future of Biodiversity. Science [Internet] 269:347–350. Available from: http://www.ncbi.nlm.nih.gov/pubmed/17841251

Pullin AS, Knight TM, Stone DA, Charman K. 2004. Do conservation managers use

scientific evidence to support their decision-making ? Biological Conservation 119:245–252.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings. Biological Sciences / The Royal Society 267:1947–1952.

R Development Core Team. 2016. R: A language and environment for statistical computing.

Schipper J, Chanson JS, Chiozza F, et al. 2008. The status of the world's land and marine mammals: diversity, threat and knowledge. Science 322:225–230.

Schwitzer C, Mittermeier RA, Rylands AB, et al. 2015. Primates in Peril: The World's 25 Most Endangered Primates 2012–2014.61-64 p.

Sitas N, Baillie JEM, Isaac NJB. 2009. What are we saving? Developing a standardized approach for conservation action. Animal Conservation 12:231–237.

Springer MS, Meredith RW, Gatesy J, et al. 2012. Macroevolutionary Dynamics and Historical Biogeography of Primate Diversification Inferred from a Species Supermatrix. PLoS ONE 7.

Sutherland WJ. 2006. Predicting the ecological consequences of environmental change : a review of the methods *. Journal of Applied Ecology 43:599–616.

Sutherland WJ, Armstrong-brown S, Paul R, et al. 2006. The identification of 100 ecological questions of high policy relevance in the UK. Journal of Animal Ecology 43:617–627.

Sutherland WJ, Pullin AS, Dolman PM, Knight TM. 2004. The need for evidence-based conservation. Trends in Ecology & Evolution [Internet] 19:305–308. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0169534704000734

Trimble MJ, van Aarde RJ. 2012. Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. Ecosphere [Internet] 3:1–16. Available from: http://www.esajournals.org/doi/pdf/10.1890/ES12-00299.1

Trimble MJ, Van Aarde RJ. 2010. Species inequality in scientific study. Conservation biology [Internet] 24:886–90. Available from: http://www.ncbi.nlm.nih.gov/pubmed/20184651

Verde Arregoitia LD, Leach K, Reid N, Fisher DO. 2015. Diversity, extinction, and threat

status in Lagomorphs. Ecography [Internet]:n/a-n/a. Available from: http://doi.wiley.com/10.1111/ecog.01063

Ward PI, Mosberger N, Kistler C, et al. 1998. The Relationship Between Popularity and Body Size in Zoo Animals. Conservation Biology 12:1408–1411.

SUPPORTING INFORMATION

Table S1. Definition of the terms used.

Term	Definition
Approach	
Empiric	Use of observed date.
Experimental	Use of manipulate date.
Theoretical	Use of secondary or simulate date.
Review	A review about a theme.
Themes	
Habitat loss and fragmentation	Investigates the effects of habitat lost, modification or fragmentation in a population
Hunting	Investigates the effects of hunting in a population
Road kill	Evaluation of the effect of the road kill in a population
Wildlife management	Investigates management strategies for species populations
Conservation medicine	Investigates wildlife wealth in response of anthropogenic influence
Habitat use	Evaluation of the use of modified, degraded or in regeneration habitat
Conservation genetics	Evaluation of the genetic viability through the genetic diversity of a population or metapopulation
Environment disasters	Investigates the effect of natural or almost natural disaster (hurricane, climate change, el nino) in a population
Population/species status	Investigates the population status of a specie or species, exploring the threats causes
Extinction	Analyzes the extinction risk or the population viability of a specie or population
Human-primate conflicts and interactions	Investigates conflicting interactions between primates and humans (such as crop-raiding) or explore the perception of humans population about primates or analyzes de influence of human population proximity on primate behavior
Environmental education	Studies about environmental education in projects of primates conservation
Conservation policies	Studies that involves policies (governmental or civil) practices for conservation or analyzes gaps of knowledge

Term	Definition
Tourism	Impact of tourism in a population or metapopulation
Animal trade	Investigates primate trade or the use of primates as pet
Invasive exotic species	Evaluation of the impact of introduction of exotic animals on primate population or the survival of introduced primates
Life in captivity	Investigates the alteration in survival or behavior of primates in captivity
Pesticides use	The impact of pesticides in a primate population or metapopulation
Umbrella species	The use primates as umbrella to conserve the it and other species

Table S2. Number of articles and threat status for each species presented in Mittermeier et al. [2013].

Espécies	Número de artigos	Threat status (IUCN, 2016)
Aotus jorgehernandezi	0	DD
Aotus zonalis	0	DD
Avahi betsileo	0	EN
Avahi mooreorum	0	EN
Avahi ramanantsoavanai	0	VU
Callibella humilis	0	VU
Callicebus aureipalatii	0	LC
Callicebus baptista	0	LC
Callicebus bernhardi	0	LC
Callicebus caquetensis	0	CR
Callicebus discolor	0	LC
Callicebus lucifer	0	LC
Callicebus lugens	0	LC
Callicebus medemi	0	VU
Callicebus ornatus	0	VU
Callicebus pallescens	0	LC
Callicebus purinus	0	LC
Callicebus regulus	0	LC
Callicebus stephennashi	0	DD
*Callicebus vieirai**	0	-
Carlito syrichta	0	NT
Cebus cesarae	0	DD
*Cebus yuracus**	0	-
Cephalopachus bancanus	0	VU
Cercocebus lunulatus	0	EN
*Cercopithecus lomamiensis**	0	-

Espécies	Número de artigos	Threat status (IUCN, 2016)
*Chiropotes sagulatus**	0	-
Chlorocebus djandjamensis	0	VU
Eulemur flavifrons	0	CR
Hylobates abbotti	0	EN
Hylobates funereus	0	EN
Hylobates klossii	0	EN
Leontopithecus chrysopygus	0	EN
Leontopithecus crysomelas	0	EN
Lepilemur ahmansonorum	0	EN
Lepilemur betsileo	0	EN
Lepilemur edwardsi	0	EN
Lepilemur fleuretae	0	CR
Lepilemur grewcockorum	0	EN
Lepilemur hollandorum	0	EN
Lepilemur hubbardi	0	EN
Lepilemur jamesorum	0	CR
Lepilemur milanoii	0	EN
Lepilemur mittermeieri	0	EN
Lepilemur otto	0	EN
Lepilemur petteri	0	VU
Lepilemur scottorum	0	EN
Lepilemur seali	0	VU
Lepilemur tymerlachsoni	0	CR
Lepilemur wrightae	0	EN
Macaca pagensis	0	CR
Macaca siberu	0	VU
Mandrillus leucophaeus	0	EN
Mandrillus sphinx	0	VU
Mico acariensis	0	DD
Mico manicorensis	0	LC
Mico rondoni	0	VU
Microcebus arnholdi	0	EN
Microcebus gerpi	0	CR
Microcebus macarthurii	0	EN
*Microcebus margotmarshae**	0	-
Microcebus mamiratra	0	CR
Perodicticus edwardsi	0	LC
Perodicticus ibeanus	0	LC
Piliocolobus bouvieri	0	CR
Piliocolobus epieni	0	CR
*Piliocolobus langi**	0	-
Piliocolobus oustaleti	0	LC

Espécies	Número de artigos	Threat status (IUCN, 2016)
*Piliocolobus parmentieri**	0	-
*Piliocolobus semlikiensis**	0	-
Piliocolobus temminckii	0	EN
Piliocolobus tholloni	0	NT
Piliocolobus waldronae	0	CR
Pongo abelli	0	CR
Presbytis bicolor	0	DD
Presbytis canicrus	0	EN
Presbytis mitrata	0	EN
Presbytis natunae	0	VU
Presbytis sabana	0	EN
Presbytis siberu	0	EN
Presbytis sumatrana	0	EN
Saimiri cassiquiarensis	0	LC
Saimiri macrodon	0	LC
Sciurocheirus cameronensis	0	LC
Sciurocheirus gabonensis	0	LC
Semnopithecus ajax	0	EN
Semnopithecus hector	0	NT
Semnopithecus hypoleucos	0	VU
Semnopithecus schistaceus	0	LC
Tarsius fuscus	0	VU
Tarsius lariang	0	DD
Tarsius pelengensis	0	EN
Tarsius tarsier	0	VU
Tarsius wallacei	0	DD
Thachypithecus laotum	0	VU
Theropithecus gelada	0	LC
Trachypithecus crepusculus	0	EN
Trachypithecus ebenus	0	EN
Trachypithecus margarita	0	EN
Trachypithecus mauritius	0	VU
*Trachypithecus selangorensis**	0	-
Trachypithecus shortridgei	0	EN
Ateles hybridus	0	CR
Ateles marginatus	0	EN
Ateles paniscus	0	VU
Aotus brumbacki	1	VU
Aotus vociferans	1	LC
Arctocebus aureus	1	LC
Avahi cleesei	1	EN
Avahi meridionalis	1	EN

Espécies	Número de artigos	Threat status (IUCN, 2016)
Avahi peyrierasi	1	VU
*Cacajao ouakary**	1	-
Callicebus brunneus	1	LC
Callicebus caligatus	1	LC
Callicebus cinerascens	1	LC
Callicebus coimbrai	1	EN
Callicebus dubius	1	LC
Callicebus hoffmannsi	1	LC
Callicebus modestus	1	EN
Callicebus olallae	1	EN
Cebus imitator	1	LC
*Cebus leucocephalus**	1	-
Cebus malitiosus	1	EN
*Cebus unicolor**	1	-
Cercopithecus kandti	1	EN
Cheirogaleus crossleyi	1	DD
Cheirogaleus minusculus	1	DD
Cheirogaleus sibreei	1	CR
Chiropotes albinasus	1	EN
Chlorocebus cynosuros	1	LC
Chlorocebus tantalus	1	LC
Euoticus pallidus	1	LC
Galagoides cocos	1	LC
Galagoides granti	1	LC
Hapalemur meridionalis	1	VU
Hoolock leuconedys	1	VU
Hylobates albibarbis	1	EN
Lagothrix cana	1	EN
Lagothrix poeppigii	1	VU
Lepilemur aeeclis	1	VU
Lepilemur ankaranensis	1	EN
Lepilemur randrianasoloi	1	EN
Lophocebus johnstoni	1	LC
Lophocebus opdenboschi	1	DD
Lophocebus osmani	1	LC
Macaca hecki	1	VU
Macaca nigrescens	1	VU
Macaca sinica	1	EN
Mico humeralifer	1	DD
Mico intermedius	1	LC
Mico marcai	1	DD
Mico mauesi	1	LC

Espécies	Número de artigos	Threat status (IUCN, 2016)
Mico saterei	1	LC
Microcebus bongolavensis	1	EN
Microcebus danfossi	1	EN
Microcebus jollyae	1	EN
Microcebus lehilahytsara	1	VU
Microcebus mittermeieri	1	EN
Microcebus simmonsi	1	EN
Miopithecus ogouensis	1	LC
Mirza zaza	1	EN
*Nomascus annamensis**	1	-
Nomascus hainanus	1	CR
Nomascus siki	1	EN
Nycticebus menagensis	1	VU
Papio kindae	1	LC
*Piliocolobus foai**	1	-
Piliocolobus preussi	1	CR
Pithecia aequatorialis	1	LC
Pithecia albicans	1	VU
Presbytis siamensis	1	NT
Pygathrix cinerea	1	CR
Pygathrix nigripes	1	EN
Saguinus fuscus	1	LC
Saguinus illigeri	1	LC
Saguinus lagonotus	1	LC
Saguinus leucogenys	1	LC
Saguinus nigrifrons	1	LC
Saguinus weddelli	1	LC
Saimiri vanzolinii	1	VU
Sapajus flavius	1	CR
Sapajus libidinosus	1	LC
Sapajus xanthosternos	1	CR
Semnopithecus priam	1	NT
Tarsius pumilus	1	DD
Tarsius sangirensis	1	EN
Tarsius tumpara	1	CR
Trachypithecus barbei	1	DD
Trachypithecus delacouri	1	CR
Trachypithecus poliocephalus	1	CR
Alouatta discolor	2	VU
Alouatta nigerrima	2	LC
Aotus griseimembra	2	VU
Aotus lemurinus	2	VU

Espécies	Número de artigos	Threat status (IUCN, 2016)
Aotus miconax	2	VU
Aotus nancymaae	2	LC
Aotus nigriceps	2	LC
Aotus trivirgatus	2	LC
Ateles chamek	2	EN
Avahi unicolor	2	EN
Cacajao melanocephalus	2	VU
Callicebus oenanthe	2	CR
Callithrix aurita	2	VU
Callithrix flaviceps	2	EN
Callithrix kuhlii	2	NT
Callithrix penicillata	2	LC
Cebus aequatorialis	2	CR
Cebus cuscinus	2	NT
Cebus kaapori	2	CR
Cercopithecus denti	2	LC
Cercopithecus doggetti	2	LC
Eulemur rufifrons	2	NT
Galago gallarum	2	LC
Galago matschiei	2	LC
Galagoides orinus	2	NT
Lepilemur sahamalazensis	2	CR
*Lophocebus ugandae**	2	-
Macaca maura	2	EN
Macaca thibetana	2	NT
Mico chrysoleucos	2	DD
Mico emiliae	2	DD
Mico leucippe	2	VU
Mico melanurus	2	LC
Mico nigriceps	2	DD
Microcebus berthae	2	EN
Microcebus myoxinus	2	VU
Microcebus sambiranensis	2	EN
Microcebus tavaratra	2	VU
Nomascus leucogenys	2	CR
Nomascus nasutus	2	CR
Nycticebus javanicus	2	CR
Phaner electromontis	2	EN
Phaner pallescens	2	EN
Phaner parienti	2	EN
Piliocolobus pennantii	2	EN
Pithecia monachus	2	LC

Espécies	Número de artigos	Threat status (IUCN, 2016)
Presbytis chrysomelas	2	CR
Presbytis femoralis	2	NT
Presbytis frontata	2	VU
Propithecus coronatus	2	EN
Rhinopithecus strykeri	2	CR
Saguinus inustus	2	LC
Saguinus martinsi	2	LC
Saguinus tripartitus	2	NT
Saimiri ustus	2	NT
Sapajus cay	2	LC
Sapajus robustus	2	EN
Trachypithecus cristatus	2	NT
Trachypithecus germaini	2	EN
Trachypithecus hatinhensis	2	EN
Trachypithecus obscurus	2	NT
Trachypithecus phayrei	2	EN
Allenopithecus nigroviridis	3	LC
Alouatta arctoidea	3	LC
Alouatta ululata	3	EN
Arctocebus calabarensis	3	LC
Callicebus barbarabrownae	3	CR
Callicebus cupreus	3	LC
Callicebus donacophilus	3	LC
Callicebus melanochir	3	VU
Callicebus nigrifrons	3	NT
Callimico goeldii	3	VU
Callithrix jacchus	3	LC
Cebuella pygmaea	3	LC
Cebus brunneus	3	LC
Cebus versicolor	3	EN
Cercocebus chrysogaster	3	DD
Cercopithecus lowei	3	LC
Cercopithecus roloway	3	EN
Cercopithecus wolfi	3	LC
Chiropotes utahickae	3	EN
Chlorocebus sabaeus	3	LC
Galagoides rondoensis	3	CR
Hylobates muelleri	3	EN
Lepilemur leucopus	3	EN
Lepilemur microdon	3	EN
Loris tardigradus	3	EN
Macaca munzala	3	EN

