UNIVERSIDADE ESTADUAL PAULISTA “JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – DEPARTAMENTO DE ECOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

Victor Gasperotto Krepschi

Respostas espaço-temporais de mamíferos de médio e grande porte em paisagens modificadas de Cerrado do nordeste do estado de São Paulo

Tese apresentada ao Instituto de Biociências da UNESP de Rio Claro, como parte das exigências para a obtenção do título de Doutor em Ecologia e Biodiversidade

RIO CLARO – SP

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TÍTULO DA TESE: Respostas espaço-temporais de mamíferos de médio e grande porte em paisagens modificadas de Cerrado do nordeste do estado de São Paulo

AUTOR: VICTOR GASPEROTTO KREPSCHI
ORIENTADOR: ADRIANO GARCIA CHIARELLO
COORIENTADOR: MILTON CEZAR RIBEIRO
COORIENTADOR: SILVIO FROSINI DE BARROS FERRAZ

Aprovado como parte das exigências para obtenção do Título de Doutor em ECOLOGIA E BIODIVERSIDADE, especialidade: Biodiversidade pela Comissão Examinadora:

Prof. Dr. ADRIANO GARCIA CHIARELLO
Departamento de Biologia / USP - Faculdade de Ciências e Letras de Ribeirão Preto - SP

Profa. Dra. KATIA MARIA PASCHOALETTO MICCHI DE BARROS FERRAZ
Departamento de Ciências Florestais / USP - Escola Superior de Agricultura Luiz de Queiroz - Piracicaba/SP

Davi Rodrigo Rossatto
Prof. Dr. DAVI RODRIGO ROSSATTO
Departamento de Biologia Aplicada a Agropecuária / UNESP - Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal - SP

Prof. Dr. RONALDO GONÇALVES MORATO
CENAP / Instituto Chico Mendes de Conservação da Biodiversidade - Atibaia/SP

Paulo Bobrowiec
Prof. Dr. PAULO ESTEFANO DINELI BOBROWIEC
Coordenação de Biodiversidade / Instituto Nacional de Pesquisas da Amazônia - Manaus/AM

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Dedico essa tese aos professores e orientadores acadêmicos, os quais dispõe de preciosos momentos de suas vidas à preparação de seus discípulos acadêmicos.

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Resumo

O efeito da redução do habitat natural na biodiversidade é idiossincrática a respeito das relações que se estabelecem entre as espécies e as características das paisagens modificadas pelo homem. Nesse contexto, as evidências científicas evidenciam cada vez mais a importância de se utilizar não somente a escala espacial na interpretação das respostas da biodiversidade, mas também a escala temporal. A correlação dos parâmetros biológicos atuais com características do ambiente pretérito mostra que respostas atrasadas das espécies às modificações podem ocorrer após um distúrbio ambiental, o que como consequência, gera interpretação errôneas da relação das espécies com os ambientes da paisagem no presente, o que vem a comprometer as subsequentes tomadas de decisão de viés conservacionista. A fim de compreender como espécies de mamíferos de médio e grande porte neotropicais estão respondendo à paisagens de Cerrado que passaram por redução de habitat ao longo de um intervalo temporal de 48 anos, a presente tese objetivou em seus capítulos: (i) caracterizar a trajetória e a transição das classes de cobertura e uso do solo de três paisagens modificadas pelo homem, (ii) Detectar a existência de respostas atrasadas de sete espécies de mamíferos neotropicais de médio e grande porte em relação ao ambiente nativo dessas três paisagens e (iii) detectar a existência de limiares ecológicos nas respostas de seis espécies de mamíferos neotropicais a ambientes nativo e antrópico. As três paisagens de estudo estão compreendidas na região nordeste do estado de São Paulo e possuem remanescentes de vegetação nativa de Cerrado e de Mata Atlântica sob diferentes graus de proteção ambiental. A partir dos limites das áreas protegidas criou-se uma zona de amortecimento de cinco quilômetros a fim de delimitar a extensão das paisagens a serem estudadas. As classes de cobertura e uso do solo dessas paisagens foi criada a partir de fotointerpretação de imagens aéreas, retroativamente no tempo, nos anos de 2010, 1983 e 1962. Foram determinadas 206 paisagens focais circulares de 200ha nas paisagens de estudo, de forma aleatória e igualmente distribuídas dentro e fora de áreas protegidas, a fim de se calcular a proporção das classes de cobertura e uso do solo em cada paisagem focal. Dessa forma, caracterizaram-se a trajetória de cada classe de cobertura e uso do solo e a transição das classes de vegetação nativa de cada paisagem, entre os períodos e entre as paisagens. Para a amostragem biológica de mamíferos de médio e grande porte foi instalada uma armadilha fotográfica durante 30 dias consecutivos em cada uma dessas paisagens focais para obtenção de registros fotográficos das espécies. Os registros de sete espécies foi individualmente estruturados em históricos de captura de 6 ocasiões de 5 dias, que juntamente com as covariáveis de paisagem específica de cada espécie, foi utilizado para as análises de respostas atrasadas (Capítulo 2) e de limiares ecológicos (Capítulo 3). O método de estimativa de ocupação considerando a detecção imperfeita de espécies, na estrutura de espécie única e estação única foi empregado para essas duas análises. Os principais resultados obtidos foram de que duas das paisagens possuíram predominância de Cerrado aberto (ambiente savânico) na primeira cena temporal da trajetória da paisagem, mostrando que a interpretação encontrada no ano de 2010, a qual indica uma similaridade das áreas em relação ao percentual de cobertura de vegetação nativa, é equivocada. Também demonstrou-se que as principais modificações no ambiente nativo ocorreram entre os anos de 1962 e 1983 em comparação com a magnitude de modificação ocorrida no segundo período, de 1983 a 2010, principalmente em decorrência da expansão agrícola, em parte incentivada por ações governamentais como o programa Pró-álcool. O terceiro resultado mais importante desse capítulo foi a de detectar que o Cerrado aberto foi drasticamente substituído não somente pelas culturas de cana e de reflorestamento comercial de eucalipto e pinus, mas também pela contínua substituição ocasionada adensamento de espécies florestais sobre as espécies da savana, um fenômeno que ocorre ao redor das savanas do mundo conhecido como “savanna enchroachment”, como uma consequência da supressão do fogo no ecossistema savânico do Cerrado. O resultado das análises de respostas atrasadas evidenciou que das sete espécies de mamíferos investigadas, três, o tamanduá-bandeira (*Myrmecophaga tridactyla*), o lobo-guará (*Chrysocyon brachiurus*) e o veado-catingueiro (*Mazama gouazoubira*), estão mais fortemente associadas com o Cerrado aberto existente em 1962 do que com as classes de cobertura do solo da paisagem atual, com exceção do lobo-guará, que também demonstrou uma resposta negativa à proporção atual de cana-de-açúcar nas paisagens. Baseando-se na literatura disponível de respostas atrasadas, estimou-se, de forma conservadora, que um intervalo de tempo entre 40 e 60 anos seria necessário para a primeira espécie de mamífero de grande porte se extinguir das paisagens, o que provavelmente já ocorreu na comunidade de mamíferos neotropicais de médio e grande porte dessa região. Em relação à ocorrência de limiares ecológicos na resposta das espécies à vegetação nativa e à silvicultura, foi encontrado que somente o caititu (*Pecary tajacu*) apresenta resposta em limiar para a floresta nativa em uma das paisagens, necessitando quantidades superiores a 50% de floresta nativa na paisagem para assegurar que declínios acentuados em sua ocupação não ocorram. Ainda que as paisagens de estudo não retenham essa quantidade de vegetação nativa como um todo (retém em torno de 27% de cobertura de vegetação nativa), o que se sugere é que a presença de um único e grande remanescente de vegetação nativa protegido como Unidade de Conservação Integral em uma das paisagens do estudo esteja exercendo efeito positivo na permanência dessa espécie de mamífero com elevada dependência dos recursos florestais. Essa evidência se contrapõe à proposição do Projeto de Lei nº 2362/2019, em tramitação no Senado Brasileiro, de revogar a existência das Reservas Legais no Código Florestal da Constituição Brasileira, essas que compreendem uma quantia fixa de ambientes nativos preservados dentro de terras privadas para assegurar o bom funcionamento e provisão de serviços do ecossistema. Os achados desse estudo indicam que o desaparecimento das savanas nas paisagens de estudo ameaça a permanência de espécies de mamíferos de médio e grande porte, incluindo duas espécies que encontram-se sob estado de ameaça de extinção. A principal medida de conservação sugerida para essas paisagens de estudo e contextos de ocupação humana similares em outras localidades é a de aumentar a proporção de vegetação nativa em paisagens modificadas pelo homem, em especial das fitofisionomias abertas do bioma Cerrado. Contudo, recomenda-se que técnicas de restauração apropriadas para a manutenção do Cerrado savânico sejam adotadas, de forma a evitar que ambientes florestais nativos aumentem em detrimento de ambientes nativos de feição aberta.

Palavras-chave: Cerrado, mamíferos de médio e grande porte, respostas atrasadas, débito de extinção, limiares ecológicos

Abstract

The effect of habitat reduction on biodiversity is idiosyncratic regarding the established relationships among species and the traits of human-modified landscapes. In this manner novel scientific evidences point to the importance of considering not only the spatial scale on the interpretation of species responses, but also the temporal scale. The correlation between biological parameters of the present and environmental traits of the past show that species might present delayed responses after a disturbance event, and as consequence, species responses to current landscape traits may be misleading for conservation purposes and environmental management actions. In order to understand how the neotropical medium and large-sized mammals are responding to human-modified landscapes of Cerrado under a 48-years interval of disturbance, the present dissertation aimed in their three chapters: (i) to describe land use and land cover trajectory and native vegetation transition of three human-modified landscapes, (ii) to detect the existence of time-lagged responses among seven neotropical medium and large-sized mammal species to their the natural environment and (iii) to detect the existence of ecological threshold responses of six neotropical medium and large-sized mammal species to natural and human-modified environments. The three studied landscapes are located in the northeastern region of São Paulo State and harbor important protected remnants of Cerrado and Atlantic Rainforest under distinct levels of environmental protection enforcement. From the edges of the protected remnants a 5 km buffer zone was stablished to settle the limits of the landscape under study. Land use and land cover categories were mapped from visual interpretation of aerial images, backwards in time, in three distinct time scenes: 2010, 1983 and 1962. A total of 206 focal landscapes with area of 200ha were randomly created in all three landscapes with a balanced distribution inside and outside of protected areas, aiming the obtaining of the proportion of each class of land cover in each focal landscape. The trajectory of land cover classes and the transition of native vegetation were characterized for each landscape separately to perform comparison within and among landscapes. Medium and large-sized mammal species were surveyed through one camera-trap device placed during 30 days in each focal landscape. The individual history of records of the seven elected species of mammals were arranged in six occasions of five days and joined to the landscape covariates chosen for each species to perform time-lag responses analysis (chapter 2 of this dissertation) and ecological thresholds analysis (Chapter 3). Occupancy estimates modelling accounting for imperfect detection was adopted for both analysis in the in the single species/single framework. The main results of landscape transition showed that two of the three landscapes were mostly covered by the open savannah in 1962 while the third landscape by the wooded savanna, showing that relying in present time native vegetation proportion in the landscape (year of 2010), which by its turn denoted similarity in vegetation composition among the studied landscapes, might be misleading. It was also detected that the main changes in natural environment occurred during 1962 and 1983 period in comparison with the magnitude of change of the second period, between 1983 to 2010, which was partially as a consequence of governmental incentives to agricultural expansion. The third important result of landscape trajectory was noticing that the opened savanna environments were replaced not only but sugar cane and forestry crops, but also encroached by the continuous growth of the wooded savanna species, a phenomena known as “savanna encroachment”, a consequence of fire suppression in the Cerrado ecosystem. The results found for time-lag responses showed that among the seven mammal species analyzed, three species, named the giant anteater (*Myrmecophaga tridactyla*), the maned wolf (*Chrysocyon brachiurus*) and the brown brocket deer (*Mazama gouazoubira*) are still responding to the opened savannah environments of 1962 instead of the current land cover types that substitute them, with the exception of the maned wolf negative response to sugar cane proportion in the landscape. Based on literature data, a conservative estimation points to a 40 to 60 years delay in medium and large-sized mammal response to the first local species extinction take place, what has probably occurred in the community of neotropical medium and large-sized mammals of the studied region. This suggests an uncertain future for the three species presenting delayed responses in the modified landscapes. Regarding the occurrence of ecological threshold responses of the mammal species to native and anthropogenic environments, it was found that collared peccary occupancy presents a steep decline in the threshold cut-value of 50% of native forest in the landscape, even though the landscape where peccary occurs present a mean proportion of 27% of this land cover type. In this sense, it is probable that the presence of the single and large remnant of wooded forest, enforced by law as a Full Protection Conservation Unit, might be exerting a positive effect in the presence of this forest dwelling species, which highly depends on native forest resources. This evidences counteract the recently proposed Law Project (number 2362/2019) processing in the Brazilian Congress, which intend to revoke the category of environmental protection of “Legal Reserves” (a fixed set-aside portion of land of native environment in private lands that assures the maintenance of biodiversity and ecosystem services) from the Brazilian Constitution in favor of agricultural expansion in the country. The evidences of this study indicates that the decrease of the opened savannas in the studied landscapes is a threat to the maintenance of medium and large-sized mammal species. Based in these findings, the most important conservation action suggested to be implemented in the landscapes of this study and other landscapes with similar environmental scenario is to increase the proportion of native vegetation in human-modified landscapes, especially the opened physiognomies of Cerrado. Notwithstanding, it is recommended the adoption of appropriated restoration management technics in order assure the maintenance of the opened Cerrado environments and prevent the savannah encroachment by forests.

Keywords: Savannah, medium and large-sized mammals, time-lagged responses, extinction debt, ecological thresholds

Sumário

Introdução

A motivação do presente estudo foi a de ampliar a compreensão de como as espécies de mamíferos neotropicais de médio e grande porte utilizam as paisagens modificadas pelo homem. Contudo, a investigação das relações entre as espécies e seu habitat foi além das condições atuais da paisagem, e incluiu a relação das espécies com a vegetação existente no passado. A lógica desse procedimento é de que, apesar de atualmente grande parte das paisagens modificadas pelo homem estarem cobertas por ambientes de uso antrópico (como por exemplo, plantações agrícolas e áreas urbanas), em outrora, essas já estiveram cobertas por vegetação nativa. A descrição da trajetória da vegetação foi a base para descobrir se algumas espécies, como as de ciclo de vida mais longo e com tolerância às mudanças ambientais, ainda respondem à vegetação nativa do passado. Essa resposta pode persistir ao longo de muitos anos após um distúrbio ambiental, o que é conhecido como resposta atrasada (em inglês, *time-lagged response*). Uma vez descartada a existência do atraso temporal nas respostas de mamíferos de médio e grande porte, pode-se então compreender o efeito que os ambientes naturais e antrópicos das paisagens modificadas atuais exercem sobre o uso que as espécies fazem do seu habitat. Nesse contexto ambiental, os remanescentes de vegetação nativa se tornam os protagonistas na persistência das espécies e pouca atenção é dada aos demais ambientes de uso humano nas respostas desses animais. Mediante às crescentes evidências de que até mesmo espécies ameaçadas persistem nessas paisagens modificadas pelo homem, buscou-se entender juntamente aos ambientes nativos, qual o efeito dos ambientes antrópicos no uso que os mamíferos fazem da paisagem. Essa constatação se deu avaliando a relação da presença das espécies com o gradual aumento dos ambientes antrópicos, a fim de encontrar tanto a influência (positiva ou negativa) desses ambientes como a existência de mudanças súbitas de resposta. A detecção dessas proporções limite nas respostas das espécies é conhecida como limiar ecológico (do termo em inglês *ecological threshold*). Uma vez que essas relações entre as espécies e os ambientes foram exploradas de forma individual, o que se espera é que as respostas encontradas reflitam as exigências ambientais dessas espécies, isso é, estejam relacionadas com as suas características biológicas e ecológicas, atingindo o que desdobra na possibilidade de propor medidas de conservação pautadas em dados empíricos. Dessa forma, o estudo que se segue nessa tese teve como objetivos gerais, primeiramente (Capítulo 1) descrever a trajetória temporal da vegetação nativa nas paisagens selecionadas para o estudo das respostas dos mamíferos de médio e grande porte, segundo constatar se as espécies de mamíferos estão respondendo à vegetação nativa do passado ou do presente (Capítulo 2) e por fim, avaliar se as respostas das espécies ao ambiente presente, tanto em relação aos ambientes nativos, como em relação aos ambientes de uso agrícola, são positivas ou negativas e se ocorrem mudanças súbitas nessas respostas à medida que a proporção desses ambientes aumenta na paisagem. Os capítulos da presente tese foram apresentados em forma de artigos científicos completos e no idioma inglês.