Espécies	Número de artigos	Threat status (IUCN, 2016)
Mico argentatus	3	LC
Oreonax flavicauda	3	CR
Papio papio	3	NT
Pithecia irrorata	3	LC
Presbytis potenziani	3	EN
Presbytis thomasi	3	VU
Propithecus candidus	3	CR
Propithecus deckenii	3	EN
Saguinus bicolor	3	EN
Saguinus niger	3	VU
Sapajus macrocephalus	3	LC
Semnopithecus vetulus	3	EN
Simias concolor	3	CR
Tarsius dentatus	3	VU
Trachypithecus leucocephalus	3	CR
Allocebus trichotis	4	VU
Alouatta sara	4	LC
Aotus azarae	4	LC
Avahi occidentalis	4	EN
Cebus olivaceus	4	LC
Cercopithecus dryas	4	CR
Chiropotes chiropotes	4	LC
Chiropotes satanas	4	CR
Eulemur cinereiceps	4	CR
Eulemur collaris	4	EN
Eulemur sanfordi	4	EN
Galago moholi	4	LC
Galagoides thomasi	4	LC
Hapalemur occidentalis	4	VU
Lepilemur dorsalis	4	VU
Lepilemur mustelinus	4	NT
Lepilemur ruficaudatus	4	VU
Lepilemur septentrionalis	4	CR
Lophocebus aterrimus	4	NT
Macaca assamensis	4	NT
Macaca cyclopis	4	LC
Macaca leonina	4	VU
Macaca ochreata	4	VU
Microcebus griseorufus	4	LC
Nomascus gabriellae	4	EN
Nycticebus coucang	4	VU
Piliocolobus tephrosceles	4	EN

Espécies	Número de artigos	Threat status (IUCN, 2016)
Presbytis comata	4	EN
Presbytis melalophos	4	EN
Propithecus coquereli	4	EN
Rhinopithecus avunculus	4	CR
Rhinopithecus brelichi	4	EN
Saguinus geoffroyi	4	LC
Saguinus imperator	4	LC
Sciurocheirus alleni	4	LC
Trachypithecus pileatus	4	VU
Varecia rubra	4	CR
Ateles belzebuth	5	EN
Ateles fusciceps	5	CR
Brachyteles hypoxanthus	5	CR
Callicebus moloch	5	LC
Callicebus personatus	5	VU
Callithrix geoffroyi	5	LC
Cercocebus agilis	5	LC
Eulemur albifrons	5	EN
Eulemur coronatus	5	EN
Eulemur mongoz	5	CR
Euoticus elegantulus	5	LC
Hapalemur alaotrensis	5	CR
Hapalemur aureus	5	CR
Hoolock hoolock	5	EN
Hylobates pileatus	5	EN
Microcebus ravelobensis	5	EN
Mirza coquereli	5	EN
Nasalis larvatus	5	EN
Nycticebus pygmaeus	5	VU
Papio hamadryas	5	LC
Phaner furcifer	5	VU
Propithecus perrieri	5	CR
Propithecus tattersalli	5	CR
Rungwecebus kipunji	5	CR
Saguinus labiatus	5	LC
Saguinus leucopus	5	EN
Saguinus mystax	5	LC
Saguinus nigricollis	5	LC
Saimiri boliviensis	5	LC
Sapajus nigritus	5	NT
Symphalangus syndactylus	5	EN
Trachypithecus auratus	5	VU

Espécies	Número de artigos	Threat status (IUCN, 2016)
Trachypithecus geei	5	EN
Allochrocebus solatus	6	VU
Cacajao calvus	6	VU
Cercopithecus sclateri	6	VU
Cheirogaleus medius	6	LC
Eulemur rufus	6	VU
Hylobates agilis	6	EN
Hylobates lar	6	EN
Hylobates moloch	6	EN
Leontopithecus caissara	6	CR
Macaca arctoides	6	VU
Macaca nemestrina	6	VU
Macaca nigra	6	CR
Miopithecus talapoin	6	LC
Nycticebus bengalensis	6	VU
Otolemur garnettii	6	LC
Perodicticus potto	6	LC
Piliocolobus gordonorum	6	EN
Pygathrix nemaeus	6	EN
Saguinus oedipus	6	CR
Semnopithecus johnii	6	VU
Allochrocebus lhoesti	7	VU
Callicebus torquatus	7	LC
Cebus albifrons	7	LC
Cercocebus sanjei	7	EN
Cercopithecus hamlyni	7	VU
Daubentonia madagascariensis	7	EN
Eulemur macaco	7	VU
Galagoides zanzibaricus	7	LC
Indri indri	7	CR
Loris lydekkerianus	7	LC
Macaca fuscata	7	LC
Macaca tonkeana	7	VU
Microcebus murinus	7	LC
Nomascus concolor	7	CR
Papio ursinus	7	LC
Presbytis hosei	7	VU
Rhinopithecus roxellana	7	EN
Saguinus midas	7	LC
Avahi laniger	8	VU
Brachyteles arachnoides	8	EN
Cebus capucinus	8	LC

Espécies	Número de artigos	Threat status (IUCN, 2016)
Cercopithecus erythrogaster	8	VU
Galagoides demidovii	8	LC
Lagothrix lagotricha	8	VU
Leontopithecus rosalia	8	EN
Piliocolobus kirkii	8	EN
Pithecia pithecia	8	LC
Prolemur simus	8	CR
Rhinopithecus bieti	8	EN
Saimiri oerstedii	8	VU
Semnopithecus entellus	8	LC
Alouatta belzebul	9	VU
Alouatta macconnelli	9	LC
Cercopithecus neglectus	9	LC
Cheirogaleus major	9	DD
Chlorocebus pygerythrus	9	LC
Colobus polykomos	9	VU
Galago senegalensis	9	LC
Hapalemur griseus	9	VU
Otolemur crassicaudatus	9	LC
Piliocolobus rufomitratus	9	LC
Procolobus verus	9	NT
Propithecus verreauxi	9	EN
Saguinus fuscicollis	9	LC
Trachypithecus francoisi	9	EN
Allochrocebus preussi	10	EN
Alouatta caraya	10	LC
Cercopithecus campbelli	10	LC
Cercopithecus diana	10	VU
Cercopithecus mona	10	LC
Colobus vellerosus	10	VU
Eulemur rubriventer	10	VU
Macaca radiata	10	LC
Microcebus rufus	10	VU
Presbytis rubicunda	10	LC
Propithecus edwardsi	10	EN
Cercocebus galeritus	11	EN
Cercocebus torquatus	12	VU
Erythrocebus patas	12	LC
Eulemur fulvus	12	NT
Lemur catta	12	EN
Papio cynocephalus	12	LC
Propithecus diadema	12	CR

Espécies	Número de artigos	Threat status (IUCN, 2016)
Colobus satanas	13	VU
Piliocolobus badius	13	EN
Cercopithecus petaurista	14	LC
Macaca mulatta	14	LC
Cercopithecus albogularis	15	LC
Macaca sylvanus	15	EN
Papio anubis	15	LC
Saimiri sciureus	15	LC
Cercocebus atys	16	VU
Cercopithecus erythrotis	16	VU
Colobus angolensis	16	LC
Gorilla beringei	16	CR
Varecia variegata	16	CR
Alouatta guariba	17	LC
Ateles geoffroyi	17	EN
Cercopithecus cephus	17	LC
Macaca silenus	17	EN
Pan paniscus	19	EN
Sapajus apella	19	LC
Pongo pygmaeus	20	CR
Cercopithecus pogonias	21	LC
Macaca fascicularis	21	LC
Chlorocebus aethiops	22	LC
Alouatta seniculus	23	LC
Cercopithecus nictitans	25	LC
Alouatta pigra	26	EN
Lophocebus albigena	28	LC
Cercopithecus ascanius	32	LC
Cercopithecus mitis	32	LC
Colobus guereza	33	LC
Gorilla gorilla	42	CR
Alouatta palliata	44	LC
Pan troglodytes	80	EN

* This species has not been assessed on The IUCN Red List

Supporting text. Keywords used in the searches

For Conservation Biology journals, we downloaded papers with one or more of these follows words in the title, abstract or keywords:

primate* or “ape” or “apes” or monkey* or simian* or baboon* or gorilla* or gibbon* or howler* or Douroucouli* or Angwantibo* or Marmoset* or Samango* or aye-aye* or tamarin* or mangabey* or macaque* or Mandrill* or Chipanzee* or bonobo* or orangutan* or Colobus or Siamang* or Tarsier* or Allenopithecus or Allocebus or Alouatta or Aotus or Arctocebus or Ateles or Avahi or Brachyteles or Cacajao or Callibella or Callicebus or Callimico or Callithrix or Cebuella or Cebus or Cercocebus or Cercopithecus or Cheirogaleus or Chiropotes or Chlorocebus or Colobus or Daubentonia or Erythrocebus or Eulemur or Euoticus or Galago or Galagoides or Gorilla or Hapalemur or Hoolock or Hylobates or Indri or Lagothrix or Lemur or Leontopithecus or Lepilemur or Lophocebus or Loris or Macaca or Mandrillus or Mico or Microcebus or Miopithecus or Mirza or Nasalis or Nomascus or Nycticebus or Oreonax or Otolemur or Palaeopropithecus or Pan or Papio or Perodicticus or Phaner or Pithecia or Pongo or Presbytis or Procolobus or Prolemur or Propithecus or Pygathrix or Rhinopithecus or Rungwecebus or Saguinus or Saimiri or Sciurocheirus or Semnopithecus or Simias or Symphalangus or Tarsius or Theropithecus or Trachypithecus or Varecia or Xenothrix or Sapajus or Marmosets or Pitheciines or atelines or cebines or platyrrhine or catarrhines or Bunopithecus or Pseudopotto or Haplorrhini or Simiiformes or Catarrhini or Hominoidea or Hominidae or Homininae or Hominini or Strepsirrhini or Langur* or Colobine* or Langur*

For Primatology journals, we choose only articles about conservation, searching in the title, title, abstract or keywords one or more these follows words:

conservation* or conserving* or impact* or anthropogenic* or anthropic* or perturbation* or disturb* or education* or degradation* or hunting* or deforestation* or translocation* or conflict* or fragmentation* or “human–primate*” or conflict* or management* or corridors* or protected* or unprotected* or logging* or Agroecosystem*

or human-modified* or “human-modification*” or Synergistic* or reintroduction* or extinction* or “climate change*” or “habitat loss*” or viability* or “re-introduction*” or bushmeat* or road* or invasive* or invasion* or enrichment* or captive* or captivity* or environment* or disease* or landscape*

Capítulo 2

Diet disparity predicts extinction risk in primates

Flávia de Figueiredo Machado[1,2]

Lucas Lacerda Caldas Zanini Jardins[2]

Marcel Cardillo[3]

Rusell Dinnage[3]

Daniel de Brito Candido da Silva[1]

Authors' affiliations:

[1]Laboratório de Ecologia Aplicada e Conservação, Departamento de Ecologia, Universidade Federal de Goiás, Brazil.

[2]Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás, Brazil.

[3]Macroevolution & Macroecology Group, Research School of Biology, Australian National University, Australia.

ABSTRACT

Human pressure on natural ecosystem has contributed to elevate species extinction. Species vary their vulnerability to extinction according to their biology, ecology, environmental factors and threats to which they are exposed. Diet is a trait that may contribute to extinction vulnerability. The influence of diet on species extinction risk has been studied in a broad way, but detailed studies on how different aspects of diet can influence species vulnerability are still lacking. Here we examined the association between diet and extinction risk in primates, using different metrics for diet and accounting for phylogeny and covariates that may be confounded with diet, in a global scale. We used the highest resolution data available on primate diet, representing all major primate habitats. Our results showed that only diet disparity predicts primate's extinction risk. Thus, primates able to consume diet items that are more different from each other are less prone to extinction. Body mass and range size also predicted extinction risk: large species, with restricted geographic distribution, being more threatened. Body mass is a proxy to slow life history, thus large species will have smaller population growth and will be more susceptible to threatening processes. Restricted range limits population size and increases the probability of species being affected by local disasters. Primates with a high diet disparity would be able to cope better with food availablity than species with similar diet items. Diet disparity was the only predictive diet metric, but we need to account for the choice of measure, as some metrics could be unable to capture an existing relationship. Our results imply that primates with limited diet disparity should receive more conservations efforts.

Keywords: diet; primates; diet disparity; diet breadth; diet diversity; extinction risk.

INTRODUCTION

Human pressure on natural ecosystems is contributing to an extinction rate much higher than so-called "background" levels inferred from the fossil record [Pimm et al., 1995, 2014; Barnosky et al., 2011]. Susceptibility to extinction varies among species, depending on their biology, ecology, environmental factors and threats to which they are exposed [Purvis et al., 2000; Purvis, 2008; Murray et al., 2014]. Understanding why some species are more vulnerable to extinction than others is of great interest in conservation biology [McKinney, 1997], helping in the assessment of species inherent risk of extinction, and helping decision-making in conservation management and triage [Boyles & Storm, 2007].

Some well discussed characteristics contributing to extinction risk include body mass [e.g. Ameca y Juárez et al., 2014; Cardillo et al., 2004; Davidson et al., 2009, Collen et al., 2011; González-Suárez et al. 2016] and range size [e.g. Isaac & Cowlishaw, 2004; Sodhi et al., 2008; Murray et al., 2011]. The influence of diet in species extinction risk has been studied in a broad way, considering the trophic level [e.g. Di Marco et al., 2012; Farneda et al., 2015; Liow et al., 2009] and the dietary breadth [e.g. Swihart et al., 2003; Walker, 2006]. Detailed studies of how different aspects of diet affect extinction risk have not been conducted.

Species with specialized diets may have more difficulty in dealing with changes in the environment compared to generalists [Vázquez & Simberloff, 2002]. Insectivorous bats with a smaller dietary breadth are more prone to extinction than more generalists bats [Boyles & Storm, 2007]. The degree of frugivory in primates can contribute with their ability to deal with habitat disturbance [Fimbel, 1994] and agriculture [Isaac & Cowlishaw, 2004]. Specialized primate folivores that devote a higher proportion of their diet to mature

leaf consumption are less prone to extinction than species that consume young leaves [Kamilar & Paciulli, 2008]. In primates, specialized diet is associated with rarity (relative to being less common) [Harcourt & Coppeto, 2002]. Although rarity is a risk factor in extinction, little is known about how the breadth or diversity of the diet of primate species influences their susceptibility to extinction. Previous extinction risk studies have used broad dietary categories to quantify diet breadth, and have focused on particular regions or taxa. Such factors, in addition to not covering the possible diet breadth, may obscure important details in species assessment [Kamilar & Paciulli, 2008].

Primates are a good group to test models of extinction risk. They are charismatic, the ecology and natural history of most of its species are well described, and it has many species, some very abundant and of wide distribution [Purvis et al., 2000]. Furthermore, they are of great interest to conservation biology, considering that about 61% of all its species are threatened [IUCN, 2017].

In this study we examine the association between diet and extinction risk in primates. We investigated if species with a broader or more diverse diet are less prone to extinction than species with a more restrictive or less diverse diet. We measured diet in different ways, including a novel approach, using phylogenetic methods, to evaluate the diet diversity in terms of item disparity.

METHODS

Primate Diet Database

We compiled diet information for 258 primate species (Table S1). We considered the diet in four different ways: (i) diet breadth, (ii) diet evenness, (iii) diet type, and (iv) diet

disparity. For diet breadth, we counted the number of different items in the diet for each species [Mittermeier et al., 2013]. We used higher taxonomic levels for animal prey (e.g. crustaceans, insects, birds, and mammals) and plant parts for plants (e.g. fruits, seeds, leaves, and nectar) consumption to categorize the different item consumed (Table S2).