Chapter 1

Spatio-temporal dynamics of anthropic landscapes reveals savanna encroachment

Victor G Krepschi [1], Nielson A Pasqualotto [4], Thiago F Rodrigues [3], Roberta M Paolino [3], Natalia F Versiani, Adriano G Chiarello [2], Milton C Ribeiro [1] and Silvio FB Ferraz [3]

[1] Universidade Estadual Paulista (Unesp), Instituto de Biociências, Câmpus de Rio Claro, São Paulo, Brasil.

[2] Universidade de São Paulo (USP), Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Ribeirão Preto, São Paulo, Brasil

[3] Universidade de São Paulo (USP), Escola Superior de Agricultura Luiz de Queiroz (ESALQ), Piracicaba, São Paulo, Brasil

**corresponding author: vkrepschi@gmail.com*

Abstract

Most of environmental and ecological research assessments is conducted based on responses to current landscape characteristics. However, this might induce erroneous interpretation of processes observed in the present if the effect of past modifications are neglected. A preventive measure to avoid this misunderstanding on environmental studies is to describe landscape trajectory, a procedure which provides background of past time events occurred in the landscape. The core environmental issue at human-modified landscapes trajectory is linked to remnants of native vegetation, which have been historically deforested to expand agricultural demands and nowadays requires a set of conservation and restoration actions to keep their ecological functionalities and biodiversity. In the context of human-modified landscapes, describing the trajectory of native vegetation becomes an even more challenging task when inserted in naturally heterogeneous regions. The present study aimed to describe the trajectory of native vegetation remnants in an ecotone zone of Cerrado and Atlantic Forest, the main anthropic land cover that replaced them and the intensity of this replacement measured along 48 years. We mapped the study areas in three distinct time scenes (1962, 1983 and 2010) by visual interpretation of aerial photomosaic and converted into raster format to perform native vegetation trajectory comparisons. We considered three covariates of native vegetation: native open vegetation, native forest and a third covariate made of both types joined, native vegetation. Comparisons were made between time periods (1962 to 1983 and 1983 to 2010) within study areas and among study areas, in order to detect dissimilarities in the trajectories of the native vegetation covariates. Intensity of landscape change was calculated by subtracting the summed percentage of land cover change from the summed percentage of land cover persistence. Our results showed that in two of the study areas the open Cerrado cover was originally predominant in the past, while the third one, was mainly covered by forest. The main replacements of native vegetation occurred during the first time period due to sugar cane and silviculture crops expansion. The native vegetation covariate didn't show difference in trajectory among study areas. However, when we dissociated this covariate into native forest and native open Cerrado, the loss of the open Cerrado occurred in all study areas during both periods, while an anomalous level of afforestation was detected in the two sudy areas where open vegetation predominates. This temporal afforestation over open native vegetation represent a strong evidence of savannah encroachment, a phenomenon threateting savanna biodiversity worldwide. We attributed this observed forest increase to fire suppression and to compliance with Brazilian environmental laws, which promoted forest restoration instead of the recovery of the open savanna. We conclude that although the replacement of native vegetation to crops has stabilized in the trajectory of the study areas, specific environmental management of the open Cerrado is needed in both public and private lands in order to ensure environmental heterogeneity and avoid savanna disappearance.

Keywords: land use and land cover, landscape transition, Cerrado, Atlantic Forest, human-modified landscapes.

Introduction

Human modified landscapes are a resultant of decades (even centuries) of successive anthropogenic interventions. Changes in land use and land cover (lulc) in the landscape are driven both by biophysical and anthropogenic factors and result mainly from political socioeconomic cycles (de Rezende et al. 2015, Silva et al. 2016, Molin et al. 2017; Moraes et al. 2017) and governamental policies (Ferraz et al. 2005; Teixeira et al. 2009). Understanding landscape transition throughout time and the processes involved in lulc change is strategic in developing guidelines in restoration and conservation of human-disturbed landscapes (Ferraz et al. 2009; Rappaport et al. 2015). Besides, landscape dynamics allows capturing ecological responses and processes still occurring, but originated in the past (Ferraz et al. 2014).

Not surprisingly, many current ecosystem processes and responses are still linked with past time landscape and not current landscape context, which might last for years, decades or even centuries (Vellend et al. 2006, Metzger et al. 2009). Assuming solely current landscape traits and neglecting past time sources of disturbance in highly dynamic landscapes, even in spatially close locations (Molin et al. 2017), has proved misleading for ecological goals (Koyanagi et al. 2017), averting prevention of long-termed extinctions (Rappaport et al. 2015) and is resource wasteful (de Rezende et al. 2015; Semlitsch et al. 2017). In this manner, concern with the temporal scale has been increasing when seeking for explanations in current environmental and ecological assessments.

The first step involved in defining landscape trajectory is measuring spatial variation of a given landscape trait (or traits) along distinct time scenes. A trait of interest is measured as independent response variable and/or as landscape indexes, generating landscape metrics adequate to correlate with the processes under investigation (Ferraz et al. 2005; Metzger et al. 2009). Among traits related to ecosystem processes, proportion of native vegetation (Fahrig 2003) and its changes resulting from anthropogenic disturbances, both loss and gain of native vegetation, are central in environmental science, particularly in understanding the effects of human disturbances on ecosystems and biodiversity (Lira et al. 2012a; de Rezende et al. 2015). In highly dynamic landscapes, such as the deforestation arc of Brazilian Amazon (Ferraz et al. 2005; Ochoa-Quintero et al. 2015), substantial changes in native vegetation may happen in short periods of time, thus temporal scale may be correspondingly shorter in order to capture changes (around two years). By the contrary, in the imperiled Brazilian Atlantic Forest (Ribeiro et al. 2009), it has been observed that changes take longer to happen (ten to fifty years), so, temporal scale may be longer for us to understand such processes (Teixeira et al. 2009; Lira et al. 2012b; de Rezende et al. 2015; Silva et al. 2016; Uezu and Metzger 2016). The reason for this time-lapse difference lies in the context related to human land use type, and as consequence, heterogeneity of lulc classes may differ. While the Amazonian context presents cattle ranching as a primer economical activity and spontaneous regeneration takes place shortly after (forming secondary forests, Ferraz et al. 2005), countryside Atlantic Forest and Cerrado have passed by successive economic cycles (coffee, sugar cane and forestry) and environmental policy change along the last century (Victor et al. 2005; Silva et al. 2016), generating diversification in crops and thus, a mosaic of high heterogeneity of anthropogenic-generated lulc classes. However, increased heterogeneity in lulc types isn’t solely originated from anthropogenic reasons, but also from natural vegetational formations.

In Southeastern Brazil, heterogeneity in natural environments occurs when the Central Brazilian savannah biome (also called Cerrado), which is comprised by distinct types of vegetational physiognomies (ranging from open savanna to closed canopy forests), reaches in its southernmost part the Atlantic Forest biome, forming a transitional and natural ecotone zone. Thus, heterogeneity of anthropogenic environments together with natural heterogeneity of native vegetation originates a complex mosaic of land cover and land use in the landscape, with distinct structure and composition. This heterogeneous lulc context occurs in São Paulo State, a Brazilian state located in southeastern Brazil, where few, yet important, remnants of native vegetation (both from Atlantic Forest and Cerrado biome) still exist in the landscape. However, most of landscape dynamics studies conducted to date have been focused in Atlantic Forest strictly (Teixeira et al. 2009; Metzger et al. 2009; Lira et al. 2012b; Uezu and Metzger 2016, among others), setting aside Cerrado environments, an equally important biodiversity hotspot (Myers et al. 2000).

Among the few studies regarding landscape dynamics at these ecotone regions of São Paulo State, a noteworthy effort has been achieved by Shida (2005), whose study area encompassed two of the largest Cerrado remnant of São Paulo State. Her study focused mainly in describing native lulc classes changes and the relationship of those changes with important socioeconomic drivers between 1960 and 2000. Similar study was recently carried out by Moraes et al. (2017) in a neighboring area, focusing on the main drivers of forest transition and socioeconomic context. Even though the study area of this research is located in a transitional vegetation zone, the current predominance of native forest cover in the study landscape led the authors to choose it as the main covariate of the analysis. Although very conclusive, these landscape dynamic studies (Shida 2005; Moraes et al. 2017) brought little attention to changes occurred to the open Cerrado physiognomy.

In this manner, considering the landscape dynamic of both Atlantic Forest and Cerrado environments at human-modified landscapes, the present study aimed at: (i) describing lulc classes trajectory that took place along 48 years in three landscapes with apparent distinct lulc contexts and three different years (2 transitory periods); (ii) comparing native vegetation trajectory as one single covariate and separately into two classes: forest and open vegetation among landscapes and among time scenes; and (iii) characterizing landscape dynamic intensity through lulc classes replacements in distinct time periods.

Material and Methods

Study areas

Our three study areas are located in the Northeastern region of São Paulo State, Brazil (21°02' – 21°43'S and 47°54' – 47°16'W; Figure 1A and 1B). Actually, these sites harbor important protected remnants of Atlantic Forest and Cerrado biomes, including Cerrado forest (wooded savanna, also called "Cerradão") and open Cerrado (the Brazilian savanna, also called "Cerrado stricto sensu"), inside and outside Protected Areas (PA), which includes Areas of Permanent Protection (APP, reserves in private land and gallery forests) and Conservation Units (biological reserve, experimental station and state forest). The extent of each studied landscape was determined by the core protected area and its surroundings, established by a 5km buffer from PA borders. The adopted PA buffer zone length is in accordance with the management plan of the Conservation Units inserted in our landscapes. Main agricultural practices in the studied region are sugar cane plantations, silviculture (*Eucalyptus* and *Pinus*), and in a less extent, pasture and orange plantations. Due the presence of a large river (Mogi-Guaçu River) and the flat relief, marshlands occur in the landscape.

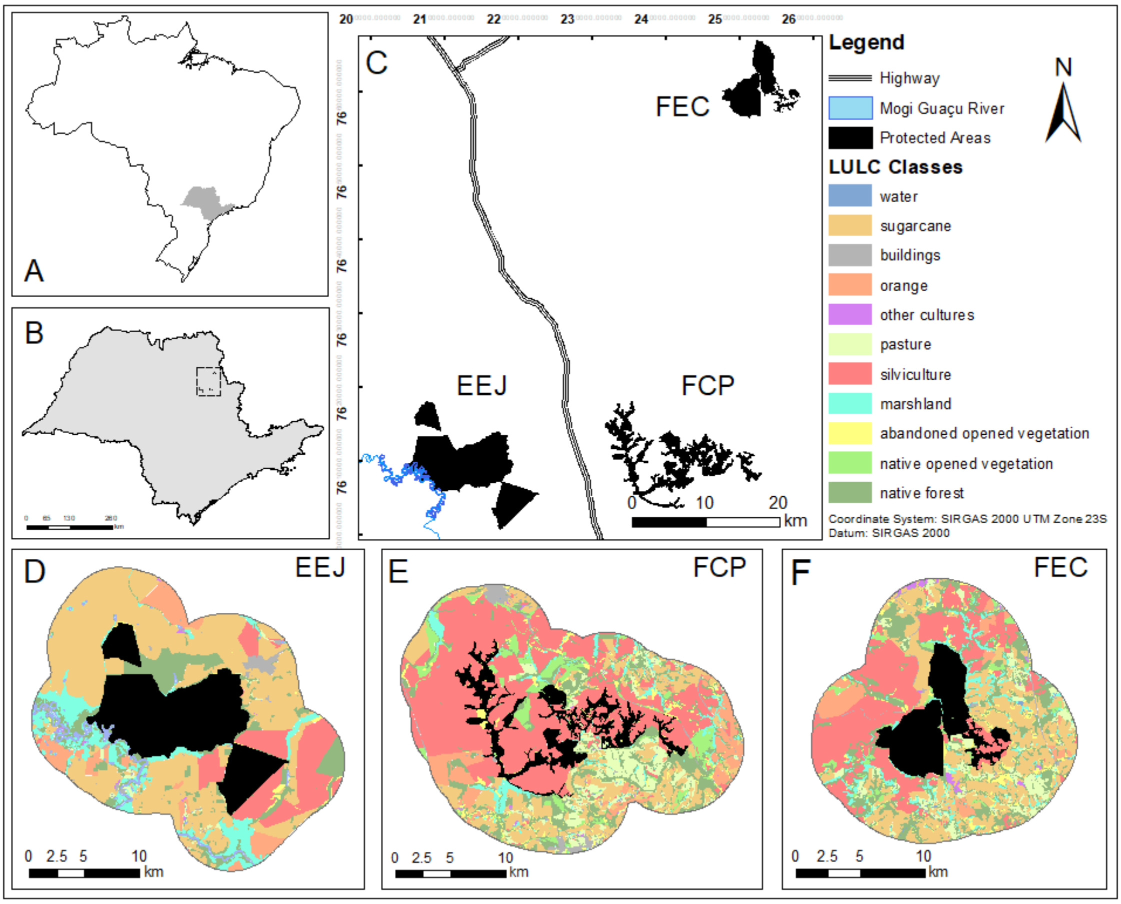

Figure 1. Location of São Paulo State (grey shaded) in Brazilian geopolitical map (A), location of studied landscapes evidenced at São Paulo State geopolitical map (B) and studied landscapes protected areas (in black) in the regional context (C). Figure D to F show each studied landscape individually, comprised by the PA (in black) and their buffer zone, determined by a 5 km radius from the PA's edge, including main current land use and land cover categories. Abbreviation of landscape names: EEJ: "Jataí" Ecological Station, FCP: "Cara Preta" Farm and FEC: "Cajuru" State Forest.