We calculated diet evenness using an adaptation of the dietary diversity index (DDI) [MacArthur, 1972], or Levin's Index [Safi & Kerth, 2004], also known as Simpson's Reciprocal Index:

$$DDI = 1/\sum P\,i^2$$

where P_i represents the proportion of item i in the diet, which we obtained from the Elton Traits database [Wilman et al., 2014]. This database contains 10 different dietary categories (for more details see Wilman et al., 2014), eight of which are found in primates. From these eight dietary categories, we combined the different vertebrate-based dietary categories and also the fruit and seeds into two single categories (vertebrates and fruits respectively), leaving six different dietary categories (invertebrates, vertebrates, fruits, exudate, and other plant material, including leaves). From these categories, we calculated diet type by classifying primate species diet as: frugivore, if the diet is composed of more than 50% of fruits and seeds; folivore if is composed of more than 50% of other plant parts; frugivore-folivore, if is composed of 50% fruits and 50% in other plant parts; gumnivore, if is composed of more than 50% of gums or other exudates; carnivore, if is composed exclusively of animal matter; and omnivore, if is composed of animal and plant matter.

For diet disparity, we applied a modification of a phylogeny-based diversity metric [Bromham et al., 2016] that accounts for similarity between diet items. We arranged all consumed items obtained from Mittermeier et al. [2013] into a hierarchical classification

(Table S1). After this, we converted the classification into a dendrogram (Figure S1) using the "ape" package [Paradis et al., 2004], in R [R Development Core Team, 2017]. For animal matter, we followed taxonomic classification. For plants, we used structural and nutritional similarity. We then calculated the diet diversity in terms of diet distinctiveness, using the index Phylogenetic Species Variability (PSV) [Helmus et al., 2007], with the "picante" package [Kembel et al., 2010], in R [R Development Core Team, 2017]. This index takes into account species relatedness, but in our case it measures how similar diet items are to each other. PSV of diets containing only a single item was set to zero. Therefore, the metric presents values varying between 0 (one food item) to 1(maximum disparity among the items, independently to number of items in the diet).

Data analysis

The IUCN Red List status was used as a response variable, and can be considered an ordinal categorization of one continuous variable [Gonzalez-voyer et al., 2016]. IUCN status was represented by an ordinal variable of increasing threat status, varying from 0 (Least Concern), 1 (Near Threatened), 2 (Vulnerable), 3 (Endangered) 4 (Critically Endangered).

We also collected data on species mean adult body mass and geographic range size to use as covariates, as weight and range size have been found to be strongly correlated with diet [Santini et al., 2014] and with IUCN threat status [e.g. Cardillo et al., 2005, 2008, Fritz et al., 2009]. We obtained species body mass from Mittermeier et al. [2013] and the range size from IUCN [2017].

For further analysis, we considered only species with complete data on diet, body mass, and range size. We did not consider species classified as Data Deficient or species

classified under IUCN criterion B (which evaluates species threat status based on reduction of geographic range size), to avoid circularity in our analyses, since we included range size as one of the predictors [Purvis et al., 2000].

One way to analyze regression models with non-Gaussian response distributions is using GLMM (Generalized Linear Mixed Models) in a Bayesian framework [Garamszegi et al., 2014]. We implemented the statistical model in MCMCglmm (MCMC Generalized Linear Mixed Models) [Hadfield, 2010], in R [R Development Core Team, 2017], which also allows control of phylogenetic non-independence [Felsenstein, 1985], by including the phylogeny as a random factor [Garamszegi et al., 2014]. We used the primate phylogeny from one mammal super tree [Fritz et al., 2009]. We matched the species from our dataset to the primate tree and inserted any missing species from our dataset at the root node of the genus containing them, using the "phytools" package [Revell, 2012]. We log transformed range size and body mass data to perform the analysis.

We modeled the relationship between IUCN Red List status as a function of each dietary measure (diet breadth, diet evenness, diet type, diet disparity), with range size, and body mass as covariates. We used the family "threshold" to model the ordinal response, as it performed better than "ordinal" family to our data. We used 300,000 MCMC iterations, thinning of 200, and burn-in of 20,000. For the priors, as suggested by Hadfield, [2010], we fixed the residual variance to 1, R-component, v=1, fix=1, and for the G-component we used v=1, nu=0.02. Convergence was verified visually by plotting parameters using the package MCMCglmm [Hadfield, 2010].

RESULTS

Diet was a significant predictor of extinction risk in primates, but only when measured as diet disparity. Diet breadth, diet evenness, and diet type models did not affect extinction risk (Table 1). Primates with lower diet disparity were more likely to have a higher threat status, suggesting that primates that are able to consume diet items that are more different from each other are less prone to extinction (Figure 1).

Both Range size and body mass predicted extinction risk in all our models (Table 1). Large-bodied primate species have higher extinction risk, as do restricted-range primate species.

Table 1. Relation between IUCN Red List status and diet (diet breadth, diet diversity, and diet type), body mass, and the size of geographical distribution in 258 primate species. (lower CI = lower 95% credible interval from 1400 models. Upper CI = upper 95% confidence interval from 1400 models. Notes: 300.000 iterations with 20.000 burn-in and thinning interval of 200).

	estimate (ß)	**lower CI**	**upper CI**
	Diet breadth		
fixed terms			
intercept	1.4811	-0.8755	3.8662
diet	-0.1049	-0.3723	0.1539
*weight	1.0173	0.3441	1.5859
*range	-1.5216	-2.0617	-1.0452
random terms			
residual variance	1	1	1
phylogenetic variance	7.521	0.9265	18.67

*Values greater than zero with 95% credibility.

Table 1. Continuation.

	estimate (ß)	lower CI	upper CI
Diet diversity - DDI			
fixed terms			
intercept	1.4337	-1.3439	3.9309
diet	-1.1887	-0.5218	0.1645
*weight	0.9022	0.288	1.4856
*range	-1.5579	-2.1382	-1.0631
random terms			
residual variance	1	1	1
phylogenetic variance	8.224	0.7057	21.44
Diet disparity - PSV			
fixed terms			
intercept	1.5047	-1.2176	4.0926
*diet	-0.4485	-0.7674	-0.1644
*weight	1.0102	0.362	1.635
*range	-1.63	-2.2938	-1.136
random terms			
residual variance	1	1	1
phylogenetic variance	8.877	0.5769	23.45
Diet type			
fixed terms			
carnivore (intercept)	-2.7448	-5.9705	0.5884
gommivore	1.8244	-1.6607	5.7195
folivore	0.1528	-2.6149	3.2081
frugivore	0.6759	-2.2005	3.6218
frugivore-folivore	-1.9338	-5.5618	1.4708
omnivore	0.2763	-2.3976	3.2403
*weight	0.7065	0.4031	1.048
*range	-0.6091	-0.7213	-0.4926
random terms			
residual variance	1	1	1
phylogenetic variance	3.284	0.8613	6.441

*Values greater than zero with 95% credibility.

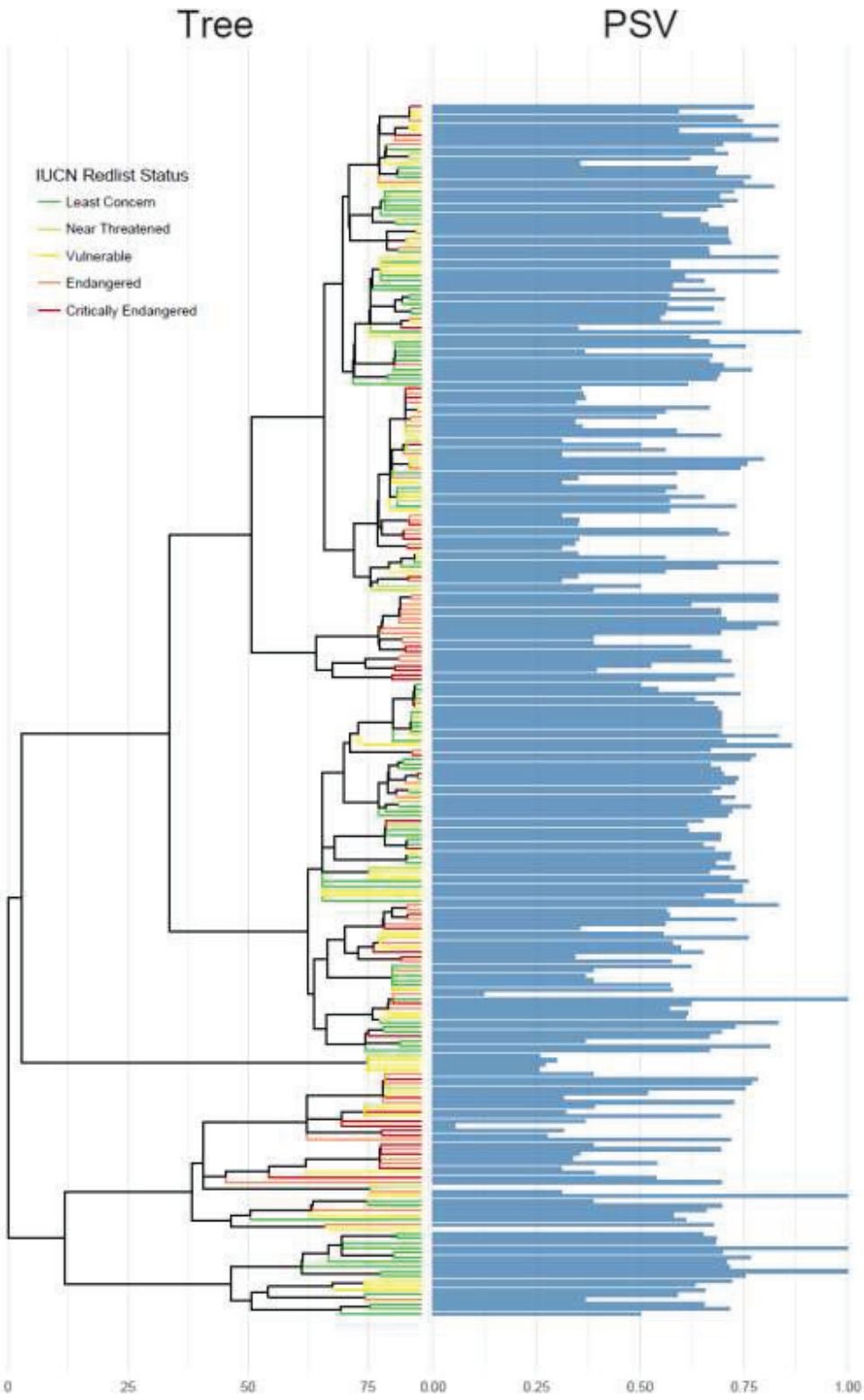

Figure 1. Diet disparity (PSV) and primate conservation status [IUCN, 2016] within the primate phylogeny.

DISCUSSION

We found that diet was a significant predictor of extinction risk. However, our results show that is does not matter whether a species is frugivorous, folivorous, omnivorous, or carnivorous (diet type), eats less or more food items (diet breadth), or have a less or more even diet (diet evenness). The important factor is how much the diet items are disparate from one other. For example, *Galagoides zanzibaricus* eats fruits and insects (plant and animal diet) and is a Least Concern species [IUCN, 2016], while *Presbytis potenziani* eats leaves, fruits and seeds (plant only diet) and is an Endangered species [IUCN, 2016]. Both consume few items, but the first one eats items much more different from one other, with a maximum disparity diet value (Table S1) and the second eats items less disparate, with a diet disparity of 0.35. Primates are a big and diverse group, having species with highly specific diets, like *Phaner furcifer* whose diet consists only of plant gums, and species with a generalist diet, such as *Papio ursinus*, whose diet includes a huge variety of items, from different animal groups and plants parts.

Our results contrast with other studies with primates, where diet type and trophic level were related with extinction risk [Purvis et al. 2000; Isaac & Cowlishaw, 2004]. Isaac & Cowlishaw [2004] found that primates with low-fruit diets are more vulnerable to agriculture. However, we evaluated the relation of diet with IUCN categories, whereas Isaac & Cowlishaw [2004] evaluated the response to specific threats (e.g. agriculture). Even though the IUCN criteria are a result of the response of species to different threats, we did not discriminate the threats the way Isaac & Cowlishaw [2004] did.

Purvis et al. [2000] showed that carnivores and primates at higher trophic levels are more prone to extinction. In order to determine trophic level they used wide diet categories

(herbivore, omnivore, insectivore, and vertebrate eater), which include more item distinctive then the categories that we used. The use of these comprehensive categories would be capturing the item disparity.

Why does having a diet with high disparity reduce extinction risk relative to those that only consume more similar items? The ability to eat items very different from each other may allow primates to cope with variation in food availability. Very different food items will vary in the nutrition content and in spatial and/or temporal availability. Species with less restrictive diet (generalists) are able to change their diet when a preferred food item is not available. These species can deal better with local events (natural or anthropogenic) that change the natural dynamics of food availability than specialists. An example might be during an insect herbivore outbreak, plant tissue may be at low availability, but insect food would be abundant. An omnivorous primate would be in a better position to take advantage of such a negative interaction between food items to maintain stability in its diet over time.

Diet specialization has been shown to increase extinction risk in the face of habitat loss and fragmentation [e.g. Farneda et al., 2015], intensity of land use [Wang et al., 2015] and landscape changes [Pavlacky et al., 2015]. In Primates, diet specialization is also related with rarity [Harcourt et al., 2002]. A specialist diet also increased extinction risk in bats [Boyles & Storm, 2007].

Diet can be evaluated as diet breadth, diet evenness, diet type, diet disparity, trophic level, percentage of item or volume of item in the diet. As we showed in this work, the metric used to evaluate diet can mask a relation that exists, but was not possible to be captured using a specific measure. Using broad categories like frugivorous or folivorous, for example, does not capture what appears to be a key property of the diet, its disparity.

Diet disparity is an important trait related to extinction risk in primates, and should be considered in the evaluation of extinction risk of this group. Our results imply that more concerted conservation effort should be targeted towards primates with limited diet disparity.

REFERENCES

Ameca y Juárez EI, Mace GM, Cowlishaw G, Pettorelli N. 2014. Identifying species' characteristics associated with natural population die-offs in mammals. Animal Conservation 17:35–43.

Barnosky AD, Matzke N, Tomiya S, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature [Internet] 471:51–57. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21368823

Boyles JG, Storm JJ. 2007. The perils of picky eating: Dietary breadth is related to extinction risk in insectivorous bats. PLoS ONE 2.

Bromham L, Dinnage R, Hua X. 2016. Interdisciplinary research has consistently lower funding success. Nature [Internet] 534:684–687. Available from: http://www.nature.com/doifinder/10.1038/nature18315

Cardillo M, Mace GM, Gittleman JL, et al. 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proceedings of the Royal Society B: Biological Sciences [Internet] 275:1441–1448. Available from: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2008.0179

Cardillo M, Mace GM, Jones KE, et al. 2005. Multiple causes of high extinction risk in large mammal species. Science (New York, N.Y.) 309:1239–1241.

Cardillo M, Purvis A, Sechrest W, et al. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology 2:909–914.

Collen B, McRae L, Deinet S, et al. 2011. Predicting how populations decline to extinction. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 366:2577–2586.

Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G. 2009. Multiple ecological

pathways to extinction in mammals. Proceedings of the National Academy of Sciences of the United States of America 106:10702–10705.

Farneda FZ, Rocha R, López-Baucells A, et al. 2015. Trait-related responses to habitat fragmentation in Amazonian bats. Journal of Applied Ecology 52:1381–1391.

Felsenstein J. 1985. Phylogenies and the Comparative Method. The American Naturalist [Internet] 125:1–15. Available from: http://search.ebscohost.com/login.aspx?direct=true&db=bth&AN=96338264&lang=es&site=ehost-live

Fimbel C. 1994. Ecological Correlates of Species Success in Modifted Habitats May fire Primates of Tiwai Island. Conservation Biology 8:106–113.

Fritz SA, Bininda-Emonds ORP, Purvis A. 2009. Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. Ecology Letters 12:538–549.