The first area (EEJ) harbors two PAs (figure 1D): "Jataí" Ecological Station (a strictly protected area, IUCN category I) and "Luiz Antonio" Experimental Station (IUCN category VI), which altogether comprise a large PA of 10,000 ha in the total landscape extent considered of 50,000 ha. The second study area has similar total extent of the former, but differs regarding the native vegetation, which is mostly comprised by gallery forests and smaller native vegetation remnants (figure 1E). This area is called "Cara Preta" Farm (FCP) and belongs to a private forestry company (International Paper do Brasil), serving commercial purposes. The third study area (FEC) is smaller than the previous ones, presenting a total extent of 30,000 ha. Currently, this landscape includes two important PAs (figure 1F): the first, a private owned 2,000 ha block of native open vegetation named "Dois Córregos" Farm, and a public area called "Cajuru" State Forest (IUCN category VI), which nowadays is mostly covered by plantations of old *Pinus* and *Eucaliptus* trees which are managed sustainably for commercial purposes.

Currently (year of 2010), all landscapes have around 25% of native vegetation cover (both native forests and savannah environments joined, see table 1 at Results session).

Brief historical background

Main changes in land use and land cover of the studied region occurred in three distinct economic moments (Victor et al. 2005, Shida 2005). The first moment happened on the beginning of 19th century, due to the searching of new lands for coffee plantations in the region. The suitability of lands and a railway construction boosted the establishment of coffee production and human settlement. In the beginning of the twentieth century, industrial dairy cattle segment also established in the region, in the same decade that coffee production started declining due to the market oscillation related to the First World War. The second economic moment happened after 1930, when coffee plantations definitively lost its strength in the region and, joined to dairy cattle farming, most of lands was converted to polycultures, as cotton, rice and peanuts. Before the 60's, governmental support and international market policies helped sugar cane and silviculture start in the region, but the huge expansion of these crops towards the poor soils of the Cerrado was about to happen after the "green revolution", promoted by the Military Regime empowered in Brazilian government, in the beginning of the 1960 decade. This third economical moment came with agricultural expansion of sugar cane crops, which consolidated in the middle of 1970 decade with the creation of the governmental "Pró-álcool" biofuel program (Moraes et al. 2017). In this same decade, governmental incentives lead to the establishment of the paper industry in the region and after 1988, few changes related to land use happened, consolidating these two segments which persist until the first decade of 2000's (Shida 2005).

Geoprocessing

Aerial images from the study areas were obtained from Geographic and Cartographic Institute (IGC, a public agency from São Paulo State Government). Present time scene (year of 2010) was obtained from a digital orthorectified mosaic of accurate precision and resolution of 5 meters (didn't require geoprocessing procedure), which was used as reference for georreferencing the remaining two past time scenes (1962 and 1983). Both 1962 and 1983 aerial images were obtained from paper photographs (20 x 20 cm in size) digitalized in a 600 dpi resolution scanner (with no corrections), and were processed as follow. Every individual digitalized image (from 1983 and 1962) was reduced to its core area (two thirds of the original size) to remove edge distortion of camera lens. The next step was georeferencing each image individually. Based on previous landscape time scene (to georreference 1983 images we used 2010 mosaic as reference and to georreference 1962 images, we used 1983 mosaic), georreferencing procedure was performed using *ArcGis georreferencing* tool, setting at least 30 control points in each digitalized image, and *spline* transformation. We chose this type of transformation to increase adjustments in overlayed edges of images. After georreferencing all images, we create a single mosaic for each time scene, which were used for mapping land use and land cover. We set as coordinate system the UTM projection, Zone 22S and datum Sirgas 2000 for all geoprocessing project.

Mapping procedure

Mapping of land use and land cover (lulc) of studied landscapes was made by visual interpretation of aerial photographs in 10:000 scale, resulting in a final map resolution of 5m. We mapped 2010 mosaic first and the remaining years backwards in time (1983 and 1962 mosaics). Imagery mosaics were superposed and vectors reshaped to establish the change occurred between time scenes. Ten lulc classes were defined through mapping procedure: native open vegetation, native forest, marshlands, pasturelands, sugarcane, silviculture (*Eucalyptus* and *Pinus* plantations), open abandoned vegetation, orange plantation, buildings and others (remaining minor lulc classes not included in the main classes). After 2010 time scene mapping, Kappa index of concordance was applied (based on google earth images comparison), obtaining 0.9 of similarity (Paolino et al. 2016).

Landscape trajectory description and dynamic intensity

For each individual landscape (EEJ, FCP and FEC) we described the proportion occupied by each lulc class along time scenes and main transitions (the substitution each lulc class by another) that occurred between them (using *ArcGis Combine* tool, described at *Statistical Analysis* below). Native open vegetation, native forest and native vegetation (both vegetation types pooled) change was compared among landscapes (in the same time scene) and between time scenes (in the same landscape). Additionally, the intensity of landscape dynamics was determined for each landscape for each time period.

Statistical Analysis

For each landscape, the lulc map (vector in *.shp* format) was converted to raster format surface (with 5m of pixel resolution). Then, the proportion of each lulc class in each time scene was determined by dividing the number of pixels of this given lulc class by the total number of pixels of the whole landscape (represented further as percentage). To quantify main transitions occurred in each period (period 1 corresponding by 1962 to 1983 interval and period 2 by 1983 to 2010 interval) we used the *ArcGis* tool *Combine,* which generates a distinct code for each lulc pixel conversion (e.g., forest to silviculture = code 1, forest to sugarcane = code 2). The final product of this tool is the counting of pixels with the same conversion code in the landscape. Further, we divided this final count by the total number of pixels of the whole landscape to obtain the proportion of each type of lulc class conversion in each period (represented further as percentage). Based on these values of class conversion, we calculated the intensity of landscape dynamic (*Dynamic*) through subtraction of the summation of percentages of all classes that changed (*Change*) in a given period from the summation of percentages of classes that remained the same in the same period (*Permanence*). We did this for both periods (1962 to 1983 and 1983 to 2010) and each landscape (EEJ, FCP and FEC), separately and we considered major changes occurring in the landscape (totaling 80% of lulc change). The interval of *intensity of landscape dynamics* ranges from -100% to 100%, in which positive values represent less intense dynamics in the landscape, while negative values represent dynamic changes occurring in lulc classes, meaning that landscape transition was more intense.

Comparisons of native vegetation cover change among study areas (in the same time scene) and among time scenes (within landscape) was based on 206 randomly selected rounded shaped sample units of 200 ha, of which, 102 belonging to EEJ landscape, 52 to FCP landscape and 52 to FEC landscape. We performed comparisons for both types of native vegetation separately (native forest and native opened vegetation), and for native vegetation (both types of native vegetation joined). Given that our data did not adhere to the parametric assumptions (normality and homoscedasticity), we adopted non-parametric tests Kruskal-Wallis analysis (non-parametric ANOVA) followed by Wilkoxon test (Mann-Whitney test) to perform comparisons among landscapes. Within landscape comparisons were performed using Pearson correlation tests, with significance when Pearson correlation coefficient was less than 0.6.

Results

Land use and land cover maps and the transition of each lulc class of each landscape are represented in figure 2 and their percentage values described in table 1.

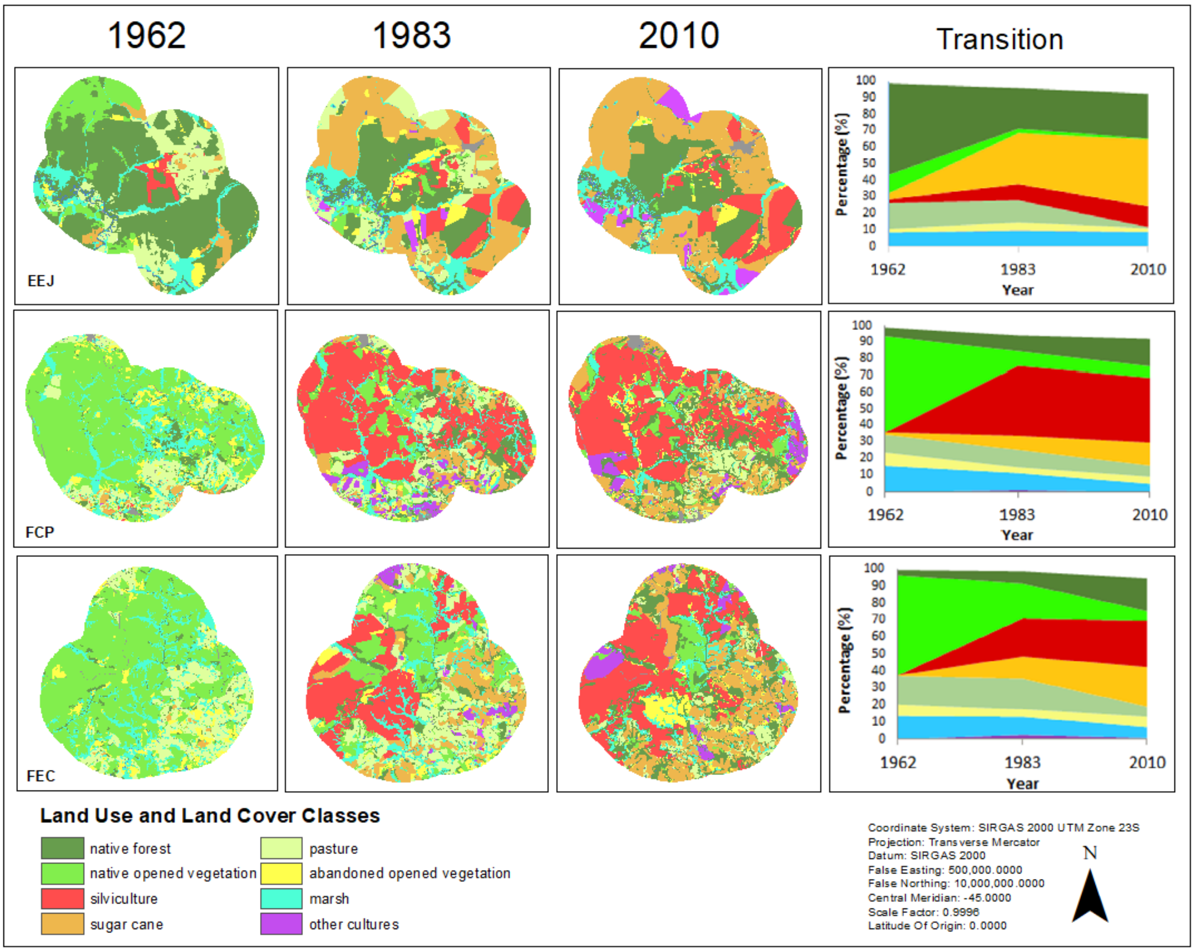

Figure 2. Land use and land cover maps of studied landscapes in 1962, 1983 and 2010 (the first three columns on the left) with their respective trajectories represented in percentage ("Transition" column on the right). Abbreviation of landscape names: EEJ: "Jataí" Ecological Station, FCP: "Cara Preta" Farm and FEC: "Cajuru" State Forest.

Table 1. Trajectory of lulc classes (in percentage of the total landscape) of the three studied landscapes. Legend: fores (native forest), noveg (native open vegetation), silvi (managed forests), sugar (sugar cane), pastu (pasture), aband (abandoned open vegetation), marsh (marshlands), other (other cultures), orang (orange plantations), build (buildings), naveg (native vegetation), EEJ ("Jataí" Ecological Station), FCP ("Cara Preta" Farm), FEC ("Cajuru" State Forest).

Landscape	**EEJ**			**FCP**			**FEC**		
LULC/Year	1962	1983	2010	1962	1983	2010	1962	1983	2010
fores	55.23	24.55	26.97	5.21	9.46	16.54	3.03	7.21	19.40
noveg	11.21	2.69	0.48	57.67	8.82	6.78	58.80	20.47	5.70
silvi	2.25	9.68	12.65	0.14	42.19	39.24	0.00	22.50	27.24
sugar	3.67	30.95	40.59	1.53	8.56	14.02	0.53	13.03	23.34
pasture	15.73	13.45	0.69	10.86	10.62	6.76	16.80	17.94	5.77
aband	2.18	4.95	2.27	8.02	3.49	4.33	6.59	4.33	6.23
marsh	8.42	9.46	8.56	15.37	9.73	4.30	13.69	10.86	6.36
other	0.00	0.16	0.17	0.03	1.27	0.13	0.00	2.36	0.67
orang	0.00	1.80	5.16	0.21	4.06	5.42	0.00	0.25	3.98
build	0.15	0.96	1.41	0.91	1.74	2.38	0.44	0.84	1.03
naveg	66.45	27.24	27.44	62.88	18.28	23.32	61.82	27.68	25.11

Native vegetation proportion was similar among landscapes (table 1) and no dissimilarity in native vegetation loss was detected among landscapes in both periods (table 2 – results of comparative tests, and figure 3). However, when we examined native vegetation separately into native forest and native opened vegetation, both initial proportion and trajectory of these land cover classes differed among landscapes. At the beginning of the trajectory (in 1962) EEJ landscape surface was mainly comprised by native forest (55%, table 1), while FCP and FEC surface was mainly covered by native opened vegetation (around 58%, table 1). Native forest and native open vegetation trajectories differed from native vegetation and this change occurred distinctively among landscapes (table 2, figures 4 and 5).

Table 2. Result of comparative tests (Kruskal-Wallys and Mann Whitney tests) of vegetation change (native vegetation –naveg, native open vegetation – noveg, and native forest – fores) in the first (1962 to 1983) and second transition periods (1983 to 2010). P-value of significance (0.05) in bold indicate detection of dissimilarities in vegetation change between the study areas.

Kruskal-Wallys	Vegetation Type		
Period	Naveg	Noveg	Fores
1962-1983	>0.05	**<0.05**	**<0.05**
1983-2010	>0.05	**<0.05**	**<0.05**
Mann-Whitney	EEJ-FCP	EEJ-FEC	FCP-FEC
Fores 1962-1983	**<0.05**	**<0.05**	>0.05
Fores 1983-2010	**<0.05**	**<0.05**	>0.05
Noveg 1962-1983	**<0.05**	**<0.05**	>0.05
Noveg 1983-2010	>0.05	**<0.05**	**<0.05**

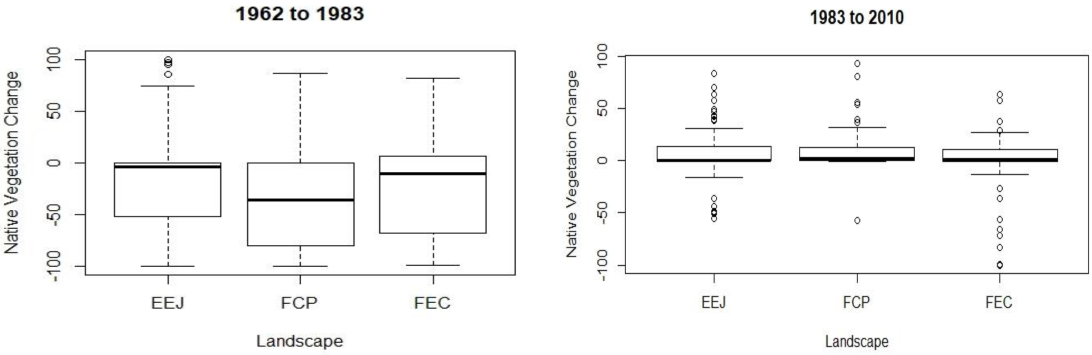

Figure 3. Comparison of native vegetation change among EEJ, FCP and FEC areas during first (1962 to 1983) and second period (1983 to 2010) measured inside 200 ha rounded-shape focal landscapes. Lines in bold represent median value. Negative values represent loss of native vegetation and positive values, native vegetation gain. Individual values of native vegetation change expressed as percentage.

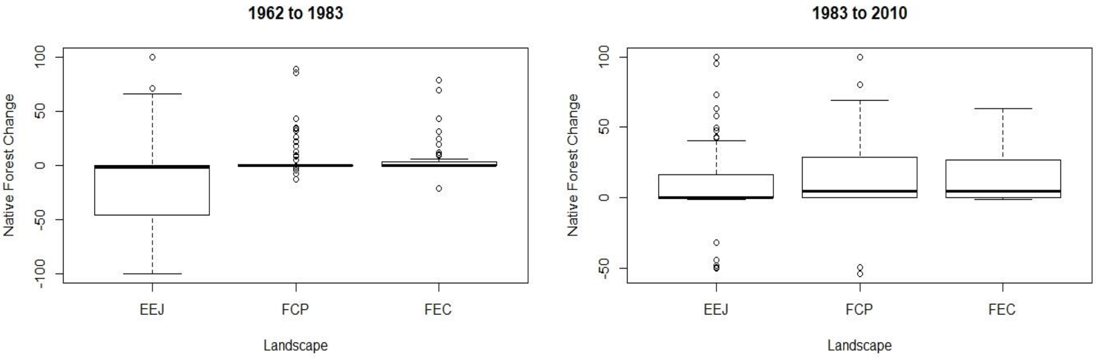

Figure 4. Comparison of native forest change among EEJ, FCP and FEC landscapes during first (1962 to 1983) and second period (1983 to 2010) measured inside 200 ha rounded-shape focal landscapes. Lines in bold represent median value. Negative values represent loss of native forest and positive values, native forest gain. Individual values of native forest change expressed as percentage.

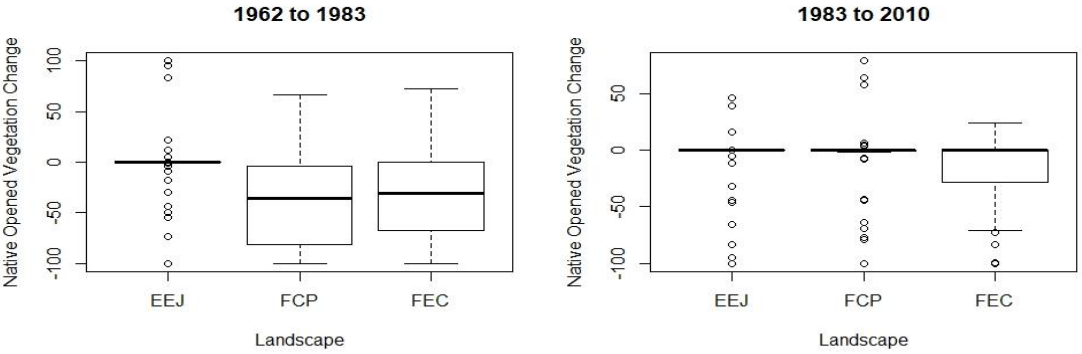

Figure 5. Comparison of native opened vegetation change among EEJ, FCP and FEC landscapes during the first (1962 to 1983) and second period (1983 to 2010) measured inside 200 ha rounded-shape focal landscapes. Lines in bold represent median value. Negative values represent loss of native opened vegetation and positive values, native opened vegetation gain. Individual values of opened native vegetation change expressed as percentage.

Native forest trajectory in EEJ was distinct from FCP and FEC both in the first and second periods (table 2 and figure 4). The first period at EEJ was marked by huge losses of native forest (loss of 55% from the initial native forest amount of 1962), while FCP and FEC landscapes showed around a 100% of gain each in native forest amount (table 1). By the other hand, all three landscapes gained native forest in the second period, but EEJ differed from FCP and FEC. While native forest amount raised only 9.8% at EEJ in the second period (2.42% of total EEJ area), FCP and FEC increased in 74% and 169%, respectively. Even though native forest was not the originally predominant native vegetation type of FCP and FEC, native forests increased 317% and 540% in these two landscapes, respectively, since 1962. Showing an opposite trend, native open vegetation decreased in all landscapes trajectories. From 1962 to 2010, native open vegetation decreased 95% at EEJ, 88% at FCP and 90% at FEC. Even though this loss was more drastic in the first period (table 1), FEC landscape faced a reduction of 14.77% of native open vegetation (from 20.47% in 1983 to 5.7% in 2010) in the second period, which represent a decline of 72% of the initial proportion of native open vegetation of second period. Similarities of native open vegetation trajectory were found between FCP and FEC in the first period and between EEJ and FCP in the second period (figure 5).

According to results of *Combine* tool analysis, native environments were replaced mainly by two anthropogenic environments: sugar cane and silviculture. Sugar cane replacement was predominant at EEJ (23.58%) during the entire transition, while silviculture predominated at FCP (37.9%; table 3 and table 4). Notwithstanding, a more diverse replacement was observed at FEC, in which native open vegetation turned into silviculture (27.67%), native forest (8.91%), sugar cane (7.48%) and pasture (7.34%, table 3). The majority of suppressions in natural environment cover occurred in the first period (table 3), whilst in the second (table 4), their natural cover remained the same, with the exception of FEC. In the later period, most of replacement occurred among anthropogenic environments, but it is worth mentioning that the conversion of native open vegetation and marshlands into native forest happened in all landscapes. In EEJ, 2% of marshlands turned into native forest at the end of the trajectory. At FCP, 7% of native open vegetation and 5.29% of marshlands became native forest. FEC showed a similar pattern, with 8.91% of native open vegetation and 4% of marshlands ending up as native forest. Besides, pasture was the only anthropogenic lulc class that turned into native forest (EEJ: 1.59% - table 3, FCP: 1.58 and FEC: 1.52% - table 4).

Landscape dynamic intensity is shown in table 5. The highest value of lulc change was observed at FCP during the first period, followed by quite similar amounts between EEJ and FEC during this same period. On the other hand, the lowest intensity of lulc change was observed at EEJ in the second time period, followed by FCP. Negative values of *Dynamics* shows that the first period was more intense than the second in all landscapes, yet FEC, distinctively from the others, still showed 45% of lulc changes during the second period.

Table 3. Main LULC transitions at the study areas during first period (1962 to 1983) calculated for all pixels of whole landscape. Legend: fores (native forest), noveg (native open vegetation), silvi (managed forests), sugar (sugar cane), pastu (pasture), aband (abandoned open vegetation), marsh (marshlands), other (other cultures), orang (orange plantations), build (buildings), naveg (native vegetation), EEJ ("Jataí" Ecological Station Area), FCP ("Cara Preta" Farm Area), FEC ("Cajuru" State Forest Area).

EEJ			**FCP**			**FEC**		
1962	**1983**	**%**	**1962**	**1983**	**%**	**1962**	**1983**	**%**
fores	fores	20.32	noveg	silvi	36.71	noveg	silvi	21.51
fores	sugar	17.55	marsh	marsh	8.35	noveg	noveg	17.13
fores	silvi	7.13	noveg	onveg	7.26	marsh	marsh	8.84
marsh	marsh	6.70	pastu	pastu	4.25	noveg	pastu	7.34
noveg	sugar	6.03	noveg	fores	3.64	pastu	pastu	7.31
pastu	pastu	5.87	noveg	sugar	2.86	pastu	sugar	5.28
pastu	sugar	4.35	noveg	pastu	2.64	noveg	sugar	5.25
fores	aband	3.61	fores	fores	2.57	noveg	fores	3.13
noveg	pastu	2.97	pastu	sugar	1.99	noveg	aband	2.82
fores	pastu	2.69	aband	silvi	1.82	fores	fores	2.27
sugar	sugar	1.91	marsh	silvi	1.73	-	-	-
pastu	fores	1.59	marsh	pastu	1.71	-	-	-
-	-	-	noveg	aband	1.66	-	-	-
-	-	-	pastu	orang	1.63	-	-	-
-	-	-	marsh	fores	1.52	-	-	-

Table 4. Main LULC transitions at the study areas during second period (1983 to 2010) calculated for all pixels of the landscape. Legend: fores (native forest), noveg (native open vegetation), silvi (managed forests), sugar (sugar cane), pastu (pasture), aband (abandoned open vegetation), marsh (marshlands), other (other cultures), orang (orange plantations), build (buildings), naveg (native vegetation), EEJ ("Jataí" Ecological Station Area), FCP ("Cara Preta" Farm Area), FEC ("Cajuru" State Forest Area).

EEJ			FCP			FEC		
1983	**2010**	**%**	**1983**	**2010**	**%**	**1983**	**2010**	**%**
sugar	sugar	26.53	silvi	silvi	34.89	silvi	silvi	17.16
fores	fores	21.27	fores	fores	6.46	sugar	sugar	9.83
silvi	silvi	8.27	sugar	sugar	3.86	pastu	sugar	7.73
pastu	sugar	7.74	marsh	fores	3.77	noveg	silvi	6.16
marsh	marsh	6.66	marsh	marsh	3.49	fores	fores	6.03
sugar	silvi	2.95	noveg	fores	3.38	noveg	fores	5.78
pastu	orang	2.75	pastu	sugar	3.33	marsh	marsh	4.19
marsh	fores	2.03	noveg	noveg	3.20	marsh	fores	4.00
aband	sugar	1.98	orang	sugar	2.64	noveg	noveg	3.94
-	-	-	pastu	pastu	2.09	silvi	aband	2.86
-	-	-	sugar	pastu	2.05	pastu	pastu	2.83
-	-	-	silvi	aband	1.95	noveg	sugar	2.23
-	-	-	silvi	sugar	1.61	pastu	silvi	2.07
-	-	-	pastu	fores	1.58	pastu	fores	1.52
-	-	-	build	build	1.45	outros	sugar	1.51
-	-	-	silvi	orang	1.40	pastu	orang	1.40
-	-	-	pastu	orang	1.26	pastu	aband	1.26
-	-	-	sugar	orang	1.23	-	-	-
-	-	-	noveg	silvi	1.19	-	-	-

Table 5. Intensity of landscape dynamics in each studied landscape during 1st (1962-1983) and 2nd (1983-2010) periods. *Dynamics* values in bold represent both highest and lowest values, with positive and negative values indicating permanence and change, respectively.

Landscape	Period	Permanence	Change	Dynamics
EEJ	1962-1983	43.10	56.89	-13.79
	1983-2010	78.23	21.46	**56.77**
FCP	1962-1983	27.91	72.08	**-44.17**
	1983-2010	68.59	31.40	37.19
FEC	1962-1983	43.94	56.06	-12.12
	1983-2010	54.62	45.37	9.25

Discussion

The detailed spatio-temporal description of lulc classes trajectory, revealed distinct legacies of human disturbance through time among the studied landscapes. Though these landscapes shifted from natural to anthropic-dominated environments throughout the analysed period, the study sites still have significant remnants of Cerrado so that they represent, currently, the “best scenarios” of the extant Cerrado landscapes in São Paulo State, serving, therefore, as strongholds for the regional biodiversity conservation (Toppa 2004; Lyra-Jorge et al. 2010; Muylaert et al. 2016; Paolino et al. 2016).

The most important findings of our study refers to the trajectory of the natural environment. They show that the dissociation of native vegetation, from a single covariate to describe native environment trajectory into two, native open vegetation and native forest, is of utmost importance for landscape level environmental studies. If we had analysed the native vegetation as a single covariate, no differences in trajectory would be detected among landscapes. Further, we wouldn’t detect the real losses in native open vegetation occurred during the second period (specially at FEC landscape). This could lead to the misleading conclusion of a stabilization trend in native vegetation loss. Additionally, the current level of native vegetation cover (25% of each landscape, on average) would be very close to an ecological threshold (Ferraz et al. 2005; Swift and Hannon 2010). This scenario would mislead us to conclude about an optimistic scenario regarding natural vegetation cover that, in fact, doesn´t fully represent the reality of Cerrado. This mistake could, misdirect decision makers in their actions regarding natural environments protection, conservation and management. In this manner, after dissociating native vegetation into two distinct classes and considering theirs trajectories separately through time, we were able to reveal that each type of native vegetation requires specific sets of conservation and management measures. Even though this perception might seem intuitive, studies of landscape dynamics conducted thus far in similar anthropogenic context in São Paulo State (Ferraz et al. 2014; Molin et al. 2017; Moraes et al. 2017) concentrated their scope solely in native forest cover and its corresponding trajectory. This limitation denies the possible idiosyncrasies of these two types of vegetation and consequently, the ecological differences they might have in ruling the distinct effects on ecosystems.

Nevertheless, some changes occurred between native vegetation and anthropogenic lulc classes corroborate the previous studies carried out in the same or similar region (Shida 2005, Moraes et al. 2017). Specifically, the strong governmental incentives to sugar cane and silviculture production from the 70’s, resulted in large replacements of natural vegetation cover in all three landscapes (Shida 2005, Moraes et al. 2017). However, sugar cane cover predominated in the EEJ landscape, probably reflecting its superior soil quality and land suitability for mechanization (Shida 2005). On the other hand, in FCP and FEC native open vegetation replacements during the first period were mainly due to silviculture. This phase of higher landscape dynamics intensity and natural cover loss (1962 to 1983) stretched the vital importance of governmental policies in natural vegetation removal. By the other hand, governmental policies also influenced the safeguarding of protected areas of native forest, as observed during the second period at EEJ landscape and the increase of this vegetation type in all landscapes. The consolidation of the "Jataí" Ecological Station in 1982 (SMA 2018) as a strictly protected reserve is reflected in the native forest persistence during the second period (from 1983 to 2010). During this second period, landscape dynamics intensity decreased, mainly due to agricultural stability in the region, with the establishment of sugar cane and silviculture as major economical crops. Dissimilar from the first period, most of lulc replacements in the second period occurred among anthropogenic environments and not at the expenses of native vegetation. Sugar cane, for example, replaced pastures, orange plantations, "other cultures" and abandoned lands. Notwithstanding, the exception for this replacement trend was observed at FEC landscape.

While minor losses of native open vegetation occurred due to silviculture replacement at FCP (1.19%), the continued loss of native open vegetation at FEC landscape occurred in the second period. Replacement by both silviculture (6.16%) and sugarcane (2.23%) represented 56% of native open vegetation total loss during the second period. This later replacement at FEC, certainly reflects the lack of protective measures (the opposite found at EEJ landscape during the same period), and is an outcome of occupation of less suitable lands with more constrains to agriculture purposes, what is prone to happen after the occupation of the more suitable lands (Grecchi et al. 2014). However, the remaining 46% of native open vegetation lost at FEC occurred due to native forests replacement.

We observed a forest gain in modified landscapes during last decades, something that has been reported from other Brazilian locations (Teixeira et al. 2009; Lira et al. 2012b; de Rezende et al. 2015; Molin et al. 2017, Silva et al. 2017). Undoubtedly, this forest gain has a long term positive effect in many ecological processes (Ferraz et al. 2005; Ferraz et al. 2014; de Rezende et al. 2015; Rappaport et al. 2015) and biodiversity conservation (Uezu and Metzger 2016; Moraes et al. 2017). This benefit is questionable, however, if regenerating forests replace mature ones (Ferraz et al. 2005; Teixeira et al. 2009; Ferraz et al 2014), if replacement encroaches the opened savannah (Bond and Parr 2010) and if at the expense of other types of natural environments.

Our findings support the two later processes and contradicts the trend observed elsewhere of forest recovery over anthropogenic lulc classes such as pastures, sugar cane, silviculture and abandoned lands (Ferraz et al. 2014; Silva et al. 2016; Molin et al. 2017; Moraes et al. 2017). In our landscapes, considerable amounts of native forests are increasing at the expense of marshlands and native open vegetation (summing 12.5% in each FCP and FEC), while only a minor amount of pastures (1.55%) turned into forest since 1962. In our understanding, marshland replacement by native forest at EEJ (around 2%) is of less concern than the savanna encroachment occurred in FCP and FEC, where savanna has predominated (and was the main original vegetation cover).