Garamszegi LZ, Pearse WD, Purvis A, et al. 2014. Modern phylogenetic comparative methods and their application in evolutionary biology. Modern Phylogenetic Comparative Methods and their Application in Evolutionary Biology.

Gonzalez-voyer A, González-Suárez M, Vilà C, Revilla E. 2016. Larger brain size indirectly increases. Evolution 70:1364–1375.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Harcourt AH, Coppeto SA. 2002. Rarity, specialization and extinction in primates (vol 29, pg 445, 2002). 29:1717–1717.

Harcourt AH, Coppeto SA, Parks SA. 2002. Rarity, specialization and extinction in primates. Journal of Biogeography 29:445–456.

Helmus MR, Bland TJ, Williams CK, Ives AR. 2007. Phylogenetic Measures of Biodiversity. The American Naturalist [Internet] 169:E68–E83. Available from: http://www.journals.uchicago.edu/doi/10.1086/511334

Isaac NJB, Cowlishaw G. 2004. How species respond to multiple extinction threats. Proceedings of the Royal Society B: Biological Sciences [Internet] 271:1135–1141. Available from: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2004.2724

IUCN. 2016. Available from: http://www.iucnredlist.org/

IUCN. 2017. Available from: http://www.iucnredlist.org/

Kamilar JM, Paciulli LM. 2008. Examining the extinction risk of specialized folivores: A comparative study of colobine monkeys. American Journal of Primatology 70:816–827.

Kembel SW, Cowan PD, Helmus MR, et al. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC. 2009. Lower Extinction Risk in Sleep-or-Hide Mammals. The American Naturalist [Internet] 173:264–272. Available from: http://www.jstor.org/stable/10.1086/595756

MacArthur R. 1972. Geographical Ecology. New York: Harper and Row. 269 p.

Di Marco M, Cardillo M, Possingham HP, et al. 2012. A novel approach for global mammal extinction risk reduction. Conservation Letters 5:134–141.

McKinney ML. 1997. Extinction Vulnerability and Selectivity: Combining Ecological and Paleontological Views. Annual Review of Ecology and Systematics [Internet] 28:495–516. Available from: http://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.28.1.495%5Cnhttp://www.annualreviews.org/doi/pdf/10.1146/annurev.ecolsys.28.1.495

Mittermeier R, Rylands A, DE W, editors. 2013. Handbook of the Mammals of the World - Volume 3. Barcelona: Lynx Edicions. 950 p.

Murray K a, Rosauer D, McCallum H, Skerratt LF. 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proceedings. Biological sciences / The Royal Society [Internet] 278:1515–23. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3081746&tool=pmcentrez&rendertype=abstract

Murray KA, Verde Arregoitia LD, Davidson A, Di Marco M, Di Fonzo MMI. 2014. Threat to the point: improving the value of comparative extinction risk analysis for conservation action. Global Change Biology [Internet] 20:483–494. Available from: http://doi.wiley.com/10.1111/gcb.12366

Paradis E, Claude J, Strimmer K. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Pavlacky DC, Possingham HP, Goldizen AW. 2015. Integrating life history traits and forest structure to evaluate the vulnerability of rainforest birds along gradients of deforestation and fragmentation in eastern Australia. Biological Conservation [Internet] 188:89–99. Available from: http://dx.doi.org/10.1016/j.biocon.2014.10.020

Pimm SL, Jenkins CN, Abell R, et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science (New York, N.Y.) [Internet] 344:1246752. Available from: http://www.ncbi.nlm.nih.gov/pubmed/24876501

Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The Future of Biodiversity. Science [Internet] 269:347–350. Available from: http://www.ncbi.nlm.nih.gov/pubmed/17841251

Purvis A. 2008. Phylogenetic Approaches to the Study of Extinction. The Annual Review of Ecology, Evolution, and Systematics [Internet] 39:301–319. Available from: http://geology.gsapubs.org/content/43/8/751.full?etoc

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings. Biological Sciences / The Royal Society 267:1947–1952.

R Development Core Team. 2017. R: A language and environment for statistical computing.

Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Safi K, Kerth G. 2004. A comparative analysis of specialization and extinction risk in temperate zone bats. Conservation Biology 18:1293–1303.

Santini L, Di Marco M, Boitani L, Maiorano L, Rondinini C. 2014. Incorporating spatial population structure in gap analysis reveals inequitable assessments of species protection. Diversity and Distributions 20:698–707.

Sodhi NS, Bickford D, Diesmos AC, et al. 2008. Measuring the meltdown: Drivers of global amphibian extinction and decline. PLoS ONE 3:1–8.

Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE. 2003. Responses of'resistant'vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity & Distributions 9:1–18.

Vázquez DP, Simberloff D. 2002. Ecological specialization and susceptibility to

disturbance: conjectures and refutations. The American naturalist 159:606–623.

Walker JS. 2006. Resource use and rarity among frugivorous birds in a tropical rain forest on Sulawesi. Biological Conservation 130:60–69.

Wang X, Zhang K, Wang Z, et al. 2004. The decline of the Chinese giant salamander Andrias davidianus and implications for its conservation. Oryx 38:197–202.

Wang Y, Thornton DH, Ge D, Wang S, Ding P. 2015. Ecological correlates of vulnerability to fragmentation in forest birds on inundated subtropical land-bridge islands. Biological Conservation [Internet] 191:251–257. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0006320715300070

Wilman H, Belmaker J, Simpson J, et al. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. Ecology 95:2027.

SUPPORTING INFORMATION

Table S1. Information about threat status, body mass, range size, and diet for the 258 primates species used in this study.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Allenopithecus nigroviridis	0	4725	41.151	0.61	8	2	Omnivore
Allocebus trichotis	2	7900	3.626	0.58	6	2	Frugivore-Folivore
Allochrocebus preussi	3	5475	1.408	0.7	7	2.78	Omnivore
Alouatta belzebul	2	6375	70.78	0.58	6	1.92	Folivore
Alouatta caraya	0	7025	261.887	0.57	6	1.92	Folivore
Alouatta guariba	0	5400	95.187	0.37	4	1.92	Folivore
Alouatta macconnelli	0	6375	143.583	0.62	6	1.92	Folivore
Alouatta palliata	0	6050	46.982	0.39	3	1.92	Folivore
Alouatta pigra	3	7050	20.494	0.39	3	1.92	Folivore
Aotus azarae	0	1257.5	263.424	0.73	6	5.56	Omnivore
Aotus brumbacki	2	665	10.1	0.66	5	5.56	Omnivore
Aotus miconax	2	800	4.874	0.75	9	5.56	Omnivore
Aotus nigriceps	0	957.5	127.238	0.75	9	5.56	Omnivore
Aotus vociferans	0	703	82.676	0.76	8	5.56	Omnivore
Arctocebus aureus	0	235	54.269	0.71	4	1.72	Omnivore
Arctocebus calabarensis	0	347.5	12.117	0.65	4	1.72	Omnivore
Ateles belzebuth	3	8100	93.818	0.73	9	2.5	Omnivore
Ateles chamek	3	6000	200.917	0.56	10	2.5	Omnivore
Ateles fusciceps	4	8450	17.621	0.36	5	2.5	Omnivore
Ateles geoffroyi	3	7950	76.23	0.56	6	2.5	Omnivore
Ateles hybridus	4	6262.5	13.619	0.57	6	2.5	Omnivore
Ateles marginatus	3	8100	42.946	0.83	3	2.5	Omnivore
Ateles paniscus	2	8925	86.359	0.56	12	2.5	Omnivore
Avahi laniger	2	1200	4.303	0.39	4	1.47	Folivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Brachyteles arachnoides	3	9350	7.639	0.58	6	2.94	Folivore
Brachyteles hypoxanthus	4	8625	8.353	0.34	8	1.85	Folivore
Cacajao calvus	2	2950	14.891	0.61	7	1.92	Omnivore
Callibella humilis	2	167.5	0.521	0.83	3	3.33	Omnivore
Callicebus brunneus	0	850	20.161	0.67	6	2.63	Omnivore
Callicebus cupreus	0	1100	63.473	0.81	6	2.63	Omnivore
Callicebus discolor	0	1005	18.837	0.37	4	2.63	Omnivore
Callicebus lucifer	0	1500	19.051	0.7	4	2.63	Omnivore
Callicebus lugens	0	1250	74.302	0.73	5	2.63	Omnivore
Callicebus melanochir	2	1400	8.403	0.67	6	2.63	Omnivore
Callicebus nigrifrons	1	1325	42.593	0.73	5	2.63	Omnivore
Callicebus oenanthe	4	800	0.745	0.67	6	2.63	Omnivore
Callicebus personatus	2	3350	12.258	0.71	4	2.63	Omnivore
Callimico goeldii	2	360.5	49.329	0.86	5	2.38	Omnivore
Callithrix aurita	2	425	13.967	0.69	11	3.33	Omnivore
Callithrix flaviceps	3	400	2.133	0.68	11	3.33	Omnivore
Callithrix geoffroyi	0	240	10.648	0.63	7	3.33	Omnivore
Callithrix jacchus	0	319.95	77.274	0.54	9	3.33	Omnivore
Callithrix kuhlii	1	375	3.844	0.74	12	3.33	Omnivore
Callithrix penicillata	0	202.5	110.877	0.5	2	3.33	Omnivore
Cebuella pygmaea	0	112.5	137.071	0.71	9	2.27	Omnivore
Cebus albifrons	0	2350	302.065	0.65	10	5.56	Omnivore
Cebus capucinus	0	2875	39.439	0.69	4	5.56	Omnivore
Cebus kaapori	4	2700	15.519	0.68	10	1.92	Omnivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Cercocebus agilis	0	7375	85.651	0.67	11	1.85	Omnivore
Cercocebus atys	1	8375	35.848	0.71	16	2.38	Omnivore
Cercocebus galeritus	3	5125	0.016	0.66	10	1.85	Omnivore
Cercocebus torquatus	2	8375	23.383	0.72	11	1.85	Omnivore
Cercopithecus ascanius	0	3700	213.48	0.65	10	3.13	Omnivore
Cercopithecus campbelli	0	3225	50.613	0.7	6	3.13	Omnivore
Cercopithecus cephus	0	3700	63.342	0.61	10	3.13	Omnivore
Cercopithecus denti	0	4050	33.206	0.68	4	3.13	Omnivore
Cercopithecus diana	2	4550	28.394	0.69	4	2.78	Omnivore
Cercopithecus dryas	4	2650	0.111	0.35	3	3.13	Omnivore
Cercopithecus erythrogaster	2	3500	5.999	0.83	3	3.13	Omnivore
Cercopithecus erythrotis	2	3700	4.55	0.57	7	3.13	Omnivore
Cercopithecus hamlyni	2	4450	19.367	0.62	9	3.13	Omnivore
Cercopithecus lowei	0	4200	27.711	0.57	6	3.13	Omnivore
Cercopithecus mitis	0	5775	192.188	0.68	10	2.78	Omnivore
Cercopithecus mona	0	4600	50.57	0.57	4	3.13	Omnivore
Cercopithecus neglectus	0	4450	186.367	0.89	5	3.13	Omnivore
Cercopithecus nictitans	0	5300	108.928	0.58	6	3.13	Omnivore
Cercopithecus petaurista	0	3200	43.485	0.57	6	3.85	Omnivore
Cercopithecus pogonias	0	3950	171.503	0.56	6	3.13	Omnivore
Cercopithecus roloway	3	4550	11.152	0.55	7	2.38	Omnivore
Cercopithecus sclateri	2	3375	2.945	0.83	3	3.13	Omnivore
Cheirogaleus medius	0	135	10.922	0.61	8	3.85	Omnivore
Chiropotes albinasus	3	2850	80.593	0.57	6	3.33	Omnivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Chiropotes chiropotes	0	2925	110.971	1	2	1.85	Omnivore
Chiropotes satanas	4	2925	22.232	0.62	8	3.33	Omnivore
Chiropotes utahickae	3	3000	28.795	0.12	3	2.63	Frugivore
Chlorocebus aethiops	0	3975	94.807	0.67	15	3.57	Omnivore
Chlorocebus cynosuros	0	3975	255.322	0.67	12	3.85	Omnivore
Chlorocebus pygerythrus	0	3975	387.575	0.37	5	3.57	Omnivore
Chlorocebus sabaeus	0	3975	125.882	0.75	22	3.57	Omnivore
Chlorocebus tantalus	0	4650	327.881	0.67	11	2.63	Omnivore
Colobus angolensis	0	8950	187.712	0.69	7	1.72	Folivore
Colobus guereza	0	9300	249.129	0.83	3	1.72	Folivore
Colobus polykomos	2	7900	28.005	0.56	6	1.72	Folivore
Colobus satanas	2	11500	26.699	0.56	6	1.72	Folivore
Colobus vellerosus	2	8400	39.055	0.35	3	1.72	Folivore
Daubentonia madagascariensis	3	2500	10.691	0.7	11	2.78	Omnivore
Erythrocebus patas	0	4825	590.782	0.77	15	2.78	Frugivore
Eulemur albifrons	3	1900	1.546	0.77	8	2.78	Omnivore
Eulemur cinereiceps	4	2000	0.159	0.78	7	1.52	Frugivore
Eulemur collaris	3	2200	0.724	0.39	3	1	Frugivore
Eulemur coronatus	3	1300	0.519	0.73	6	1.72	Folivore
Eulemur fulvus	1	1500	4.121	0.75	11	1.72	Folivore
Eulemur mongoz	4	1200	0.702	0.32	4	2.63	Gumnivoro
Eulemur rubriventer	2	2000	4.235	0.52	6	1.72	Folivore
Euoticus elegantulus	0	315	63.61	0.77	5	2.27	Omnivore
Euoticus pallidus	0	230	7.82	0.7	6	2.27	Omnivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Galago moholi	0	177.5	357.042	1	2	1.92	Omnivore
Galago senegalensis	0	202.5	692.045	0.68	6	1.92	Omnivore
Galagoides granti	0	52.5	44.389	0.75	5	1.47	Omnivore
Galagoides thomasi	0	105	367.498	0.71	4	1.47	Omnivore
Galagoides zanzibaricus	0	150	0.581	1	2	1.52	Omnivore
Gorilla beringei	4	121750	5.297	0.52	6	1.22	Folivore
Gorilla gorilla	4	116500	56.559	0.39	3	1.22	Folivore
Hapalemur alaotrensis	4	1250	0.018	0.32	4	1	Folivore
Hapalemur aureus	4	1400	0.209	0.05	2	1	Folivore
Hapalemur griseus	2	890	7.325	0.69	7	1	Folivore
Hapalemur occidentalis	2	948	3.35	0.39	4	1	Folivore
Hoolock hoolock	3	6500	28.323	0.78	9	1.85	Omnivore
Hylobates agilis	3	6075	31.378	0.83	3	1.85	Omnivore
Hylobates albibarbis	3	5950	16.23	0.83	3	1.72	Frugivore
Hylobates klossii	3	6000	0.488	0.83	3	1.85	Omnivore
Hylobates lar	3	5350	53.386	0.71	6	1.85	Omnivore
Hylobates moloch	3	6400	3.211	0.69	4	1.85	Omnivore
Hylobates muelleri	3	5650	42.715	0.69	4	1.85	Omnivore
Hylobates pileatus	3	5542.37	10.145	0.62	5	1.85	Omnivore
Indri indri	4	7400	2.553	0.54	7	1.72	Folivore
Lagothrix cana	3	7250	112.3	0.58	6	1.85	Frugivore
Lagothrix lagotricha	2	7250	53.211	0.6	9	1.92	Omnivore
Lagothrix poeppigii	2	7250	54.327	0.76	9	1.85	Frugivore
Lemur catta	3	2200	8.826	0.72	9	1.47	Frugivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Leontopithecus caissara	4	625	0.03	0.78	8	2	Omnivore
Leontopithecus chrysomelas	3	552.5	1.698	0.67	10	2	Omnivore
Lepilemur edwardsi	3	965	0.765	0.31	4	1	Folivore
Lepilemur mustelinus	1	1000	2.203	0	1	1	Folivore
Lophocebus albigena	0	6575	118.856	0.66	7	2	Frugivore-Folivore
Lophocebus aterrimus	1	6800	58.615	0.64	8	2.78	Frugivore
Loris lydekkerianus	0	276.5	17.515	0.59	11	1	Carnivore
Loris tardigradus	3	152.5	1.26	0.37	2	1.92	Omnivore
Macaca arctoides	2	10500	124.623	0.36	5	3.33	Omnivore
Macaca assamensis	1	9500	161.357	0.62	8	3.33	Omnivore
Macaca cyclopis	0	9950	2.41	0.68	12	3.33	Omnivore
Macaca fuscata	0	10450	15.51	0.76	15	3.33	Omnivore
Macaca hecki	2	8250	1.95	0.83	3	2.38	Omnivore
Macaca leonina	2	6350	130.396	0.59	9	1.52	Omnivore
Macaca maura	3	7400	0.391	0.83	3	3.33	Omnivore
Macaca mulatta	0	5525	680.615	0.69	15	3.33	Omnivore
Macaca nemestrina	2	9150	111.206	0.73	8	1.92	Omnivore
Macaca nigra	4	9175	0.623	0.77	8	1.92	Omnivore
Macaca pagensis	4	7375	0.174	0.77	4	2.38	Omnivore
Macaca radiata	0	6350	52.228	0.68	11	3.33	Omnivore
Macaca siberu	2	6375	0.314	0.82	6	2.38	Omnivore
Macaca silenus	3	5750	2.313	0.75	17	3.33	Omnivore
Macaca sinica	3	4775	3.809	0.7	7	3.33	Omnivore
Macaca sylvanus	3	12200	4.049	0.75	6	3.33	Omnivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Macaca thibetana	1	16250	122.279	0.71	11	3.33	Omnivore
Macaca tonkeana	2	10250	6.613	0.59	5	3.33	Omnivore
Mandrillus leucophaeus	3	3850	3.597	0.71	17	3.57	Omnivore
Mandrillus sphinx	2	1875	26.413	0.71	13	3.57	Omnivore
Mico intermedius	0	295	5.163	0.7	9	2.63	Omnivore
Mico leucippe	2	330	1.21	0.7	9	2.78	Omnivore
Mico mauesi	0	357.5	2.413	0.7	9	3.33	Omnivore
Mico melanurus	0	330	71.642	0.7	9	3.57	Omnivore
Mico saterei	0	430	1.572	0.7	9	3.33	Omnivore
Microcebus griseorufus	0	45	3.199	0.39	3	4.55	Omnivore
Microcebus murinus	0	60	7.818	0.7	11	4.55	Omnivore
Microcebus myoxinus	2	42	2.66	1	2	4.55	Omnivore
Miopithecus ogouensis	0	1250	39.568	0.69	7	1.47	Omnivore
Miopithecus talapoin	0	1012.5	31.872	0.68	9	2	Omnivore
Mirza coquereli	3	308	4.261	0.66	14	2.5	Omnivore
Nasalis larvatus	3	16000	43.809	0.34	5	1.47	Folivore
Nomascus concolor	4	7500	2.307	0.7	7	1.52	Omnivore
Nomascus gabriellae	3	5200	7.934	0.39	3	1.52	Omnivore
Nomascus leucogenys	4	6500	4.464	0.62	5	1.52	Omnivore
Nomascus siki	3	7250	2.265	0.39	3	1.52	Omnivore
Nycticebus bengalensis	2	1375	177.078	0.72	6	3.33	Omnivore
Nycticebus coucang	2	742.5	51.381	0.63	11	3.33	Omnivore
Nycticebus pygmaeus	2	424	41.212	0.66	7	3.33	Omnivore
Oreonax flavicauda	4	7425	2.219	0.65	9	1.85	Frugivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Otolemur crassicaudatus	0	1400	468.087	0.68	12	2.27	Omnivore
Otolemur garnettii	0	822.5	43.155	0.65	10	2.27	Omnivore
Pan paniscus	3	35250	33.894	0.72	14	2.38	Omnivore
Pan troglodytes	3	42000	203.212	0.7	12	2.17	Omnivore
Papio anubis	0	21000	644.342	0.7	19	3.33	Omnivore
Papio cynocephalus	0	17250	353.489	0.73	17	2.38	Omnivore
Papio hamadryas	0	15675	50.745	0.66	12	1.52	Omnivore
Papio papio	1	16750	36.955	0.69	10	3.85	Omnivore
Papio ursinus	0	23000	297.714	0.72	19	3.85	Omnivore
Perodicticus potto	0	925	319.169	0.5	2	1.52	Omnivore
Phaner furcifer	2	390	1.768	0	1	1	Gumnivoro
Phaner pallescens	3	333	4.194	0.68	3	1	Gumnivoro
Piliocolobus badius	3	9125	35.875	0.31	4	1.47	Folivore
Piliocolobus preussi	4	8865.71	0.31	0.35	3	1.47	Folivore
Piliocolobus tholloni	1	8591.69	40.522	0.5	2	1.47	Folivore
Pithecia aequatorialis	0	3500	10.172	0.83	3	3.57	Omnivore
Pithecia albicans	2	3500	5.309	0.61	8	3.57	Omnivore
Pongo abelii	4	60000	0.643	0.73	10	1.52	Omnivore
Pongo pygmaeus	4	60000	10.38	0.68	10	1.52	Omnivore
Presbytis chrysomelas	4	7050	3.241	0.5	2	2.78	Frugivore
Presbytis comata	3	6875	2.213	0.74	9	2.78	Frugivore
Presbytis femoralis	1	7050	12.198	0.56	6	2.78	Frugivore
Presbytis frontata	2	5700	25.379	0.31	4	2.78	Frugivore
Presbytis hosei	2	6125	20.054	0.76	7	2.78	Frugivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Presbytis melalophos	3	7250	23.57	0.31	4	2.78	Frugivore
Presbytis potenziani	3	6450	0.488	0.35	3	2.78	Frugivore
Presbytis rubicunda	0	6125	40.952	0.59	5	2.78	Frugivore
Presbytis siamensis	1	6250	13.072	0.31	4	2.63	Frugivore
Presbytis thomasi	2	7500	4.929	0.8	9	2.78	Frugivore
Procolobus verus	1	4225	32.873	0.39	3	1.52	Folivore
Prolemur simus	4	2350	0.148	0.37	4	1.22	Folivore
Propithecus coquereli	3	3700	2.598	0.34	6	1.72	Folivore
Propithecus diadema	4	6250	1.401	0.36	5	1.72	Folivore
Propithecus edwardsi	3	5500	0.268	0.69	7	2.38	Frugivore-Folivore
Propithecus perrieri	4	4450	0.005	0.39	3	1.72	Folivore
Propithecus tattersalli	4	3500	0.144	0.31	4	1.72	Folivore
Propithecus verreauxi	3	2900	5.973	0.54	7	1.72	Folivore
Pygathrix cinerea	4	9225	2.072	0.35	3	1.85	Folivore
Pygathrix nemaeus	3	8400	7.953	0.35	6	1.47	Folivore
Pygathrix nigripes	3	8300	7.917	0.31	4	1.72	Folivore
Rhinopithecus avunculus	4	11250	0.893	0.35	6	1.85	Folivore
Rhinopithecus bieti	3	13300	2.73	0.71	10	1	Folivore
Rhinopithecus roxellana	3	12500	29.796	0.69	12	1.52	Folivore
Saguinus bicolor	3	540	0.824	0.73	5	2.94	Omnivore
Saguinus fuscicollis	0	333	141.348	0.77	9	2.94	Omnivore
Saguinus geoffroyi	0	496.95	6.161	0.74	6	2.94	Omnivore
Saguinus imperator	0	475	19.321	0.69	4	2.94	Omnivore
Saguinus inustus	0	465	30.945	0.71	3	2.94	Omnivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Saguinus labiatus	0	455	23.459	0.67	6	2.94	Omnivore
Saguinus leucopus	3	462	4.655	0.73	5	2.94	Omnivore
Saguinus midas	0	440	70.21	0.67	7	2.94	Omnivore
Saguinus mystax	0	505	48.114	0.77	9	2.94	Omnivore
Saguinus niger	2	429.5	47.881	0.69	4	4.55	Omnivore
Saguinus nigricollis	0	460	17.349	0.72	6	2.94	Omnivore
Saguinus oedipus	4	410.85	4.282	0.7	8	2.94	Omnivore
Saguinus tripartitus	1	400	2.088	0.69	4	2.94	Omnivore
Saimiri boliviensis	0	900	113.543	0.72	6	5	Omnivore
Saimiri sciureus	0	925	360.405	0.68	9	5	Omnivore
Saimiri vanzolinii	2	800	0.238	0.72	3	5	Omnivore
Sapajus apella	0	2950	275.071	0.69	9	5.56	Omnivore
Sapajus libidinosus	0	3050	217.561	0.62	9	3.85	Omnivore
Sapajus nigritus	1	3700	78.004	0.61	9	3.85	Omnivore
Sapajus xanthosternos	4	2875	38.89	0.65	8	3.85	Omnivore
Sciurocheirus alleni	0	355	7.795	0.71	6	1.92	Omnivore
Semnopithecus entellus	0	15500	49.45	0.73	9	1.22	Folivore
Semnopithecus hector	1	17350	9.298	0.57	11	1.85	Folivore
Semnopithecus hypoleucos	2	13100	1.115	0.65	8	1.85	Folivore
Semnopithecus johnii	2	11625	1.402	0.57	11	1.72	Folivore
Semnopithecus priam	1	NA	19.865	0.56	6	1.92	Folivore
Semnopithecus schistaceus	0	17350	29.4	0.59	11	1.52	Folivore
Simias concolor	4	7875	0.488	0.31	4	1.52	Folivore
Symphalangus syndactylus	3	10950	27.696	0.69	4	1.52	Omnivore