Savanna encroachment is an issue debated worldwide and it is assumed to be driven mainly by climatic (increase of atmospheric CO_2 concentration) and human-induced factors (fire suppression and overgrazing, Bond and Parr 2010). The consequences of this process may be irreversible if setting objectives and management aren´t applied (Cava et al. 2017), leading to environmental homogenization, the decrease of species abundance (Soto-Shoender et al. 2018) and species loss (Livingston et al. 2016; Pinheiro et al. 2016, Abreu et al. 2017). Under the scope of the present study, it is not possible to pinpoint the specific anthropogenic and environmental factors acting in this process of forest gain (Silva et al. 2016). Notwithstanding, based on literature reports and the regional context of these agricultural landscapes, we consider three factors that might be causing afforestation in the studied landscapes.

The first potential factor favorable to forest increase during the studied period is the increasing compliance to Brazilian environmental laws, specifically the Forest Code (Brasil 1965), which includes in its terms the protection and restoration of forests along riverbeds (called Areas of Permanent Protection, APP). According to Brancalion and collaborators (2016), the onset of effective compliance by landowners started after the promulgation of the Law of Environmental Crimes (1998), which made authorities capable to control and punish landowners responsible by environmental irregularities. At that time, the regularization of native vegetation cover of public and private lands emphasized the protection of water bodies (springs, rivers and reservoirs) and didn't accounted for specific Cerrado restoration guidelines. These became available in São Paulo State in 2014 (under the Resolution nº 32/2014, SMA 2014), but through passive and active restoration (planting seeds or saplings). Thus, with water availability along riverbeds, tree restoration/grow was favored (Silva et al. 2008) with consequent changes into abiotic conditions of the soil, all facilitating the substitution of open vegetation areas into native forests (Pinheiro et al. 2016; Targa et al. 2017) instead of open Cerrado (Cava et al. 2017).

Simultaneously to the above-mentioned legislation-driven transformations, another factor that might have contributed to this increasing compliance to environmental laws was social and environmental requirements for international certification, aiming at commodities and other agricultural goods for exportation (Brancalion et al. 2016). This certification process is older and consolidated for the forestry industry (Silva et al. 2016, Molin et al 2017). The commitment of forestry companies to environmental requirements for certification in the long term includes, for example, the reduction of the area necessary to produce cellulose and promotion of environmental restauration of thousands of hectares (proportional to the silvicultural farm size) inside their own lands. Contrary to other sectors (Moledo et al. 2016), forestry industry does not compensate for this using lands available elsewhere. Similarly, Silva and collaborators (2016), in a study conducted at Atlantic Forest region, pointed out the silviculture among the main drivers of native forest regeneration. In this manner, considering the highest levels of forest recover found at FCP and FEC, where silviculture predominates for decades and replaced much of native open vegetation, it seems reasonable to consider this aspect as a proximate cause of native forest gain. The last important aspect to be mentioned is the contemporary management of fire suppression practiced both at silviculture and sugarcane plantations.

Valduga and collaborators (2016) indicate fire suppression among the positive ecological impacts cited for silviculture in Brazil. It is also an agricultural and environmental commitment established at São Paulo State for sugar cane production a decade ago, that resulted in a permanent program called “Greener Ethanol Program” (SMA, 2017), an initiative sealed between environmental agencies and sugar cane producers to improve the reduction of atmospheric emission of gases. This pact included the complete banishment of fire management in sugar cane crops during the pre-harvesting phase (among other objectives). It is unquestionable that fire suppression is a beneficial practice for agricultural purposes, as it reduces atmospheric emissions and protect small forest remnants (in general). However, it may exert a negative effect into the management of natural savanna ecosystem, where spontaneous burn is a natural environmental element. Seasonal fires are a key component that maintain savannas and grasslands environments structurally open, controlling the establishment and growth of fire sensitive trees (Bond and Parr 2010) preventing, therefore, the enclosure of the open savannah in the medium and long term. Indeed, this is an issue of even higher concern for savanna-protected areas immersed in human-modified landscapes.

It is known that gallery forests are a natural part of savanna pristine areas of Brazil and its natural occurrence reaches the proportion of 5% at the landscape level (Silva et al. 2008). These forests along riverbeds harbors one third of total Cerrado's species richness (specially climbers species and trees) and, in this manner, are contributing both for biodiversity and heterogeneity surplus. Notwithstanding, at the landscapes of the present study, the percentage of forest at the open vegetation study landscapes (FCP and FEC), started at this proportion (or under at FEC) in 1962 and showed a sharp rise (far above the natural proportion) in the last temporal landscape considered in this study (2010), what represents an anomalous increase for savanna dominated landscapes. The effects of this vegetation turnover for neotropical biodiversity is still poorly known (Abreu et al. 2017).

Based on our findings, we insight that due to decreased landscape dynamic and consolidation of large crops in the region, anthropogenic-dominated Cerrado landscapes might face stabilization in terms of vegetation loss. However, increasing forest cover in detriment of open savannas represent a conservation challenge for environmental agencies in promoting the maintenance of environmental heterogeneity of native open vegetation remnants, both at private and public lands. The chances of losing Cerrado heterogeneity and its inherent biodiversity is contemporary and real (not a prediction) and thus, governmental and private consent are necessary to conserve and maintain the open Cerrado. Our objective recommendation for similar or analogous naturally heterogeneous landscapes is simple (yet not always feasible): obtaining aerial images old enough to represent the beginning of the transition period of interest with the best resolution quality as possible, raise geoprocessing efforts to achieve better mapping resolution in order to differentiate land cover classes of interest and follow similar rationale described in this study in order to check if the original proportion of distinct vegetation types maintain itself throughout landscape trajectory and finally, set the appropriated restoration technics for that specific environment if necessary.

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Chapter 2

Time-lagged response of mammals in human-dominated Cerrado landscapes

Authors: Victor G Krepschi[1]*, Larissa L Bailey[2], Nielson AS Pasqualotto[4], Thiago F Rodrigues[4], Natalia F Versiani[3], Roberta M Paolino[4], Milton C Ribeiro[1] and Adriano G Chiarello[3]

[1] Universidade Estadual Paulista (Unesp), Rua 24ª 1515, Instituto de Biociências, Departamento de Ecologia, Rio Claro, São Paulo, Brasil

[2] Colorado State University (CSU), Fish and Wildlife Conservation Biology Department, Fort Collins, Colorado, United States of America

[3] Universidade de São Paulo (USP), Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Ribeirão Preto, São Paulo, Brasil

[4] Universidade de São Paulo (USP), Escola Superior de Agricultura Luiz de Queiroz (ESALQ), Piracicaba, São Paulo, Brasil

**corresponding author: vkrepschi@gmail.com*

Abstract

The understanding of species responses to their primary habitat changes comprehends an issue of utmost importance given the effects of anthropogenic activities on the environment. However, the timing of biological responses doesn’t necessarily occur just after habitat disturbance and might take years to happen. These delayed responses differ among species due to their biological idiosyncrasies, such as life-span and sensitiveness to habitat change. If the new characteristics of the modified environment do not fulfill species ecological needs, they face populational decline and even local extinction. The medium and large-sized mammal community is a biological group of interest in delayed-response arena due to their higher longevity, the important role that species play in the ecosystem and their persistence in agricultural human-modified landscapes. However, they have been little studied on this respect. Thus, we aimed at detecting the existence of time-lagged responses in seven species of neotropical medium and large-sized mammal species with distinct tolerance to habitat loss in human-modified landscapes of the Cerrado biome (the Brazilian savanna). We selected two landscapes harboring important remnants of native vegetation and used occupancy estimation model in the single season/single species framework (accounting for imperfect detection of species) in order to test if the current species occupancy is associated with present or past time native environment cover. Our results showed that three species still present time-lagged responses to native open vegetation: the giant anteater (*Myrmecophaga tridactyla*), the maned wolf (*Chrysocyon brachyurus)* and the brown brocket deer *(Mazama gouazoubira)*. The maned wolf also presented, however, a negative response to sugar cane of the present landscape. The delays in species response lasts 48 years and according to a literature-based estimation, a range of 40 to 60 years is expected to the first species disappearance. Additionally, we found that unpaved roads are important elements in species detection at the modified landscape, influencing both positively and negatively species movements, which is also an issue of conservationist concern. Considering that all delayed responses were found in the landscape covered by open Cerrado environment and that our analysis were based on species-area relationship, we conclude that in order to revert species decline and safeguarding biodiversity is necessary to enforce protection of remnants and adopt specific management to restore the open Cerrado.

Keywords: occupancy, time-lag, delayed responses, extinction debt, maned wolf, giant anteater, brown brocket deer

Introduction

The loss of biodiversity occurring in the Anthropocene is comparable to a mass extinction event (Dirzo et al. 2014). Human activities are responsible for environmental changes, being habitat loss the main threat for continental species persistence (Fahrig 2003). The conversion of continuous natural ecosystems into smaller and disconnected remnants immersed in human-dominated matrix (Ribeiro et al. 2009) modify the biological community composition originally inhabiting the landscape (Jorge et al. 2013; Beca et al. 2017, Magiolli et al. 2016), but such modification might not necessarily occur right after disturbance, but involves a time delay to happen. This interval of time between environment modification and the establishment of a new stationary equilibrium in community composition is known as relaxation time (Diamond 1972, Brooks et al. 1999). During relaxation time, species (or community) are still adapting to the new conditions of the modified environment and both immigration and extinction may happen in the landscape (Jackson and Sax 2010). If no immigrations occurs and habitat requirements are no longer available for one or more species of the community during this time lapse, populations are expected to face reproductive and competitive failure, what may account for local extinctions (Jackson and Sax 2010). Even though realized extinctions can only be accounted at the end of the relaxation time, it is possible to predict the number of species expected to go extinct in a landscape (Kuussaari et al. 2009), an ecological process named extinction debt (Tilman et al. 1994).

Extinction debt can be detected in distinct hierarquical levels (Hylander and Ehrlén 2013) and several mechanisms influence its magnitude (amount of species to be lost) and duration (Hanski and Ovaskainen 2002). There exist many ways of detecting extinction debt and most of them relies on species area relationship (Kuussaari et al. 2009; Chen and Peng 2017). One practical way (given the difficulty of obtaining standardized past biological data) consists in comparing the correlation of present biological data with both present and past landscape traits (Kuussaari et al. 2009). If the correlation with past landscape traits is stronger than with the present landscape traits, it is assumed that species present(s) time-lagged response(s), and as consequence, exists an evidence of extinction debt. Up to date, different biological groups have been investigated regarding time-lagged responses in the extinction debt approach: herbaceous plants (Alofs et al. 2014), insects (Bommarco et al. 2014), trees (Lindborg and Eriksson 2004, Vellend et al. 2006, Metzger et al. 2009), amphibians (Metzger et al. 2009, Piha et al. 2007, Semlitsch et al. 2017), reptiles (Halstead et al. 2014), birds (Ferraz et al. 2003, Uezu and Metzger 2016), small mammals (Pardini et al. 2010) and bats (Yamanaka et al. 2015). Notwithstanding, knowledge regarding time-lagged responses of medium and large-sized mammal (mlsm) species are still scarce and controversial in literature (Colishaw 1999, Sales et al. 2015, Semper-Pascual et al. 2018).

Current knowledge regarding mlsm delayed responses is mainly supported by two recent studies at community level (Colishaw 1999, Semper-Pascual et al. 2018) and another, at species level (Sales et al. 2015). Two of them indicate mlsm delayed responses higher than 11 years (up to 25 years in terrestrial mlsm species) after disturbances (Sales et al. 2015, Semper-Pascual et al. 2018) and is attributed to mlsm lower reproductive rates (Sales et al. 2015). By the other hand, African primates still present extinction debt even after half century since disturbance (Cowlishaw 1999). Altogether, these evidences of delayed responses in distinct mlsm groups corroborates that duration may also vary among species according to life span (Halley et al. 2016). Regarding detection of such time-lagged responses, mlsm species are not an exception from the general consensus that dependence on natural habitat improves species responses detection (Kuussaari et al. 2009; Pardini et al. 2010; Yamanaka et al. 2015). Through model selection comparison, strength of mlsm forest-dwelling species group response was higher than the whole mlsm community altogether (Semper-Pascual et al. 2018), leading to the conclusion that species with broader environmental use (e.g., the giant anteater), lack habitat specificity and make use of ecotone zones and heterogeneous landscapes, decreasing detection of their responses (Semper-Pascual et al. 2018). Notwithstanding, this landscape scenario is common in savannah environments, which includes opened natural environments besides native forests, as well in human-modified landscapes, and the understanding of mlsm species delayed responses requires a step forward in disentangling distinct environmental types and species specific responses.

When aiming to the species level approach, monitoring population is necessary. For mlsm, this requires substantial efforts and financial support and choosing a reliable method is of utmost importance. Among methods available, estimating species occupancy (Mackenzie et al. 2017), has been proving practical (not being necessary to mark individuals at field) and accurate due accounting for imperfect detection, a statistical framework which diminishes the bias of false absences (Mackenzie et al. 2006). Currently, there is a wide array of occupancy estimates appliances in mlsm studies (Paolino et al. 2016; Heim et al. 2017; Rodrigues et al. 2017; Massara et al. 2017; Xavier et al. 2018) and specifically for time-lagged studies, attempts has been scarce but proved successful (Sales et al. 2015). Thus, in the present study we aim detecting time-lag responses of neotropical mlsm species that persist (Lyra-Jorge et al. 2010; Paolino et al. 2016) in natural remnants of anthropic modified landscapes at an ecotonic region between Atlantic Rainforest and Brazilian savannah (Cerrado), where drastic replacement of native vegetation cover occurred almost fifty years ago (Shida 2005).

Among the studied mlsm species occurring in the study areas, we predict that those species with more specializations to native vegetation are also the more sensitive to habitat modification (also recognized as specialized species). As consequence, they may present longer delay in response to habitat change. The maned wolf (Dietz 1984) and collared peccary (Keuroghlian et al. 2004) are species of which we expect time-lagged responses to past native vegetation, respectively to native open vegetation and native forest. By the other hand, those species with less specificity to habitat and less sensitive to habitat modification, such as the giant anteater, crab-eating fox, brown brocket deer, puma and ocelot might not present delayed responses to neither vegetation types, resembling their plasticity and generalist behavior in terms of habitat requirements.

Material and Methods

Study areas

Our three study areas are located in the Northeastern region of São Paulo State, Brazil (21^{o}02’ – 21^{o}43’S and 47^{o}54’ – 47^{o}16’W; Figure 1). This region harbor important protected remnants of Cerrado forest (also called “Cerradão”), open Cerrado (also called “Cerrado stricto sensu”) and Areas of Permanent Protection (APP), enforced as Conservation Units. We included a 5km buffer zone around them, which comprises remnants of native vegetation immersed in matrix of anthropogenic use. Sugar cane plantations and forestry (*Eucalyptus* and *Pinus*) are the main agricultural activities and, in a less extent, pasture and orange plantations. Due the presence of a large river (Mogi-Guaçu River) and the flat relief, marshlands occur in the landscape. Climate varies from a warm and wet season (October – March) to a cold and a dry season (April – September), with most of annual precipitation (1470mm) concentrated in the former and an average temperature of 21.6°C (annual range: 14 – 28°C; CEPAGRI, 2014).

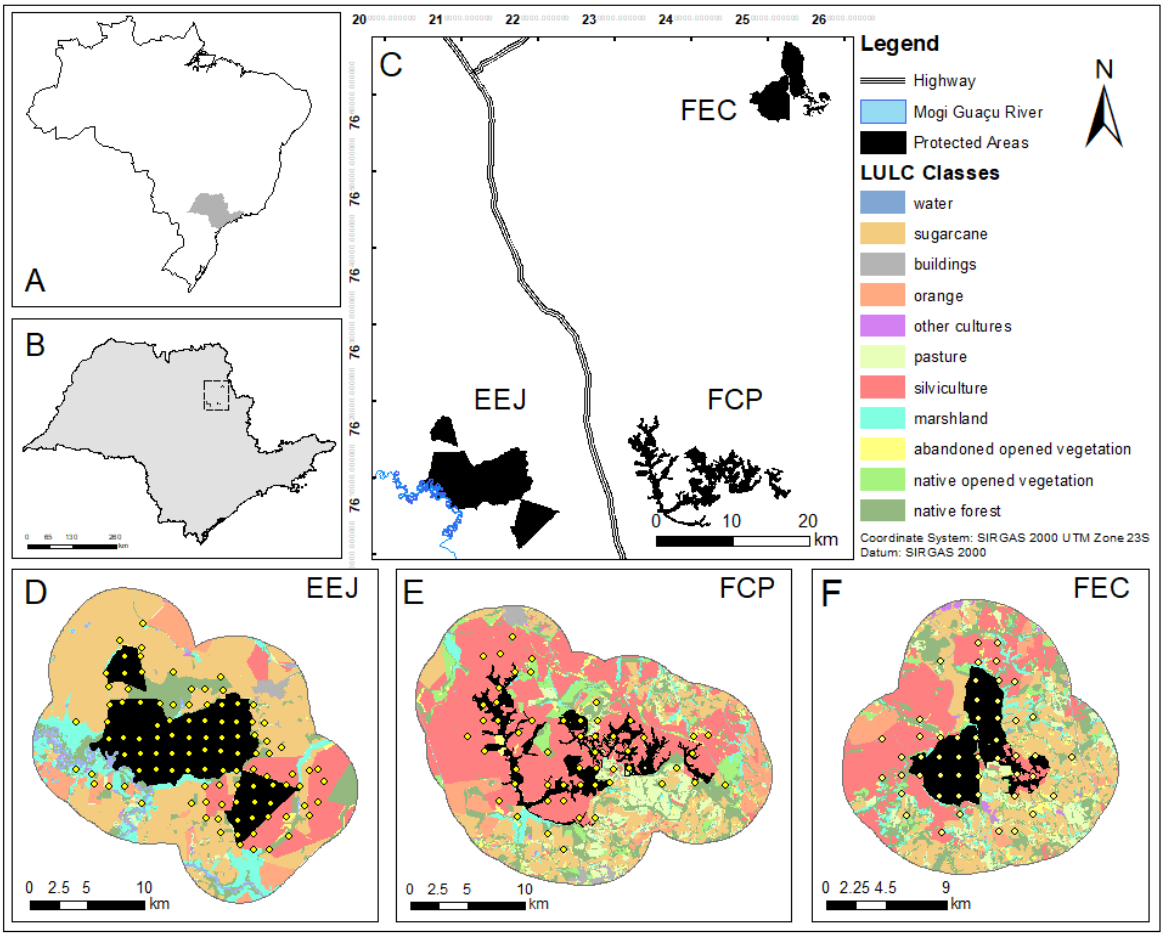

Figure 1. Location of São Paulo State (grey shaded) in Brazilian geopolitical map (A), location of studied landscapes evidenced inside the dashed square at São Paulo State geopolitical map (B) and studied landscapes protected areas (in black) in the regional context (C). Figure D to F show each studied landscape individually, comprised by the PA (in black) and their buffer zone, determined by a 5 km radius from the PA's edge, including main current land use and land cover classes (distinct colors) and the yellow dots the location of camera-trap station settlement. Abbreviation of landscape names: EEJ: "Jataí" Ecological Station, FCP: "Cara Preta" Farm and FEC: "Cajuru" State Forest.

Land use and land cover characterization and landscape covariates

We classified land use and land cover (lulc) of the areas in 1962, 1983 and 2010 time scenes by visual identification of aerial photographs in a 1:10,000 scale (for detailed description, see mapping procedure section in Chapter 1). The mapping procedure resulted in eleven lulc classes (native forest (vnf), native open vegetation (vna), marshlands (var), sugar cane (can), managed forests (silv), orange plantations (lar), pasturelands (pas), open abandoned vegetation (vaa), urban area (ua), water and others (out)). For each lulc class we generated one landscape covariate calculating its proportion on the focal landscape (200 ha circular landscape around sampling point) through moving window procedure in GrassGIS (Grass Development Team, 2015). In addition, we included distance measurements from the sampling point as site covariates (urban distance (ud), native forest distance (nd) and water distance (wd), mean temperature (temp), edge (30 m of width from interface inward native forest), area of water surface (wa) and density of rivers (dens). All covariates used in mammals modelling were selected based on mammal species literature (table S1; Supplementary Material).

Sampling design

For each study area, we overlaid a squared grid of 200 ha cells to maximize independency between sampling points on the basis of giant anteater ranging (see Paolino et al. 2016 and Rodrigues et al. 2017). Cell centers were assigned as potential sampling points, of which we randomly selected 206 (102 in EEJ and 52 in FCP and 52 in FEC). Half of the selected points occurred inside protected areas and half of them outside protect area (buffer zone). We assumed that this sampling design satisfied the independence assumption among adjacent sampling points (average distance of 1400m between sampling points) and assured a balanced effort inside and outside protected areas. Some selected points were replaced due to logistic limitations (inaccessibility) and those located within sugarcane crops were relocated (for safety reasons) to the nearest native vegetation fragment but facing this environment.

Mammal surveying

We surveyed medium and large-sized mammals through camera-trapping during two consecutive dry seasons (April through September of years 2013 and 2014, totaling 12 months). At each selected sampling point, one camera-trap station (Reconyx HC500 HyperFire®) was deployed in tree trunks (~ 40cm above the ground); vegetation that could interfere in camera view was cleared and cameras were tested for triggering. Each camera trap station remained operational during 30 consecutive days. At the end of this period, the camera-trap device was recovered for batteries replacement, to substitute the memory card and to be settled in the next sampling point. Eighteen camera-trap stations operated simultaneously every month, resulting a total sampling effort of 6,240 camera-trap days during the entire mammal survey.

Native vegetation transition in the landscapes

We compared native vegetation transition among studied areas in order to verify that all three areas could be grouped (or not) in mammals occupancy analysis (for detailed description see Statistical Analysis section from Chapter 1). We found that the predominant vegetation type of EEJ in 1962 and its main changes occurred in native forest, while in FCP and FEC, the original vegetation type and main changes occurred in native open vegetation (see detailed description in results of Chapter 1). Thus, we analyzed EEJ landscape (n=102 sampling points) separately from FCP and FEC landscapes (n=104 sampling points), which were treated as a single landscape (FCP+FEC). Additionally, we made paired comparisons of native vegetation between time scenes within landscapes. This comparison showed that native vegetation of 1983 time scene was correlated to 2010 time scene in all landscapes (Pearson correlation coefficient > 0.6), which led us to exclude 1983 time scene from all analyses.

Mammal species

We tested time-lagged responses for seven medium and large-sized mammal species: maned-wolf (*Chrysocyon brachiurus*), collared peccary (*Pecari tajacu*), giant anteater (*Myrmecophaga tridactyla*), brown brocket deer (*Mazama gouazoubira*), ocelot (*Leopardus pardalis*), puma (*Puma concolor*) and crab-eating fox (*Cerdocyon thous*). These species were selected due their longevity, responsiveness to natural environment changes and data sufficiency (highest number of presences in the history of detection of our dataset and elevated number of camera-trap records).

Statistical Analysis

Occupancy estimation models

We adopted occupancy estimation models accounting for imperfect detection, using a single-season/single-species approach (MacKenzie et al. 2017) incorporated in MARK (White and Burnham 1999). Our primary goal was to determine if each species occurrence was better explained by natural vegetation conditions in the past (1962) or in the present (2010), the occupancy covariates. Based on the 30 days of monitoring at each camera trap, we generated a detection history (detection/non-detection data) consisting of six independent occasions of 5 days each (e.g., 100101). The set of detection histories for each species for each landscape was joined with species-specific covariates thought to influence detection (z-scored and not correlated - Pearson correlation coefficient value < 0.6). We tested all possible combinations of the detection covariates selected for each species (Supplementary Material, table S1), with the occupancy covariates of native vegetation of the present or from the past. This procedure resulted in a balanced model set (covariates of the model set occur in the same number of times), allowing multi-model inference (Burnham and Anderson 2002) to compare multiple hypothesis (models) to determine which best explains our data. Akaike Information Criterion (AIC) was used to rank models and those with $\Delta\text{AIC} < 2$ were considered equally plausible. We evaluate the importance of each covariate through cumulative model weights (Burnham and Anderson 2002). Even though the top ranked model represent the most parsimonious model, given our data, in some cases, equally plausible models were also interpreted, mainly due biological meaningfulness. We evaluated the precision of covariates effects by reporting/examining upper and lower 95% confidence intervals from selected models and reporting if these confidence intervals overlapped zero.

Time-lagged responses

Time-lagged responses were assumed if species occupancy was best modeled by past (1962) rather than the current (2010) native vegetation. Because landscapes differed in the original (1962) native vegetation type, we used detection data from EEJ to test species responses for native forest and we used detection data from FCP and FEC (combined) to test species responses to changes in open native vegetation. By doing so, we focused on the effect of the vegetation that originally (1962) covered most of the area in each one of these landscapes. Among the seven species analyzed, time-lagged responses of collared peccary was tested only at EEJ due to the low number of camera trap records at FCP+FEC landscape. All the remaining six species were tested separately for both landscapes. If time-lagged response was found for a given species, we performed a “post hoc” modelling comparing the best past native vegetation model with models containing distinct combinations of current land cover classes. We did this to access how much better (or worse) the response from past vegetation on occupancy is when compared to the current anthropogenic landscape (sugar cane, managed forest, current native open vegetation and current native forest).

Results

Detection Covariates

The best set of covariates of detection for each species at FCP+FEC and EEJ landscapes is reported in tables 1 and 2, respectively. Unpaved roads (roads) was the most important covariate of detection among medium and large-sized mammals in the landscapes of this study, influencing detection of six of seven species. Ocelot was the only species we couldn´t find a good structure of detection, probably due the low number of records in our sampling. Maned wolf, giant anteater, crab eating fox and puma responded positively to unpaved roads, that is, detection probability was higher when camera traps were placed on unpaved roads. On the other hand, brown brocket deer and collared peccary responded negatively.

Additively to roads, both temperature (temp) and density of rivers (dens) influenced positively the collared peccary detection. The negative influence of unpaved roads in detection was also observed for brown brocket deer in FCP+FEC, together with open abandoned vegetation and water distance (both positively). At EEJ landscape, the best set of covariates for detection of the brocket deer was pasture and abandoned open vegetation, both increasing detection. The remaining species presented the same structure of covariates of detection for both landscapes (tables 1 and 2), but the effect of some covariates differed.

Table 1. Top ranked models (ΔAICc < 2) at FCP+FEC for the studied mammal species.

Species	**AICc**	**ΔAICc**	**wAICc**	**L**	**K**	**deviance**
Maned wolf						
p(road)Ψ(vna62)	467.90	0.00	0.54	1.00	4	459.50
Giant anteater						
p(protec+road+wa)Ψ(vna62)	440.84	0.00	0.25	1.00	6	427.97
p(protec+wa)Ψ(vna62)	441.44	0.60	0.19	0.74	5	430.82
p(protec+road+wa+ua)Ψ(vna62)	442.35	1.51	0.12	0.47	7	427.17
Brown brocket deer						
p(road+wd+vaa)Ψ(vna62)	327.95	0.00	0.17	1.00	6	315.08
p(road+wd+vna10+vaa)Ψ(vna62)	328.46	0.51	0.14	0.78	7	313.29
p(road+wd)Ψ(vna62)	329.35	1.39	0.09	0.50	5	318.73
p(wd+vaa)Ψ(vna62)	329.45	1.49	0.08	0.47	5	318.83
p(wd+vna10+vaa)Ψ(vna62)	329.74	1.78	0.07	0.41	6	316.86
Puma						
p(protec+road+ud)Ψ(.)	271.88	0.00	0.25	1.00	5	261.26
p(protec+road)Ψ(.)	273.15	1.27	0.13	0.53	4	264.75
p(protec+road)Ψ(vna62)	273.47	1.59	0.11	0.45	5	262.85
p(protec+road+UD)Ψ(vna62)	273.72	1.83	0.10	0.40	6	260.84
Crab-eating fox						
p(road+temp+wa)Ψ(.)	333.30	0.00	0.21	1.00	5	322.69
p(protec+road+temp+wa)Ψ(.)	333.82	0.52	0.16	0.77	6	320.94
p(road+temp+wa)Ψ(vna10)	335.00	1.70	0.09	0.43	6	322.13
p(road+temp)Ψ(.)	335.17	1.86	0.08	0.39	4	326.76

Table 2. Top ranked models (ΔAICc < 2) at EEJ for the studied mammal species.

Species	AICc	ΔAICc	wAICc	L	K	deviance
Maned wolf						
p(road)Ψ(vnf10)	252.84	0.00	0.97	4.00	244.43	244.43
Collared peccary						
p(road+temp+dens)Ψ(vnf10)	344.89	0.00	0.16	1.00	6	332.00
p(road+temp)Ψ(vnf62)	345.04	0.15	0.15	0.93	5	334.41
p(road+temp)Ψ(vnf10)	345.04	0.15	0.15	0.93	5	334.42
p(road+temp+dens)Ψ(vnf62)	345.70	0.81	0.11	0.67	6	332.82
Giant anteater						
p(vnf10+road+wa)Ψ(vnf62)	377.73	0.00	0.17	1.00	6	364.84
p(wa)Ψ(vnf62)	379.36	1.63	0.07	0.44	4	370.95
p(road+wa)Ψ(vnf62)	379.63	1.90	0.07	0.39	5	369.00
p(vnf10+road+wa+ua)Ψ(vnf62)	379.66	1.94	0.06	0.38	7	364.47
Brown brocket deer						
p(vaa)Ψ(.)	407.82	0.00	0.12	1.00	3	401.58
p(past+vaa)Ψ(.)	407.87	0.05	0.12	0.97	4	399.46
p(past+vaa+silv)Ψ(.)	408.97	1.15	0.07	0.56	5	398.35
p(vaa+silv)Ψ(.)	409.56	1.73	0.05	0.42	4	401.14
p(vaa)Ψ(vnf10)	409.65	1.83	0.05	0.40	4	401.24
Puma						
p(vnf10+ud+road)Ψ(vnf62)	294.04	0.00	0.27	1.00	6	281.15
p(vnf10+ud+road)Ψ(.)	294.09	0.05	0.27	0.97	5	283.46
p(vnf10+road)Ψ(.)	295.32	1.28	0.14	0.53	4	286.91
p(vnf10+ud+road)Ψ(vnf10)	295.71	1.68	0.12	0.43	6	282.83
p(vnf10+road)Ψ(vnf62)	295.73	1.69	0.12	0.43	5	285.11
Crab-eating fox						
p(road+temp+wa)Ψ(vnf10)	204.65	0.00	0.42	1.00	6	191.77
p(road+temp)Ψ(vnf10)	204.89	0.24	0.37	0.89	5	194.27
Ocelot						
p(.)Ψ(.)	285.54	0.00	0.21	1.00	2	281.42
p(.)Ψ(vnf10)	286.72	1.18	0.12	0.55	3	280.48
p(wa+temp)Ψ(.)	287.36	1.81	0.09	0.40	4	278.94

Time-lagged responses

We constructed 13 model sets to explore time-lagged responses for our selected mammal species (tables 1 to 3). We found evidence of time-lagged responses for three species: maned wolf, brown brocket deer and giant anteater in FCP+FEC landscape (table 3). The remaining species (collared peccary, puma, crab-eating fox and ocelot) didn´t present temporal responses; their occupancies were either affected more strongly by the current vegetation or were constant across all sites/camera stations (table 3). No time-lagged responses were found in EEJ landscape (table 3); top ranked models (ΔAICc < 2) of each model set are shown in table 1 (FCP+FEC) and table 2 (EEJ).