Table S1. Continuation.

Species	Threat status	Body mass (g)	Range size (km2)	Item disparity (PSV)	Diet breadth	Proportion of item (DDI)	Diet type
Tarsius bancanus	2	114.39	68.943	0.26	6	1	Carnivore
Tarsius dentatus	2	115.91	2.848	0.27	3	1	Carnivore
Tarsius syrichta	1	115.91	9.861	0.26	5	1	Carnivore
Tarsius tarsier	2	100.5	11.565	0.3	3	1	Carnivore
Theropithecus gelada	0	19500	8.605	0.55	7	1	Folivore
Trachypithecus auratus	2	9719.6	11.146	0.69	4	1.72	Folivore
Trachypithecus cristatus	1	6150	98.676	0.34	5	1.72	Folivore
Trachypithecus delacouri	4	7750	0.52	0.37	4	1.72	Folivore
Trachypithecus francoisi	3	6925	22.367	0.34	7	1.72	Folivore
Trachypithecus geei	3	11625	0.673	0.56	6	1.72	Folivore
Trachypithecus germaini	3	6750	28.622	0.54	7	1.72	Folivore
Trachypithecus hatinhensis	3	7550	1.607	0.36	5	1.72	Folivore
Trachypithecus obscurus	1	7200	21.285	0.59	5	1.72	Folivore
Trachypithecus phayrei	3	7175	99.218	0.36	6	1.72	Folivore
Trachypithecus pileatus	2	11625	27.2	0.67	8	1.72	Folivore
Trachypithecus poliocephalus	4	8050	0.083	0.36	5	1.72	Folivore
Varecia rubra	4	3300	0.443	0.32	4	1.22	Frugivore
Varecia variegata	4	3650	0.83	0.28	5	1	Frugivore

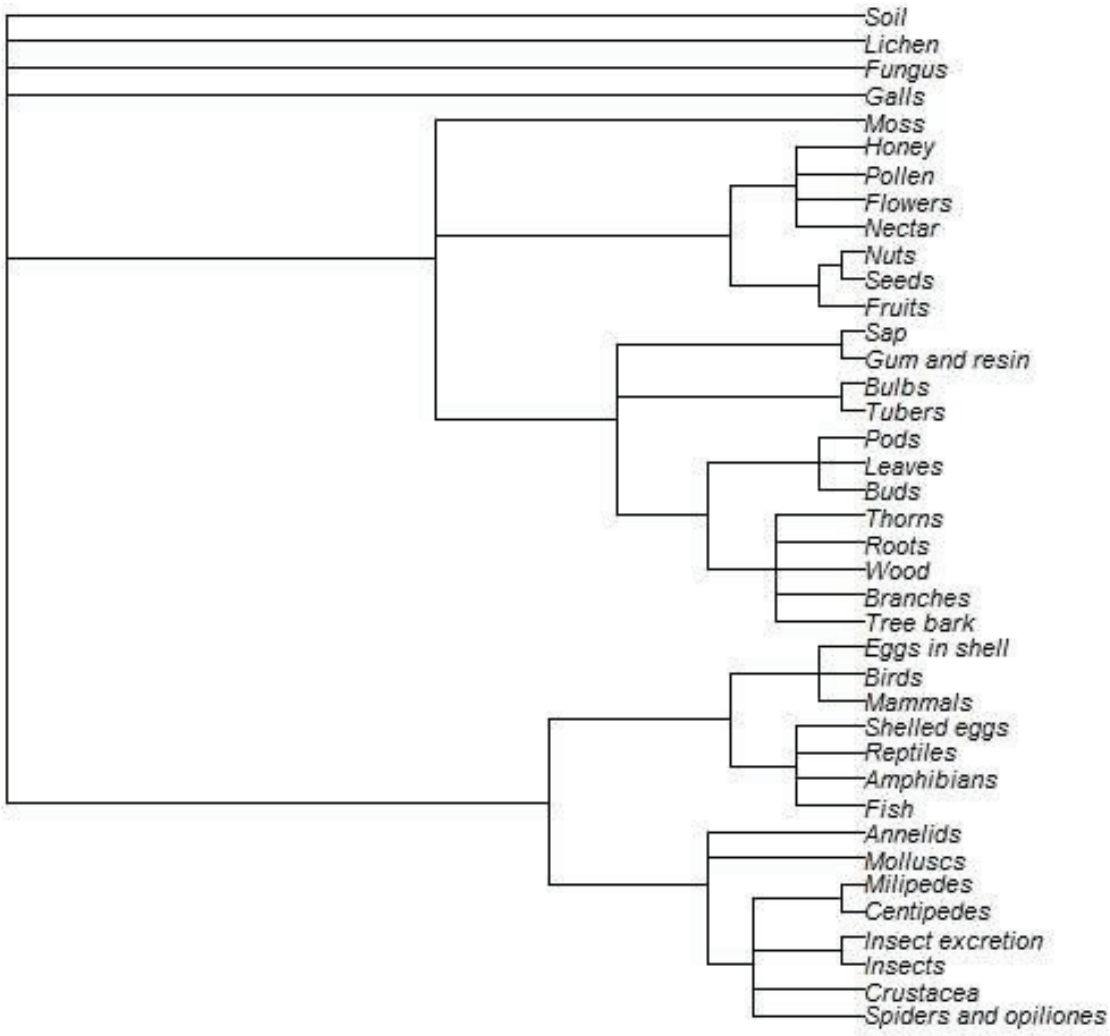

Figure S1. Dendrogram created from the hierarchical classification of the diet items, based on taxonomic classification to animals and structural and nutritional similarity to plants.

Table S2. Food items categories created to analyze primate diet breadth and diet hierarchy.