Table 3. Summary of results from time-lagged models of each mammal species in each landscape. Positive result for time-lagged responses highlighted in bold. Response to occupancy covariates column indicates if species responded positively, negatively or imprecisely to present or past native vegetation cover. "Low number of detections" indicates insufficient number of camera-trap records to perform the occupancy estimates analysis.

Species	Landscape	Time lag	Best structure of detection	Response
Maned wolf	EEJ	no	p(road)	negative to vnf10
	FCP+FEC	**yes**	p(road)	positive to vna62
Giant anteater	EEJ	no	p(vnf+road+wa)	negative to vnf62
	FCP+FEC	**yes**	p(protec+road+wa)	positive to vna62
Brown brocket deer	EEJ	no	p(past+vaa)	negative to vnf62
	FCP+FEC	**yes**	p(road+wd+vaa)	positive to vna62
Collared peccary	EEJ	no	p(road+temp+dens)	positive to vnf10
Puma	EEJ	no	p(vnf10+ud+road)	negative to vnf62
	FCP+FEC	no	p(protec+ud+road)	imprecise to vna62
Crab-eating fox	EEJ	no	p(road+temp+wa)	negative to vnf10
	FCP+FEC	no	-	low number of detections
Ocelot	EEJ	no	p(.)	low number of detections
	FCP+FEC	no	-	low number of detections

The best occupancy model for maned wolf at FCP+FEC landscape indicates a strong and positive relationship with native open vegetation of 1962 (figure 2A). Model weight was high (wAICc = 0.54) and there was no other equally plausible model (ΔAICc < 2) among the top ranked models (table 1). *Post hoc* modeling showed this species occurrence as negatively influenced by current amounts of sugar cane (figure 2B), but an equally plausible response to past native environment (table 4; see also table S2 of Supplementary Material for the complete model set). At EEJ landscape, the only top ranked occupancy model (ΔAICc < 2, table 3) of maned-wolf showed a precise and negative response to current native forest (figure 2C).

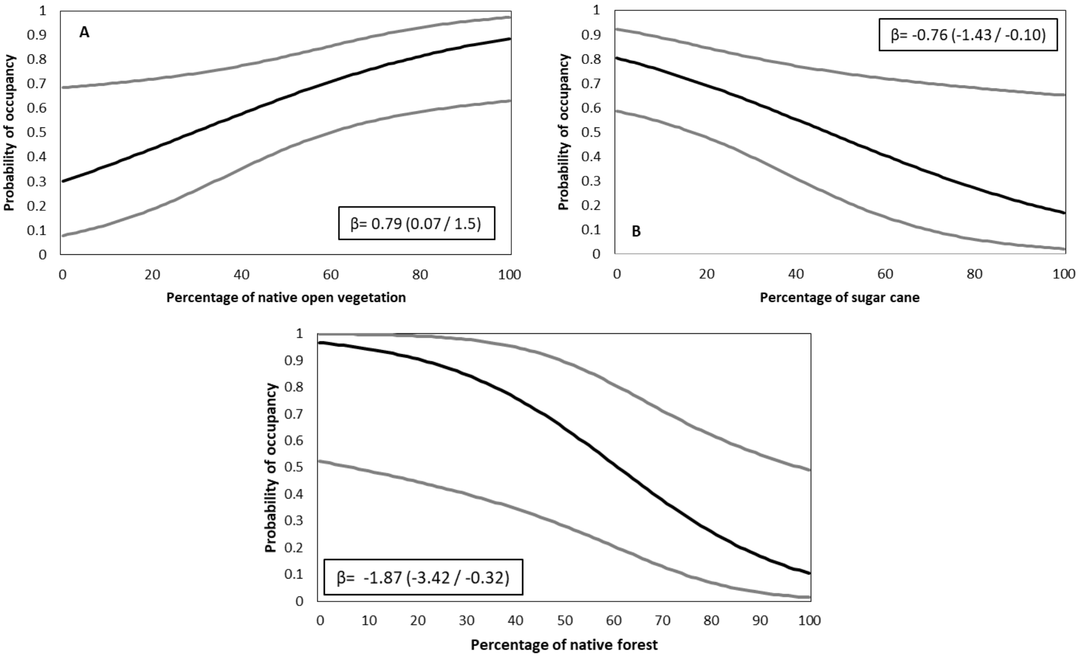

Figure 2. (A) Maned wolf responses to the proportion of native open vegetation available in 1962 at FCP+FEC, (B) to the percentage of sugar cane available in 2010 in this same landscape and (C) to native forest in 2010 at EEJ landscape. Dark lines represent the occupancy estimates and grey lines its upper and lower 95% confidence interval. Beta estimates followed by its lower/upper coefficient interval values is displayed into chart.

Table 4. Top four models of maned wolf, giant anteater and brown brocket deer from *post hoc* modeling at FCP+FEC.

Species	AICc	ΔAICc	wAICc	L	K	deviance
Maned wolf						
p(road)Ψ(can)	467.64	0.00	0.27	1.00	4.00	459.24
p(road)Ψ(vna62)	467.91	0.26	0.24	0.88	4.00	459.50
p(road)Ψ(can+silv)	469.49	1.84	0.11	0.40	5.00	458.87
p(road)Ψ(silv)	469.50	1.85	0.11	0.40	4.00	461.09
Giant anteater						
p(protec+road+wa)Ψ(vna62)	440.84	0.00	0.51	1.00	6.00	427.97
p(protec+road+wa)Ψ(.)	444.11	3.27	0.10	0.20	5.00	433.49
p(protec+road+wa)Ψ(silv)	444.64	3.80	0.08	0.15	6.00	431.77
p(protec+road+wa)Ψ(can)	444.82	3.98	0.07	0.14	6.00	431.95
Brown brocket deer						
p(road+wd+vaa+vna10)Ψ(vna62)	328.46	0.00	0.57	1.00	7.00	313.29
p(road+wd+vaa+vna10)Ψ(.)	332.19	3.73	0.09	0.16	6.00	319.32
p(road+wd+vaa+vna10)Ψ(can)	332.90	4.43	0.06	0.11	7.00	317.72
p(road+wd+vaa+vna10)Ψ(silv)	333.01	4.55	0.06	0.10	7.00	317.83

Similarly, the current occupancy of giant anteater in FCP+FEC landscape was best modeled as a function of past native vegetation (figure 3A and table 1), supporting a time-lagged response to native open vegetation (weight of evidence of vna62 = 0.735). *Post hoc* modeling showed that no current landscape covariate explained variation in this species' occurrence better than the past amount of open native vegetation (wAICc = 0.51, table 4 and table S2). The third mammal species presenting time-lagged effect, brown brocket deer, also included in all top ranked models (ΔAICc < 2) the precise and positive response (figure 3C) to native open vegetation of 1962 as covariate of occupancy (weight of evidence of vna62 = 0.81, table 1). *Post hoc* modeling supported a stronger effect of past natural vegetation than current landscape land cover (wAICc = 0.57, table 4 and table S2).

We didn't find effect of past native forest on brown brocket deer occupancy at EEJ (table 2), thus, no time-lagged response was detected for this landscape. Giant anteater's top ranked models from EEJ (table 2) supported past native forest responses on occupancy (weight of evidence of vnf62 = 0.60; figure 3B), but the trend of this response was negative. The best ranked model presented an imprecise and negative response to 1962 native forest (vnf62), but the second, a precise and negative response to past native forest (Figure 3B). This type of response for vnf62 was also found for collared peccary, our forest dwelling species.

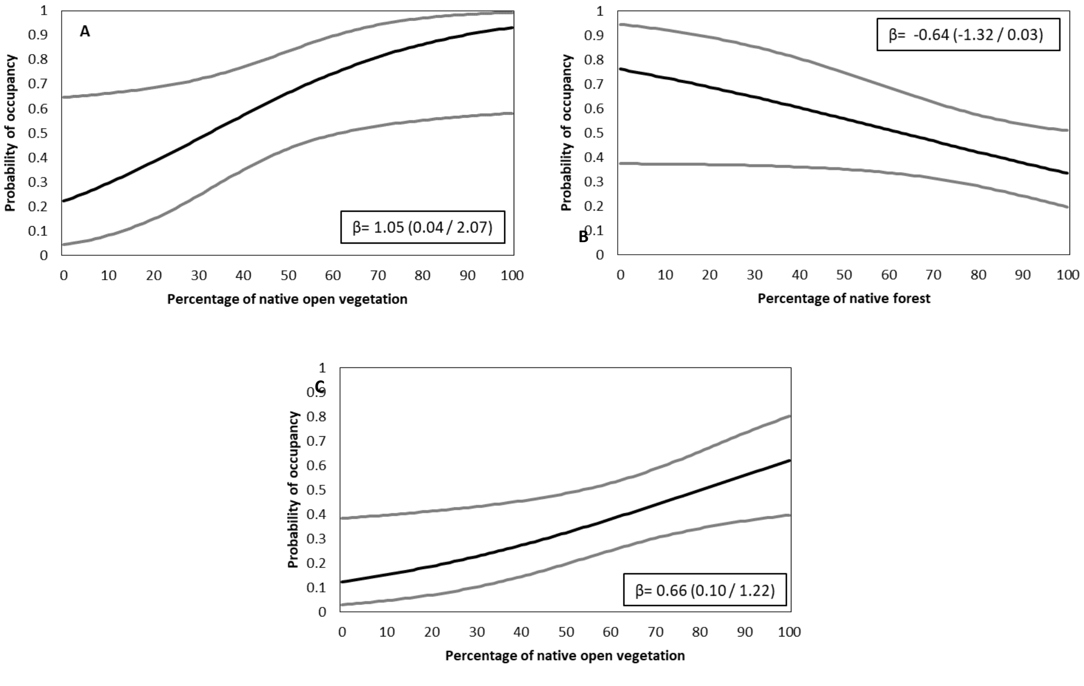

Figure 3. (A) Giant anteater probability of occupancy to past (1962) native open vegetation at FCP+FEC, (B) giant anteater probability of occupancy to past native forest at EEJ and (C) brown brocket deer probability of occupancy to past native open vegetation at FCP+FEC. Dark lines represent the occupancy estimates and grey lines its upper and lower 95% confidence interval. Beta estimates followed by its lower/upper coefficient interval values is displayed into chart.

The best ranked model for collared peccary occupancy (table 2) supported a positive and precise response to current native forest (weight of evidence of vnf10 = 0.48, figure 4A).

However, similarly to giant anteater, a precise and negative occupancy response to past native forest (weight of evidence of vnf62 = 0.35, figure 4B) was found in the second best supported model of the model set (table 2). This effect was inconsistent with our *a priori* expectation for these species and even though these two species support responses to past native forest, we didn’t consider this negative effect of past native forest as evidence of time-lagged responses (table 3). We didn’t detect time-lagged responses for the remaining three carnivore species (crab-eating fox, ocelot and puma) in both landscapes.

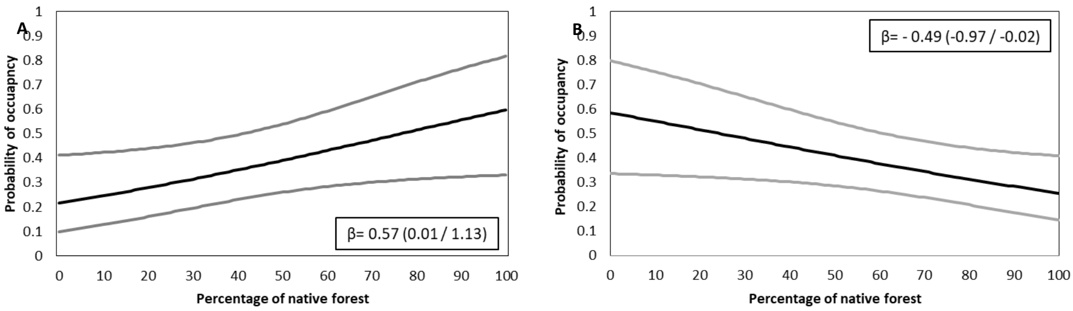

Figure 4. (A) Collared peccary probability of occupancy on current native forest proportion and (B) to past native forest proportion. Dark lines represent the occupancy estimates and grey lines its upper and lower 95% confidence interval. Beta estimates followed by its lower/upper coefficient interval values is displayed into chart.

Crab-eating fox occurrence showed no precise response to native open vegetation in FCP+FEC landscape (table 1), but this fox occurrence was negatively related to current native forest in EEJ landscape (figure 5A and table 2). We suspect that this imprecision we observed for FCP+FEC landscape is due the low number of recordings (34 records of the crab-eating fox from only 13 of 104 camera-trap stations). Similarly, small sample size (only 18 records at 8 camera-trap stations) is probably behind the imprecision we also found for ocelot modelling in this landscape. However, at EEJ landscape, ocelot showed a positive response to current native forest, yet this specific response was weak and imprecise (beta estimates interval overlapped 0), what led us to assume the null model (constant occupancy across stations/sites), the most parsimonious model, as the most reliable in this species occupancy analysis (table 3). The null model means that none of the chosen covariates explained ocelot occupancy.

The puma model set for FCP+FEC supported no occupancy covariate among their top ranked models (weight of evidence of Ψ(.) = 0.52; table 1), however, we found an imprecise, but positive response to past native open vegetation (weight of evidence of vna62 = 0.29; figure 5B). At EEJ, top ranked models included both past and current native forest in occupancy, however, response to these covariates were imprecise (confidence interval of the estimated betas overlapped 0; see table 2). Thus, similarly to FCP+FEC, we found no covariates affecting the occupancy of this cat in EEJ.