Plant	Animal	Animal/plant	Substrate	Plant/parasite	Fungi	Lichen
Tree bark	Spiders/opiliones	Honey	Soil	Gall	Fungi in general	Lichen in general
Branches	Crustaceans					
Wood	Insects					
Roots in general	Insects excretion					
Thorns	Centipedes					
Buds	Milipedes					
Leaves	Molluscs					
Pods	Annelids					
Tubers	Fish					
Bulbs	Amphibians					
Gum/resin	Reptiles					
Sap	Mammals					
Fruits	Birds					
Seeds	Eggs in shell					
Nuts	Shelled eggs					
Nectar						
Flowers						
Pollen						
Moss						

Capítulo 3

Primates extinction risk: spatial, phylogenetic and biological components

Flávia de Figueiredo Machado[1,2]

Marcel Cardillo[3]

Rusell Dinnage[3]

Daniel de Brito Candido da Silva[1]

Authors' affiliations:

[1]Laboratório de Ecologia Aplicada e Conservação, Departamento de Ecologia, Universidade Federal de Goiás, Brazil.

[2]Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de Goiás, Brazil.

[3]Macroevolution & Macroecology Group, Research School of Biology, Australian National University, Australia.

ABSTRACT

Current extinction rates present high levels, moving towards a mass extinction event, being human activities the main responsible for that. Understanding why some species are more prone to extinction than others is an important goal of conservation biology and might contribute to prevent future declines. Although there are many studies about mammal extinction risk, most of them do not consider biological, phylogenetic and spatial components combined in the analysis. Ignoring phylogenetic or spatial signal leads to pseudo replication, which can lead to inaccurate interpretation of extinction risk s. In this study, we explored patterns of extinction risk in primates, using a method that partitions the variation in extinction risk into spatial, phylogenetic, and independent components. We found a spatial and phylogenetic pattern in extinction risk, where species that are spatial or phylogenetically close to each other will present similar extinction risk. Primates more susceptible to extinction are those with longer weaning age, diurnal crepuscular activity period, restricted range size, lower habitat breadth and living in the Madagascar region or in places that are more impacted by humans, with high precipitation and high NDVI. Besides that, our results also show that space is an important component of extinction risk, more than phylogeny and independent components. This study reinforce the importance of space in extinction risk and the necessity to consider it, as well as phylogeny, in extinction models. This kind of analysis can also be used to predict species threat status, contributing of their conservation.

Keywords: primates, extinction risk, conservation, phylogenetic signal, spatial signal.

INTRODUCTION

Extinction is the last step of the evolutionary process [Purvis et al., 2000a]. However, even though it is a natural process, present day anthropogenic activities increased extinction rates to mass extinction event levels [Pimm et al., 1995, 2014; Barnosky et al., 2011]. This rate of continuous species loss is moving towards a mass extinction event [Barnosky et al., 2011; Ceballos et al., 2015; De Vos et al., 2015], and human activities are the main cause of species decline [Dirzo et al., 2014; Pimm et al., 2014].

One of the main goals of conservation biology is to understand species extinction patterns and which attributes predisposes them to extinction [McKinney, 1997]. The first studies about extinction risk were interested in understanding how biological and ecological traits contribute to species extinction proneness [e.g. Bodmer et al., 1997; Jernvall & Wright, 1998]. However, the use of these predictors explain just a part of the extinction risk [Cardillo et al., 2008]. The remaining of this variation would be explained by the extrinsic factors and the interaction of them with the traits [Fisher et al., 2003; Cardillo et al., 2005; Price & Gittleman, 2007].

The control of phylogenetic signal is commonplace in extinction risk analyses, in order to avoid pseudo-replication, as species are not independent evolutionary units [Felsenstein, 1985]. However, environmental variables within a species distribution may be spatially auto correlated [Gaston et al., 2008]. This is usually ignored in extinction risk models, violating the statistical assumption of non-independence for data [Cardillo & Skeels, 2016]. Few extinction risk analysis consider both spatial and phylogenetic signal [Safi & Pettorelli, 2010; Jetz & Freckleton, 2015; Cardillo & Skeels, 2016]. Ignoring either

the spatial or phylogenetic signals increases the chances of pseudo-replication, and part of the extinction risk will not be explained.

Although previous studies explored extinction risk in mammals in general [e.g. [Brashares, 2003; Davidson et al., 2012; Farneda et al., 2015] and specifically in primates [Isaac & Cowlishaw, 2004; Kamilar & Paciulli, 2008], none of them considered both the spatial and the phylogenetic components investigating patterns in extinction risk. Jetz & Freckleton [2015] used an approach of partitioning the variance of extinction risk in order to predict mammal's threat status, but they were interested neither in the influence of each particular component nor how the predictors contribute to extinction risk individually.

Primates is a well-studied mammal order, with ecological and biological data available both quantitatively and qualitatively [Purvis et al., 2000b]. Furthermore, this order is of great interest to conservation biology, considering that 61% of all primate species are threatened [IUCN, 2017]. Understanding the causes of extinction is an important step to comprehend the current decline of species, allowing us predict future declines [Cardillo et al., 2008] and making possible the strategic planning for their conservation [Cardillo et al., 2004].

In this study, we explored patterns of extinction risk in primates, partitioning variation in extinction risk into spatial, phylogenetic, and independent components. We included species traits, geographical distribution, environmental variables and threats to investigate which contributes to some primates being more prone to extinction than others, and the influence of phylogeny, space and independent variables in the extinction risk.

METHODS

Predictor variables and variable selection

We compiled a traits database (see variables description in Table S1) for all 434 extant primates species [IUCN, 2017]. The traits database includes variables related with species' physical characteristics (i.e. body mass), reproductive traits associated with species reproductive rate (i.e. gestation length), and reproductive timing (i.e. weaning age) [Bielby et al., 2007]. We also included species' diet, which is known to be part of species spatial requirements [Santini et al., 2014], and habitat breadth (i.e. habitat used), as a measure of habitat specialization. Finally, we also included species dependence on the forest canopy (i.e terrestriality), as it can influence their susceptibility to specific threats, such as agriculture [Isaac & Cowlishaw, 2004], and species habit (i.e. diurnal, nocturnal, and crepuscular), because has it been observed that diurnal species tend to be more prone to extinction [Purvis et al., 2000b].

As our traits database contains missing data, we did data imputation. For habit and terrestrially, we used genus information. For all other traits (body mass, weaning age and gestation length), we used the missForest method [Stekhoven & Bühlmann, 2012], which performs data imputation using a random forest algorithm [Verde Arregoitia et al., 2013]. We performed data imputation including the primates' phylogeny of Springer et al. [2012], as missForest perform a better result using phylogeny [Penone et al., 2014]. For it, we obtained the phylogenetic eigenvectors to include as predictor, using only the first four of them, as this was the number with a minor error for all imputed traits. For all IUCN primates' species that were not in the tree used, we randomly inserted them in the clade node, 1.000 time, resulting in 1.000 trees. As the imputation error did not vary significantly between the different trees, we selected randomly one of them to do the imputation.

We also considered the region which each species occur (Neotropical, mainland Africa, Asia or Madagascar) [Estrada et al., 2017] and extrinsic factors related to environmental characteristics, ecological flexibility and human impact in the species range (see variables description in Table S1). For environmental characteristics and ecological flexibility, we selected variables which would be limiting species distribution: mean annual temperature, mean annual precipitation, minimum and maximum temperature, and NDVI (Normalized Difference Vegetation Index). We considered canopy height , as it has been observed as a good predictor of primate diversity [Gouveia et al., 2014]. As proxies of human impact, we included human population growth and density, human poverty, distance between major cities, forest cover lost and forest cover, and Human Footprint map. For all these variables, we extracted the mean value in each cell (0.5° x 0.5° resolution) within the species range.

For all predictor variables, we used the "powerTransform" function in library "car" for R, which finds a power to raise the data that maximizes a fit to a Gaussian distribution. To avoid including correlated variables we calculated the correlation between them. For all variables with a correlation higher than 0.8 we kept and used them in multimodel analysis to do variable exclusion based in AIC inference, keeping that with lowest AIC. Therefore, we used 16 variables instead of 23: range size, weaning age, gestation length, human footprint, human population growth, human poverty, distance between major cities, mean annual temperature, mean annual precipitation, maximum temperature, NDVI, tree cover lost, habit, diet, habitat, terrestriality, and region. We also included interactions between traits and extrinsic variables, region and traits and between traits and extrinsic variables.

Data analyses

We used the IUCN Red List status (here after referred to as "threat status") as a response variable, where each category was transformed into a number, varying from 0 (Least Concern), 1 (Near Threatened), 2 (Vulnerable), 3 (Endangered) to 4 (Critically Endangered).

We tested the relation between the predictors and threat status using a GLS ("Generalized least-squares") model [Freckleton & Jetz, 2008]. In this model, the variance is partitioned in phylogenetic, spatial and independent components (neither phylogenetic nor spatial). The model is represented by the equation:

$$\boldsymbol{V}(\phi, \lambda) = \gamma \boldsymbol{h} + \lambda' \sum + \phi \boldsymbol{W}$$

Where $\sum$ is a variance-covariance matrix describing the phylogenetic distances among species, W is a variance-covariance matrix describing the spatial distances among species, and h is a vector of tip heights from the phylogeny. The phylogenetic component is obtained by Pagel's measure of phylogenetic signal (λ) [Pagel, 1999], which is represented by $\lambda' = (1 - \phi)\ \lambda$. The spatial component is given by ϕ, and $(1 - \phi)$ is the non-spatial component. The part that is not explained by space or phylogeny is the independent component, given by $\gamma = (1 - \phi)\ (1 - \lambda)$.

We generated the Primates phylogenetic matrix using the function "vcv.phylo" in the "ape" library for R [Paradis et al., 2004]. To obtain the spatial matrix we calculated the distance between each species from the centroids, using the "earth.dist" function in the "fossil" package [Vavrek, 2011] for R. We used the "regress" function from the "regress" package [Clifford and McCullagh, 2006] for R to estimate the spatial, phylogenetic, and independent component in the GLS model.

To fit the models, we ran univariate tests including the phylogeny and space together to see the influence of each predictor independently of each other, and of

phylogeny and space. After that, we ran a multivariate model with all predictors, including the interactions, and we simplified it in a Minimum Adequate Model (MAM) where all predictors were significant. We used Akaike Information Criterion (AIC) to compare which model better explain Primates extinction risk (predictor + space + phylogeny; predictor + space; predictor + phylogeny; phylogeny + space; or only predictor).

RESULTS

The phylogenetic and spatial pattern in the distribution of threat status are represented in the Figure 1 and Figure 2, respectively. There is a pattern in the phylogenetic distribution of threat status, where closely-related species present similar threat status (Figure 1). This pattern is corroborated by the high phylogenetic signal observed in the threat status ($\lambda = 0.64$, $p < 0.001$). There is also a spatial pattern in threat distribution. However, it is no high (Moran's $I = - 0{,}054$, $p < 0.001$). It is possible to observe some "hotspots" of elevated extinction risk. These "hotspots" are more concentered in the extremities of the Primates distribution, mainly in the mainland Africa and Asia regions.

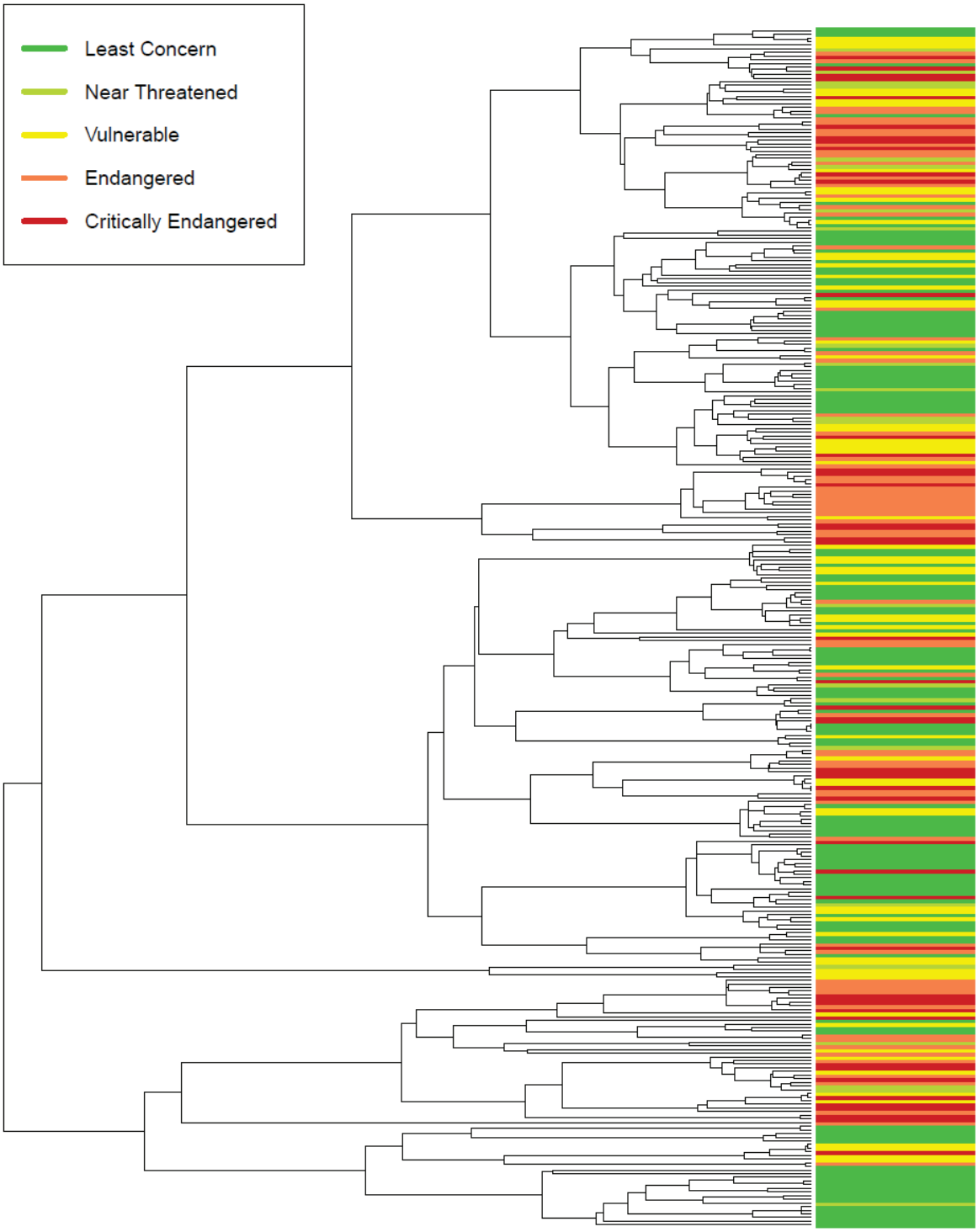

Figure 1. Phylogenetic pattern in the distribution of threat status.

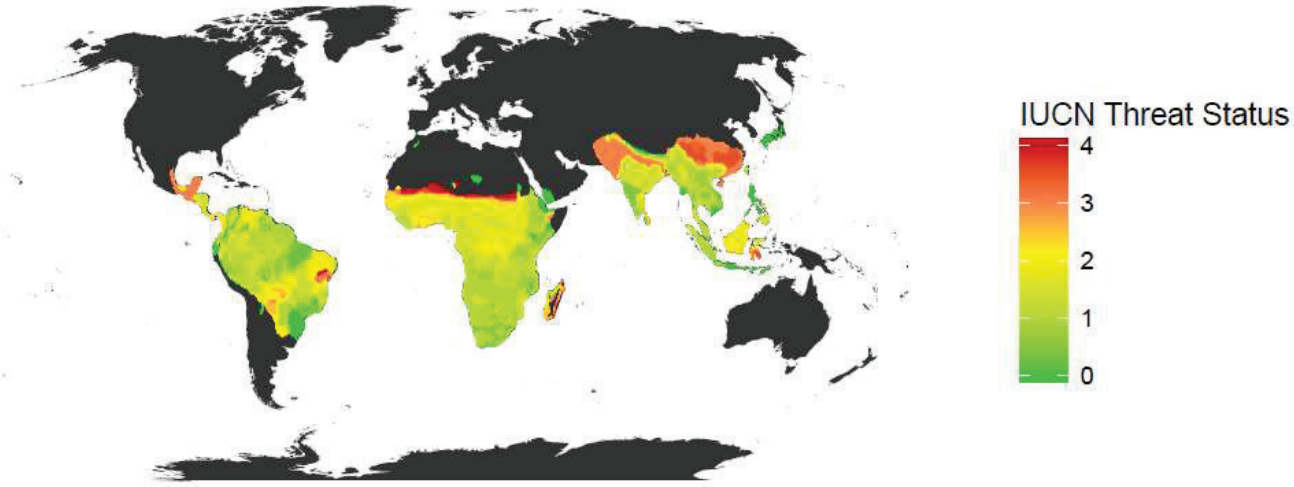

Figure 2. Spatial pattern in the distribution of extinction risk. The values represents the average of species threat status per 0.5° x 0.5° grid cell, where 0 is (Least Concern), 1 (Vulnerable), 2 (Near Threatened), 3 (Endangered), and 4 (Critically Endangered).

The results did not present a significant difference between the different phylogenetic trees generated (Figure S1), then we show the results for one of them chosen randomly. The predictors significantly related with extinction risk, independently of phylogeny and space were: range size, weaning age, human footprint, human population growth, human poverty, distance between major cities, mean annual precipitation, NDVI, and habitat (Table 1).

Table 1. Results of univariate test, showing the importance of each predictor, independently of each other, phylogeny, and space.

Predictor	Intercept	Slope estimate	Slope s.e.	p
Range size*	1.536	-0.8194	0.0624	< 0.001
Weaning age*	1.7302	0.6622	0.101	< 0.001
Gestation length	1.468	0.1819	0.1005	0.2372
Human footprint*	1.523	0.3904	0.1075	0.0028
Human population growth*	1.5048	-0.2654	0.097	0.0396
Human poverty*	1.1974	-0.3708	0.17	0.0161
Distance between major cities*	1.6526	-0.3743	0.0905	0.0005
Mean annual temperature	1.4958	-0.0732	0.0925	0.5958
Maximum temperature	1.5217	-0.1874	0.0882	0.1534
Mean annual precipitation*	1.2622	0.2588	0.0993	0.0468
Tree cover	1.4658	0.0035	0.1044	0.5958
Tree cover loss	1.4595	0.063	0.089	0.5958
NDVI*	1.2962	0.2679	0.1008	0.0468
Habit	2.9641	-1.7767	0.9542	0.1165
Diet	0.1768	1.6413	0.9311	0.1741
Habitat*	1.6818	-0.1358	0.2099	0.0059
Terrestriality	1.4922	-0.5326	0.5383	0.4756
Region	-0.4367	1.6985	0.7551	0.3857

*variables significantly related with primates extinction risk.

In the multipredictor model, human population growth, human poverty and NDVI dropped out of the model with $p > 0.05$, but two other variables were significant: habit and region. Four variables and two interactions also were significant in this model: range size, human accessibility, weaning age, tree cover loss, human footprint: region, and tree cover

loss: range size. We used these variables and interactions to future analyses and to model comparison.

The predictors and interaction that remained significant, composing the minimum adequate model (MAM), were range size, weaning age, human footprint, habit, region, region, and range size: weaning age (Table 2).

Table 2. Predictors that remained significant in the multipredictors models, composing the minimum adequate model (MAM).

Predictor	chi test	p	Estimate	Error
Range size	122.4476	<0.01	-0.725	0.058
Weaning age	23.8214	<0.01	0.542	0.102
Human footprint	10.1423	0.0014	0.261	0.082
Habit	12.2010	0.0321	-	-
Habit crepuscular diurnal	-	-	-1.968	0.729
Habit diurnal	-	-	-0.797	0.600
Habit nocturnal	-	-	-0.689	0.652
Habit crepuscular	-	-	1.043	1.383
Habit nocturnal crepuscular	-	-	-0.161	1.125
Habit nocturnal crepuscular diurnal	-	-	0.306	1.014
Region	10.2289	0.0167	-	-
Region Asia	-	-	1.29	0.532
Region Madagascar	-	-	1.749	0.818
Region Neotropics	-	-	1.610	1.091
Region mainland Africa	-	-	1.043	1.383
Range size: weaning age	5.2425	0.0220	-0.131	0.059

The best model to explain primate extinction risk was the one that include the predictors, phylogeny and space (Table 3). The second best model includes phylogeny and

space. The worst model excludes the predictors and keeps phylogeny and space. The best model explains 50% of all variation found in primates extinction risk (Table 3). In this model, space is the most important component, and the phylogenetic and independent components presents similar contribution (Table 3).

Table 3. Model comparison. The model that better explain the Primates extinction risk is the one that include the predictors, space and phylogeny.

Model	AIC	R^2	Variance components		
			Independent (γ)	Phylogenetic (λ')	Space (ϕ)
Predictors only	317.9306	0.6083	-	-	-
Predictors + space	297.4262	0.4862	0.1785	-	0.8215
Predictors + phylogeny	293.6435	0.5884	0.4492	0.4308	-
Phylogeny + space	450.8368	-0.0239	0.0572	0.1200	0.8228
Predictors + space + phylogeny	276.0307	0.5037	0.1585	0.1846	0.6570

DISCUSSION

In this work we found a spatial and phylogenetic pattern in the extinction risk of primates. Our results indicate that primate species tend to have a higher extinction risk if they have older weaning age, diurnal/crepuscular activity period, restricted range size, small habitat breadth, and if they live in Madagascar or in places with high human impact, with higher precipitation, and high NDVI. We also found that space is highly important in primate extinction risk, being more important than phylogenetic and independent components.

We found that spatially and/or phylogenetically close species present similar threat status. Phylogenetically related species will have similar life history traits, and then share traits that contribute to be more prone to extinction. For example, closer species will present similar weaning age, an important trait to extinction risk, as ours results showed. This trait show a strong phylogenetic signal ($\lambda = 0.95$, $p < 0.001$), justifying the clustered phylogenetically pattern observed in extinction risk.

The same way, spatially close species will live in similar environmental conditions and may be subject to the same local threats. Interestingly, the higher threat status are concentrated in the extremities of the Primates distribution, mainly in the mainland Africa and Asia regions. In these places, the main threats to primates are agriculture, hunting and trapping and logging and wood harvesting [Estrada et al., 2017]. Is possible that the extremities of these regions are more impacted by those threats.

In order to highlight the importance of the spatial component, primate extinction risk varies according with the region the species occurs. Madagascar is the worst region for a primate. It presents the higher primate diversity in the world and also the largest number of threatened species [Estrada et al., 2017] and primates suffer with agriculture expansion, hunting and trapping [Estrada et al., 2017].

Range size, weaning age and habit were the only variables from species related to extinction risk in the univariate tests. Range size has been related with extinction risk [e.g. Cardillo et al., 2008; Davidson et al., 2009; Redding et al., 2010; Di Marco et al., 2014] as restrict distribution is associate with small population and in case of be overlapping by high human impact the species will be in high risk. A long weaning age is a proxy to slow life history, meaning slow population growth. A population with slow growth presents a low renewal rate of individuals, taking more time to reestablish in face environmental

perturbations [Owens & Bennett, 2000; Purvis et al., 2000b]. Slow life history like weaning age was related with extinction risk in other studies [e.g. Price & Gittleman, 2007; Fritz et al., 2009; Hanna & Cardillo, 2013]. The interaction between longer weaning age and restricted range size may be even worse to primates extinction, as we showed in our results.

Di Marco & Santini [2015], in a global analysis to compare the power of traits and extrinsic factors like human impact and environmental variables to predict mammal range size, found that extrinsic factors influence more the size of the range than species traits. The variables temperature, precipitation, human population density and accessibility from humans (i.e. distance between major cities) were associated with smaller species ranges. These factors are a kind of human encroachment and contribute to habitat loss and restriction of mammal distribution [Hoffmann et al., 2011]. Geographic range size is directly related to extinction risk [Rabinowitz, 1981], limiting the species abundance and determining how the species will deal with stochastic events [Purvis et al., 2000a; Ceballos & Ehrlich, 2002; Diniz-Filho et al., 2005].

Human footprint, human population growth, human poverty and the distance between major cities were all threats significantly related to extinction risk. Human footprint covers different human impacts like built environments, croplands, pasture lands, population density and others. These human impacts contribute to decrease the areas available to primates. Besides that, human population growth, human poverty and the distance between major cities would be related to increase of primates hunting. Poor population tend to live in fragile habitat (many being highest conservation priority, probably many of them inhabited by primates), depending of natural resources to survive [Hines, 1998].

Restricted habitat and high mean annual temperature also predicted high extinction risk. Environmental variables and habitat type delimit the species niche and then its distribution. High annual precipitation would be limiting primates ranges favoring its vulnerability to extinction. High seasonality in precipitation was associated with small ranges in mammals in general [Di Marco & Santini, 2015] and also in amphibians [Whitton et al., 2012]. Primates living in fewer habitats types showed higher extinction risk, as observed in Kamilar & Paciulli [2008]. Species more specialists and with higher habitat restriction trend to be more rare [Harcourt & Coppeto, 2002], due its inability to explore more habitats in case of habitat perturbations.

Contrary as we expected, primates living in areas with a higher NDVI are more prone to extinction. We expected to find a higher risk in areas with smaller NDVI, less productive, as low productive areas tend to present less biodiversity. This relation is not so clear, but a possibility is that the range distribution of threatened species would be confined in productive areas.

The primates habit influenced its susceptibility to extinction, with diurnal and crepuscular species less vulnerable, contrary to what we expected. It would be expected that higher activity during the day makes the species more prone to extinction, as observed by Purvis et al. [2000b], mainly by direct human impact as hunting, because these species are more easily observed. However, is possible that this pattern is related with the hunter behavior, that prefer to hunt at night avoiding to be seen. This period, nocturnal primates are easier to be finding. This relation is not clear and need to be more investigated.

As Jetz and Freckleton [2015] and Safi and Pettorelli [2010] found, the phylogenetic and spatial components were important in our models. The space was the most important, then the predictors selected suffer a greater influence of space than the

phylogeny and other variables here not represented (independent component). Except by range size, weaning age and habit, all other important predictors are environmental characteristics or threats. These change in each place exercising great influence in the extinction risk. Although biological traits are important predictors to extinction risk, how the species respond to it depend on the threats that are exposed, being the traits mediating this exposition [Cardillo et al., 2004].

This study reinforces the importance to consider phylogenetic and spatial components in extinction risk analyses. Their omission, besides incurring in autocorrelations errors, the estimate of extinction risk may be wrong. As the importance of space and phylogeny in primate's extinction risk, is possible to reproduce these models to predict the status of data deficient species, using biological/ecological, environmental and threats information. This, beyond to extend the knowledge of the group, can contribute to conservations plans.

REFERENCES

Barnosky AD, Matzke N, Tomiya S, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature [Internet] 471:51–57. Available from: http://www.ncbi.nlm.nih.gov/pubmed/21368823

Bielby J, Mace GM, Bininda-Emonds ORP, et al. 2007. The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. The American Naturalist [Internet] 169:748–757. Available from: http://www.journals.uchicago.edu/doi/10.1086/516847

Bodmer RE, Eisenberg JF, Redford KH. 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology 11:460–466.

Brashares JS. 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. Conservation Biology 17:733–743.

Cardillo M, Mace GM, Gittleman JL, et al. 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proceedings. Biological sciences / The Royal Society 275:1441–1448.

Cardillo M, Mace GM, Jones KE, et al. 2005. Multiple causes of high extinction risk in large mammal species. Science (New York, N.Y.) 309:1239–1241.

Cardillo M, Purvis A, Sechrest W, et al. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology 2:909–914.

Cardillo M, Skeels A. 2016. Spatial, Phylogenetic, Environmental and Biological Components of Variation in Extinction Risk: A Case Study Using Banksia. Plos One [Internet] 11:e0154431. Available from: http://dx.plos.org/10.1371/journal.pone.0154431

Ceballos G, Ehrlich PR. 2002. Mammal Population Losses and the Extinction Crisis. Science 296:904–907.

Ceballos G, Ehrlich PR, Barnosky AD, et al. 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. Sciences Advances 1:1–5.

Clifford D, McCullagh P. 2006. The regress function. R News 6:6–10.

Davidson AD, Boyer AG, Kim H, et al. 2012. Drivers and hotspots of extinction risk in marine mammals. Proceedings of the National Academy of Sciences [Internet] 109:3395–3400. Available from: http://www.pnas.org/content/109/9/3395.abstract%5Cnhttp://www.pnas.org/content/109/9/3395.full.pdf

Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G. 2009. Multiple ecological pathways to extinction in mammals. Proceedings of the National Academy of Sciences of the United States of America 106:10702–10705.

Diniz-Filho JAF, Carvalho P, Bini Mauricio L, Tôrres NM. 2005. Macroecology , geographic range size – body size relationship and minimum viable population analysis for new world carnivora. Acta Oecologica 27:25–30.

Dirzo R, Young HS, Galetti M, et al. 2014. Defaunation in the Anthropocene. Science [Internet] 345:401–406. Available from: http://www.sciencemag.org/cgi/doi/10.1126/science.1251817%5Cnhttp://www.sciencemag.org/content/345/6195/401.short

Estrada A, Garber PA, Rylands AB, et al. 2017. Impending extinction crisis of the world's primates: Why primates matter. Science Advances 3.

Farneda FZ, Rocha R, López-Baucells A, et al. 2015. Trait-related responses to habitat fragmentation in Amazonian bats. Journal of Applied Ecology 52:1381–1391.

Felsenstein J. 1985. Phylogenies and the Comparative Method. The American Naturalist [Internet] 125:1–15. Available from: http://search.ebscohost.com/login.aspx?direct=true&db=bth&AN=96338264&lang=es&site=ehost-live

Fisher DO, Blomberg SP, Owens IPF. 2003. Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. Proceedings. Biological sciences / The Royal Society 270:1801–1808.

Freckleton RP, Jetz W. 2008. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. Proceedings. Biological sciences / The Royal Society 276:21–30.

Fritz SA, Bininda-Emonds ORP, Purvis A. 2009. Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. Ecology Letters 12:538–549.

Gaston KJ, Chown SL, Evans KL. 2008. Ecogeographical rules: Elements of a synthesis. Journal of Biogeography 35:483–500.

Gouveia SF, Villalobos F, Dobrovolski R, Beltrão-Mendes R, Ferrari SF. 2014. Forest structure drives global diversity of primates. Journal of Animal Ecology 83:1523–1530.

Hanna E, Cardillo M. 2013. A comparison of current and reconstructed historic geographic range sizes as predictors of extinction risk in Australian mammals. Biological Conservation [Internet] 158:196–204. Available from: http://dx.doi.org/10.1016/j.biocon.2012.08.014

Harcourt AH, Coppeto SA. 2002. Rarity, specialization and extinction in primates (vol 29, pg 445, 2002). 29:1717–1717.

Hines D. 1998. Strategy and policy division UN WFP. Improving food security in marginal, low-potential areas.

Hoffmann M, Belant JL, Chanson JS, et al. 2011. The changing fates of the world's

mammals. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 366:2598–2610.

Isaac NJB, Cowlishaw G. 2004. How species respond to multiple extinction threats. Proceedings of the Royal Society B: Biological Sciences [Internet] 271:1135–1141. Available from: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2004.2724

IUCN. 2017. Available from: http://www.iucnredlist.org/

Jernvall J, Wright PC. 1998. Diversity components of impending primate extinctions. Proceedings of the National Academy of Sciences [Internet] 95:11279–11283. Available from: http://www.pnas.org/cgi/doi/10.1073/pnas.95.19.11279

Jetz W, Freckleton RP. 2015. Towards a general framework for predicting threat status of data-deficient species from phylogenetic, spatial and environmental information. Philosophical Transactions of the Royal Society B: Biological Sciences [Internet] 370:20140016–20140016. Available from: http://rstb.royalsocietypublishing.org/cgi/doi/10.1098/rstb.2014.0016

Kamilar JM, Paciulli LM. 2008. Examining the extinction risk of specialized folivores: A comparative study of colobine monkeys. American Journal of Primatology 70:816–827.

Di Marco M, Santini L. 2015. Human pressures predict species' geographic range size better than biological traits. Global Change Biology [Internet] 21:2169–2178. Available from: http://doi.wiley.com/10.1111/gcb.12834

McKinney ML. 1997. Extinction Vulnerability and Selectivity: Combining Ecological and Paleontological Views. Annual Review of Ecology and Systematics [Internet] 28:495–516. Available from: http://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.28.1.495%5Cnhttp://www.annualreviews.org/doi/pdf/10.1146/annurev.ecolsys.28.1.495

Owens IP, Bennett PM. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America [Internet] 97:12144–8. Available from: http://www.pnas.org.libproxy.lib.unc.edu/content/97/22/12144.short

Pagel M. 1999. Inferring the historical patterns of biological evolution. Nature [Internet] 401:877. Available from: http://dx.doi.org/10.1038/44766

Paradis E, Claude J, Strimmer K. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Penone C, Davidson AD, Shoemaker KT, et al. 2014. Imputation of missing data in life-history trait datasets: Which approach performs the best? Methods in Ecology and Evolution 5:1–10.

Pimm SL, Jenkins CN, Abell R, et al. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science (New York, N.Y.) [Internet] 344:1246752. Available from: http://www.ncbi.nlm.nih.gov/pubmed/24876501

Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The Future of Biodiversity. Science [Internet] 269:347–350. Available from: http://www.ncbi.nlm.nih.gov/pubmed/17841251

Price SA, Gittleman JL. 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. Proceedings of the Royal Society B: Biological Sciences [Internet] 274:1845–1851. Available from: http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2007.0505

Purvis A, Jones KE, Mace GM. 2000a. Extinction. Bioessay 22:1123–1133.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000b. Predicting extinction risk in declining species. Proceedings. Biological Sciences / The Royal Society 267:1947–1952.

Rabinowitz D. 1981. Seven forms of rarity. In: Hugh Synge, editor. The biological aspects of rare plant conservation. Chichester, UK: John Wiley & Sons. p 205–217.

Redding DW, Dewolff C V., Mooers a. Ø. 2010. Evolutionary distinctiveness, threat status, and ecological oddity in primates. Conservation Biology 24:1052–1058.

Safi K, Pettorelli N. 2010. Phylogenetic, spatial and environmental components of extinction risk in carnivores. Global Ecology and Biogeography 19:352–362.

Santini L, Di Marco M, Boitani L, Maiorano L, Rondinini C. 2014. Incorporating spatial population structure in gap analysis reveals inequitable assessments of species protection. Diversity and Distributions 20:698–707.

Springer MS, Meredith RW, Gatesy J, et al. 2012. Macroevolutionary Dynamics and Historical Biogeography of Primate Diversification Inferred from a Species Supermatrix. PLoS ONE 7.

Stekhoven DJ, Bühlmann P. 2012. Missforest-Non-parametric missing value imputation for mixed-type data. Bioinformatics 28:112–118.

Vavrek MJ. 2011. Fossil: Palaeoecological and Paelaeogeogrpahical Analysis Tools. Palaeontologia Electronica [Internet] 14:1–16. Available from: http://palaeo-electronica.org/2011_1/238/index.html

Verde Arregoitia LD, Blomberg SP, Fisher DO. 2013. Phylogenetic correlates of extinction risk in mammals: species in older lineages are not at greater risk. Proceedings. Biological sciences / The Royal Society [Internet] 280:20131092. Available from: http://www.ncbi.nlm.nih.gov/pubmed/23825210

De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL. 2015. Estimating the normal background rate of species extinction. Conservation Biology [Internet] 29:452–462. Available from: http://doi.wiley.com/10.1111/cobi.12380

Whitton FJS, Purvis A, Orme CDL, Olalla-tárraga MÁ. 2012. Understanding global patterns in amphibian geographic range size : does Rapoport rule? Global Ecology and Biogeography 21:179–190.

SUPPORTING INFORMATION

Table S1. Description of all variables used in the analysis.

Variable	Description	Source
Body mass	Life-history and ecologital requirements trait	Mittermeier et al. [2013], Myhrvold et al. [2015], Wilman et al. [2014]
Diet	Diet category: frugivore (>50% of fruits and seeds), folivore (>50% of other plant parts), frugivore-folivore (50% of fruits and seeds and 50% of other plant parts), gumnivore (>50% of gums or other exudates), carnivore (composed exclusively by animal matter), and omnivore (composed of animal and plant matter).	Wilman et al. [2014]
Gestation length	Parameter of reproductive rate	Myhrvold et al. [2015], Mittermeier et al. [2013]
Weaning age	Parameter of reproductive timing	Myhrvold et al. [2015], Mittermeier et al. [2013], Tucutu et al. [2013]
Habitat	Macrohabitat categories preference: Forest, Savanna, Shrubland, Grassland, Wetlands, Rocky areas, Caves and Subterranean Habitats, Artificial, Other, Unknown, or two or more of these categories.	IUCN [2017]
Terrestriality	Foraging stratum categories: Scansorial, arboreal, and aerial	Wilman et al. [2014]
Habit	Activity period: diurnal, nocturnal, and crepuscular	Wilman et al. [2014]
Mean annual temperature	Mean annual temperature	Fick & Hijmans, 2017
Mean annual precipitation	Mean annual precipitation	As above
Minimum temperature	Mean minimum temperature	As above

Table S1. Continuation.

Variable	Description	Source
Maximum temperature	Mean maximum temperature	As above
NDVI	Normalized Difference Index, proxy of primary productivity. The mean of the values registered bewteen 2010 and 2016 were used.	https://neo.sci.gsfc.nasa.gov/view.php?datasetId=M(
Canopy height	Global forest hight, proxy for vertical forest structure	https://webmap.ornl.gov/wcsdown/wcsdown.jsp?dg_
Human population growth	Human population growth, proportional increase in humane population between 2010 and 2015	CIESIN [2016]
Human population density	Human population density registered in the year 2015	As above
Human poverty	The Global Subnational Infant Mortality Rates, estimates of infant mortality rates for the year 2000, proxy of human poverty	CIESIN [2005]
Tree cover	Percentage tree cover registered in year 2000	Hansen et al. [2013]
Tree cover loss	Tree cover loss registered between 2010 and 2016	As above

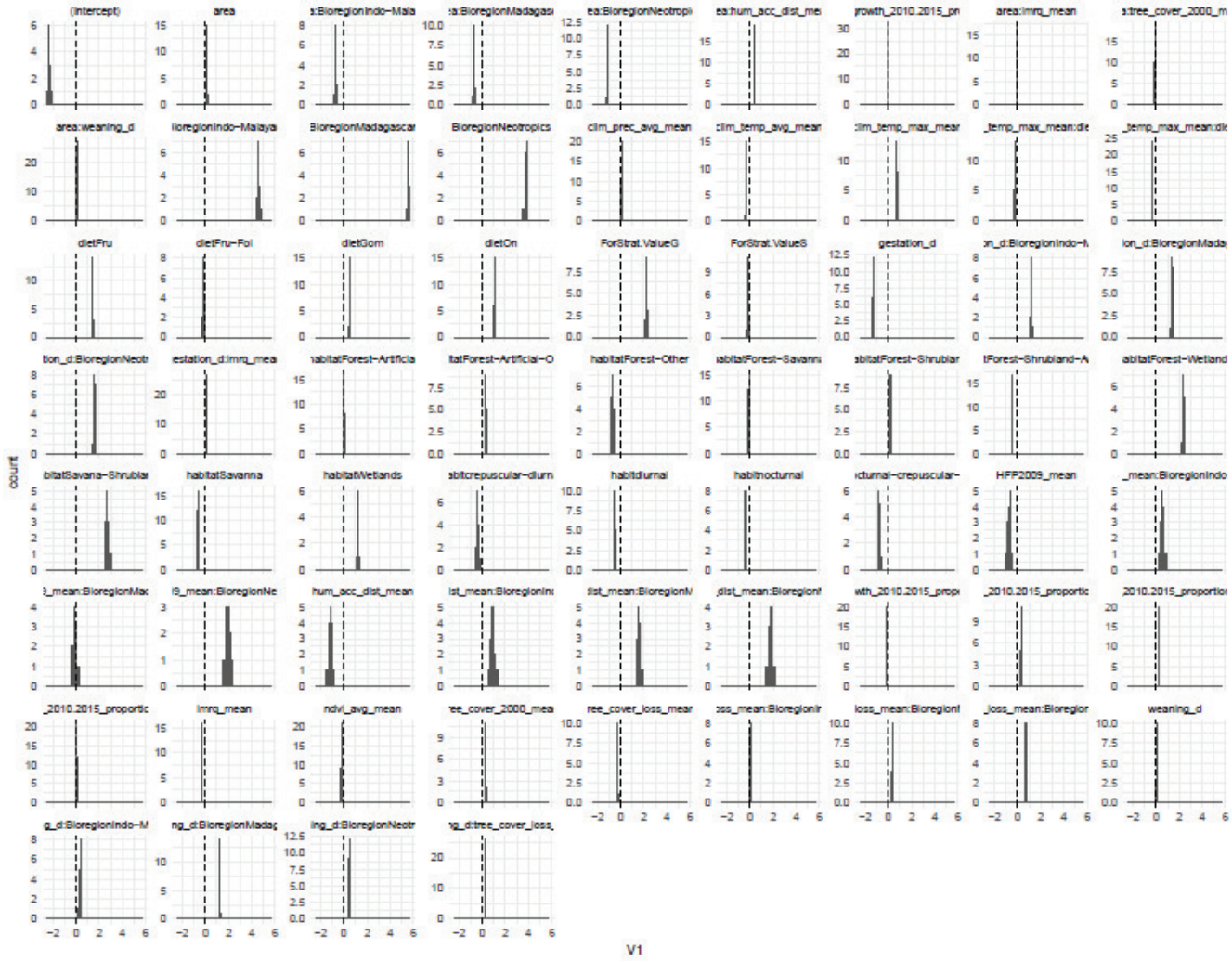

Figure S1. Graphic representation of the p values obtained in the models for each predictor for the 1.000 trees generated randomly. Here is possible to see that the p values do not change significantly to each tree.

REFERENCES

Center for International Earth Science Information Network - CIESIN - Columbia University. 2005. Poverty Mapping Project: Global Subnational Infant Mortality Rates. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC).

Center for International Earth Science Information Network - CIESIN - Columbia University. 2016. Gridded Population of the World, Version 4 (GPWv4): Population Density. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC).

Fick SE, Hijmans RJ. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology.

Hansen MC, Potapov PV, Moore R et al. 2013. High-resolution global maps of 21st-century forest cover change. Science, 342, 850–853.

Mittermeier RA, Rylands AB, Wilson DE (eds.). 2013. Handbook of the Mammals of the World - Volume 3: Primates. Barcelona: Lynx Edicions. 950p.

Myhrvold NP, Baldridge E, Chan B, et al. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology [Internet] 96:3109–0. Available from: http://doi.wiley.com/10.1890/15-0846R.1

Wilman H, Belmaker J, Simpson J, et al. 2014. EltonTraits 1.0: species-level foraging attributes of the world' s birds and mammals. Ecology, 95, 2027

CONCLUSÃO GERAL

Ao final desta tese foram obtidas as seguintes conclusões:

Capítulo 1

- Os estudos de conservação com primatas têm aumentado na primatologia, mas não na área de conservação de forma geral.
- A fragmentação de habitat é o tema mais recorrente nas pesquisas e atropelamento o menos abordado.
- A maior parte das pesquisas é empírica, seguido por pesquisas teóricas e de revisão.
- As Universidades são as instituições que mais executam as pesquisas de conservação com primatas.
- Essas pesquisas são conduzidas principalmente em áreas protegidas e áreas naturais não protegidas.
- Dos 49 países que lideraram pesquisas empíricas relacionadas à conservação de primatas, os Estados Unidos possui o maior número de trabalhos, apesar de não ser área de ocorrência de nenhuma espécie de primata não humano.
- Dos 55 países que foram área de estudo para essas pesquisas, Madagascar e Indonésia lideram com o maior número de estudos.
- Existe um padrão filogenético nos esforços de pesquisa, onde espécies mais próximas filogeneticamente recebem atenção semelhante.
- A espécie com maior número de estudos foi *Pan troglodytes* (80 artigos) e 102 espécies (27% de todos os primatas) não foram representadas nos esforços de pesquisas.

- A alocação dos esforços de pesquisa com conservação de primatas não é motivada pelo status de conservação das espécies e pelo tamanho da sua distribuição geográfica, mas sim pelo seu peso corporal e idade (tempo desde a sua descrição).

Capítulo 2

- A dieta de primatas pode predizer o risco de extinção das espécies, mas apenas quando avaliada pela métrica de disparidade de itens.
- As demais métricas de dieta (amplitude de dieta, diversidade de dieta e tipo de dieta) não mostraram efeito na predição do risco de extinção.
- Primatas que possuem dieta com baixa disparidade de itens tendem a possuir status de ameaça mais elevado do que aqueles de dieta com maior disparidade. Isso sugere que as espécies capazes de consumir itens mais distintos entre si tendem a serem menos propensos à extinção.
- Espécies de maior peso corporal e menor área de distribuição geográfica tendem a apresentar maior risco de extinção.

Capítulo 3

- Existe um padrão espacial e filogenético no risco de extinção em primatas, onde espécies mais próximas na filogenia e no espaço tendem a apresentar status de ameaça semelhantes.
- Existem alguns "hotspots" de elevado status de ameaça dentro da distribuição dos primatas, com maior concentração na extremidade da distribuição do grupo, especialmente nas regiões "mainland Africa" e Ásia.
- Independentemente da filogenia e do espaço, os preditores significantemente

relacionados ao risco de extinção foram: tamanho da distribuição geográfica, tempo de desmame, "human footprint", crescimento populacional humano, pobreza humana, distância entre as principais cidades, precipitação anual média, NDVI e habitat da espécie.

- Na análise multivariada, incluindo a filogenia e o espaço, os preditores significantemente relacionados ao risco de extinção foram: tamanho da distribuição geográfica, tempo de desmame, "human footprint", região e a interação entre região e tempo de desmame.
- O modelo incluindo o espaço, a filogenia e os preditores foi o melhor modelo e foi capaz de explicar 50% da variação encontrada no risco de extinção em primatas. Nesse modelo, o componente espacial foi o de maior importância e os componentes filogenético e independente tiveram contribuição semelhante para o risco de extinção.

Em resumo, nessa tese mostramos que as pesquisas na área de conservação de primatas não refletem as reais necessidades de conservação, já que os esforços de pesquisas não estão relacionados ao status de ameaça das espécies e o tamanho da sua área de distribuição. Discutimos que a dieta pode ser um bom preditor do risco de extinção de primatas, mas dependendo da forma como ela for mensurada. Mostramos também que primatas próximos no espaço e na filogenia tendem a apresentar status de ameaça semelhantes e que o espaço é um importante componente do risco de extinção do grupo, não devendo ser desconsiderados nesse tipo de análise.