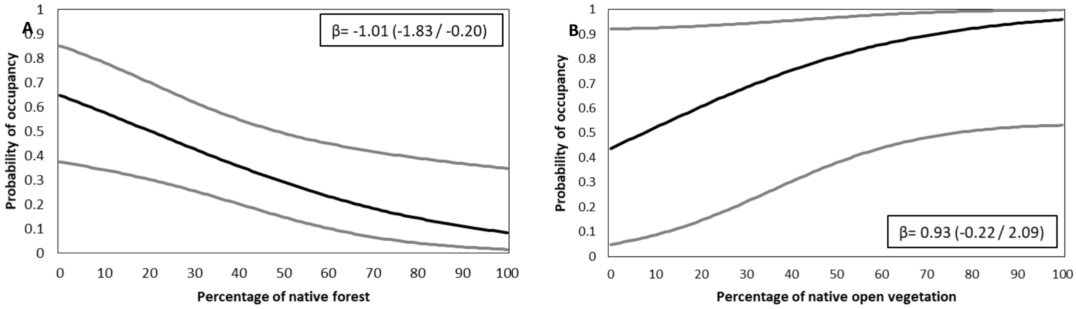

Figure 5. (A) Crab-eating fox occupancy to current native forest at EEJ and (B) imprecise occupancy response of puma to past native open vegetation at FCP+FEC landscape. Dark lines represent the occupancy estimates and grey lines its upper and lower 95% confidence interval. Beta estimates followed by its lower/upper coefficient interval values is displayed into chart.

Discussion

To our knowledge, this is the first assessment of extinction debt for terrestrial medium and large-sized mammals in a detailed species level occupancy approach. The evidence of an underrun 48 years time-delayed responses is far above other vertebrate taxa delay (Metzger et al. 2009; Halley et al. 2016) and for non-arboreal medium and large-sized mammals (Sales et al. 2015; Semper-Pascual et al. 2018). We attribute the longer delay in response of mlsm mainly to the long life-span of the studied species and the lower turnover rates of medium and large-sized mammals, resulting in longer duration of relaxation time after habitat disturbance (Kuussaari et al. 2009; Metzger et al. 2009; Sales et al. 2015). Regarding that, if we develop a conservative approach, supported by recent findings regarding dynamics of extinction debt for small mammals (Halley et al. 2016), an average length of four generations would be necessary until the first species would be extinguished from the landscape. In this manner, assuming a 10 to 15-years life-span for species of this group in the wild (which may be also an underestimation) it would take at least 40 to 60 years interval to the first extinction take place in the modified landscape. Thus, regardless other threats that might affect survival of populations in modified landscapes (e.g. poaching and ecological traps, such as roadkills and poisoning), it is reasonable to assume that we have already lost important and habitat sensitive species of medium and large-sized mammals that potentially occurred at FCP+FEC landscape (such as jaguar, tapir, pampas deer and white-lipped peccary) in the first 40 years after habitat disturbance (since 1962). Further, we are still facing the debt of more resilient species, a populational relaxation that we might face in the next few years until total occupancy find a stationary state to current landscape structure.

Among the many described mechanisms involved in extinction debt phenomena (Hanski and Ovaskainen 2002; Kuussaari et al. 2009; Hylander and Ehrlén 2013; Essl et al. 2015; Kitzes and Harte 2015), two of them make more sense given our landscape reality. The first mechanism possibly affecting delay of species response is the intensity of disturbance (Hylander and Ehrlén 2013). It is known that in intermediary levels of native vegetation loss species takes longer to respond than either low and high levels of native vegetation removal (Hylander and Ehrlén 2013). This may be the case of our landscapes, which lost the majority of their native vegetation (around 70% of their original cover) at the beginning of the observed land cover trajectory, but retained an intermediate level of native vegetation cover nowadays. This intermediary level of native vegetation cover remaining in the landscapes is around 30% of the total landscape cover in 2010, what lead us believing that a second ecological mechanism, critical thresholds (Andrén 1994, Swift and Hannon 2010, Banks-Leite et al. 2014), is also responsible for the longer delays observed in some species responses. According to theoretical approaches developed by Hanski and Ovaskainen (2002) communities close to an ecological threshold show higher delays in species extinction due to a temporary accumulation of species at the landscape level, what in turn, may extent relaxation time and as consequence, extinction debt duration.

Besides these two general landscape mechanisms that might be elongating species responses, it is worth mentioning that marked differences in species responses between savanna environment and forests were found by Semper-Pascual and collaborators (2018) in an extinction debt study conducted in the Argentinean Chaco. This South American biome resembles the Cerrado due to the presence of both forest and open savannah environments. In their study, the extinction debt detected was higher for medium and large-sized mammals forest-dwelling species than the whole community analyzed together. They concluded that the reason behind it is the heterogeneity of savannahs and the many ecotones naturally found in this environment, which poses a challenge in detecting less specialized mammal responses, such as the giant anteater (Semper-Pascual et al. 2018). This fact is congruent with our indebted landscape (FCP+FEC), a heterogeneous savannah landscape, which harbors from open grass fields to closed canopy gallery forest. However, this limitation in detecting less habitat specialized species responses at the community level approach (Semper-Pascual et al. 2018) was improved in the present study by using the species level occupancy estimates.

Among the three species in which we detected time-lagged responses, the highest specificity to open savannah environment was expected for manned wolf (Jácomo et al. 2004;

Dietz 1985; Vynne et al. 2011). This species is a well-known “forest avoider” (Lyra-Jorge et al. 2009; Beca et al. 2017), whilst giant anteater and brown brocket deer make mixed use of the native forest environment (Andrade-Núñez and Aide 2010; Bertassoni et al. 2017; Rodrigues et al. 2017). In this manner, it was rather surprising finding occupancy debt for giant anteater and brown brocket deer in the open savannah environment of FCP+FEC landscape. This is due our expectations that they would find their resources in current forest environments instead of looking for them in the relictual open savannah scattered in the landscape, or in few words, would present a more generalist behavior. Thus, it seems that this “generalist behavior” regarding habitat requirements, commonly attributed for these three species (Andrade-Núñez and Aide 2010; Beca et al. 2017), should be reviewed under the lens of delayed responses. Instead of considering them strictly as species with high environmental “plasticity”, it seems reasonable to start looking at them as “resilient” to environmental changes (Tchabovsky et al. 2016). In this manner, even though these three medium and large-sized mammal species have been proving able to exploit and survive in a modified landscape 48 years after disturbance, it shouldn´t lead us to the simplistic and non-conservative conclusion that anthropic environments found in modified landscapes poses a benefit or are “biodiversity friendly”, until this occupancy debt is completely paid and species responses are correlated with present time native vegetation of the landscape. On the other hand, in our landscapes, puma and crab-eating fox could be considered as more generalist species (non-sensitive to habitat disturbance), as in many other studies (Michalski and Peres 2005; Andrade-Núñez and Aide, 2010; Ferraz et al. 2010; Ferreira et al. 2017; Magioli et al. 2016) due to the absence of a pronounced response to native environments (Uezu and Metzger 2016).

When we compared past natural environment with all possible combinations of current landscape environments (including current native ones) in our *post hoc* models, in exception of maned wolf negative response to proportion of sugarcane, no combination of current landscape covariates explained species occupancy better than past native environment, neither was current native vegetation. This reinforce that species are still responding to past time landscape native vegetation and not solely on the new environments that replace them. One example of that is the previously published study of brown brocket deer in the same landscapes (with the same dataset) of the present study (Rodrigues et al. 2017). The main result of this study was that the brocket deer uses both managed forest (best ranked model) and sugarcane/forest interface more than native environments, which lead the authors to conclude that managed forests might be regarded as a new suitable habitat for brown brocket deer in modified landscapes (Rodrigues et al. 2017). However, the mentioned study didn’t account for species time-delayed responses. With this confrontation, we are not denying the behavioral ability of brown brocket deer and other species in using anthropogenic modified environments, nor the possibility of these environments to provide specific valuable resources for mlsm community. The unresponsiveness for current native vegetation found for giant anteater (Ferreira et al. 2017; Versiani unpublished data; Zimbres et al. 2013) also raises the evidence that this species is still responding past landscape modification (Zimbres et al. 2013). The overall and concerning issue for future time-lag and extinction debt studies should focus, therefore, on assessing how good are these “new” resources in reverting occupancy debt, and which landscape-level measures should be implemented before the end of relaxation time. Yet without response to these questionings, studies addressing this type of goals demonstrate that disturbed areas (such as buffer zones) are not as good as protected and core habitats (Massara et al. 2012, Vynne et al. 2011, Vynne et al. 2014) even for vagile species capable of exploiting the modified environment.

Vagility is one biological trait known to counteract population decline (Semlitsch et al. 2017). However, recent findings show that even vagile medium and large-sized mammals’ movements in anthropogenic landscapes are being negatively affected by human footprint (Tucker et al. 2018). In our studied landscapes, the low density of humans settlements and workers in agricultural management together with the maintenance of 30% of native vegetation (summing forested and opened native environments) seems to be allowing species movements (Villard and Metzger 2014). Notwithstanding, species are exploiting the landscapes in distinct ways, an effect evidenced by the influence of unpaved roads in species detection, leading us to conclude that instead of using generalized community approach, searching for species-specific behavioral responses is necessary to truly assess functional connectivity, even in a highly vagile biological group such as medium and large sized mammals.

The relevance of unpaved roads as covariates of detection for medium and large-sized mammal community was an important result of our study, corroborating the previously described results in literature (Ferreira et al. 2017; Versiani unpublished data; Zimbres et al. 2013). Thus, we strongly suggest that further studies with mlsm community in modified landscapes keep conserving unpaved roads (and trails) as potential covariate of detection. This feature may be involved in species movements, mainly for carnivore species. However, dissimilar responses to unpaved roads were found among species, suggesting that it is enhancing movement for some of them (maned wolf, crab eating fox, puma and giant anteater), in the search for resources in the patchy landscape, but being avoided from others (collared peccary and brown brocket deer). The fact that these prey species may be avoiding predators routes is intuitive, and for them, environments such as managed forests and gallery forests may represent better or safer dispersal routes (Paolino et al. 2018; Rodrigues et al. 2017). Thus, if unpaved roads are being used by many mlsm species as means for exploring the landscape, roadkill incidents must be of conservation concern in modified landscapes. Indeed, this is one of the main threats for many mlsm species (Fahrig 2003, Hanski 2015, Pinto et al. 2018). In the same level of importance, if species avoid unpaved roads to explore the environment, other safer options may be implemented and maintained in the landscape, such as environments that acts as corridors, to increase connectivity and avoid the restriction of their movements (Magioli et al. 2016). The absence of dispersal routes can result in population isolation, another important threat to mlsm in modified landscapes (Smith et al. 2018). In this manner, landscape management should take these individual differences in order to achieve enough connectivity for species (Boscolo and Metzger 2009; Uezu and Metzger 2016; Martensen et al. 2012). Evaluation of connectivity of our landscapes is beyond the scope of this study, however, studies conducted in similar agricultural landscapes point to the importance of connectivity in keeping mlsm functional diversity (Magioli et al. 2016). Nevertheless, considering that the detection of occupancy debt in the opened savannah was based on species area relationship, the restoration and maintenance of this environment is necessary to keep the whole mlsm community composition (Andrade-Núñez and Aide 2010).

As mentioned above, around 30% of native vegetation cover both landscapes nowadays. However, at FCP+FEC landscape, this amount is accountable only if considering the income (reforestation) of native forest since 1962 (see detailed description on Chapter 1). Open savannahs, by the other hand, declined since 1962 in this landscape (lasting around 11% from the initial amount) and no regeneration occurred on it (see results of Chapter 1). In this manner, areas designated to conservation purposes in the modified landscape are turning into forests instead of being kept as open savannah environments. The effect of savannah encroachment by forests is a research issue of global interest (Bond and Parr 2010; Stanton-Jr et al. 2018) and it has been reported that this phenomena results in drastic biodiversity decline and homogenization (Abreu et al. 2017; Stanton-Jr et al. 2018). Implementing restoration of open savannah in Brazil is still unpractical mainly due restrictions in Brazilian law regarding open savannah management with prescribed fires (Durigan and Ratter 2016), becoming harder to achieve management objectives and biodiversity needs (Cava et al. 2018). In our context, the loss of open savannah environment to native forests may accelerate the payment of the occupancy debt, effect that might be seeing earlier in maned wolf responses than in the other species.

Maned wolf is a threatened species of special conservation concern (Bressan et al. 2009) with habitat requirements centered on open environments (Dotta and Verdade 2011; Ferreira et al. 2017; ICMBio 2018), even though, this species may benefit at some level from contact zones between forests and open environments (association with low proportions of edges, in Lyra-Jorge et al. 2010). In this regard, it has been considered that deforestation of Atlantic Forest may be resulting in expansion of maned wolf geographical range (Beca et al. 2017), however, such conclusion didn’t accounted real suitability and fate of these deforested lands. If such ecotonic zone is composed of a single agricultural activity, such as sugar cane, there is a strong evidence in our results that maned wolf isn’t going to abide due to the negative effect of this crop on occupancy. At EEJ landscape, for example, maned wolf occupied mostly regions outside protected areas (Paolino et al. 2016), which is mainly dominated by sugar cane plantations and lacks open savannah environments, besides the negative occupancy trend to native forests environments.

Conclusions

Until the present, few ecological studies concerned with understanding time-lagged responses of medium and large-sized mammals before assessing current species responses. If scientific research and monitoring programs neglects the temporal aspect in interpreting species responses, upcoming consequences may be harmful to species and ecosystems. The immediate consequence of this fact is the misinterpretation of current species responses to habitat (current occupancy and distribution), which in turn, affects scientific knowledge and monitoring programs. Medium and long-term consequences of this omission may result in population decline and, eventually, local species extinction. This fate depends on landscape and species traits, which are subjects of major interest in mammal ecology. Some of the investigated medium and large-sized mammal species inhabiting human modified landscapes are still responding to past open savannah environment of 48 years ago. This delay is longer than previously reported and it is not associated with evidences indicating that indebted species are responding to current landscape environments, except the negative response found for maned wolf to sugar cane. We attribute the accuracy in detection of delayed responses of mlsm to occupancy estimates applied at species level approach. Considering that we based our findings on species-area relationship approach, the main conservation advice to revert the negative trend of species occupancy is to maintain the environments of savannah and increase the proportion of this land cover class in the indebted landscape. Notwithstanding, such goal requires active restoration management with the objective of keeping this environment as an open savannah instead of a forest environment.

Acknowledgements

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Supplementary Material

Table S1. Detection covariates selected for occupancy modeling of mammal species based on literature search. Type of covariate “Ca” and “Co” correspond to Categorical or Continuous data. Description column describes the measurement of the covariate and the reference column the literature source were the covariates were taken. The full references are available at *Literature cited* section of the main manuscript.

Mammal species	Covariates of detection	Abreviature	Type	Description	References	
Maned wolf	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Vynne et al. 2011	Ferreira et al. 2017
	protected area	protec	Ca	camera placement (0 inside of protected area)	Massara et al. 2012	Paolino et al. 2016
Collared peccary	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Breda unpublished data	-
	density of rivers	dens	Co	linear measurement of rivers inside focal landscape	Breda unpublished data	-
	mean temperature	temp	Co	month temperature average in the camera trap location	Breda unpublished data	-
Giant anteater	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-
	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Ferreira et al. 2017	-
	water area	wa	Co	proportion of water surface in the focal landscape	Versiani unpublished data	-
	urban area	ua	Co	proportion of urban area in the focal landscape	Versiani unpublished data	-
Brown brocket deer	pasture	pas	Co	proportion of pas in the focal landscape	Nanni et al. 2015	Dotta and Verdade 2011
	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Rodrigues et al. 2017	-
	open abandoned vegetation	vaa	Co	proportion of vaa in the focal landscape	Ferreira et al. 2017	-
	water distance	wd	Co	distance from sampling point to a source of water	Rodrigues et al. 2014	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Rodrigues et al. 2014	-
	open native vegetation	vna	Co	proportion of vna in the focal landscape	Rodrigues et al. 2017	-
Crab-eating fox	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Dotta and Verdade 2011	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-
	mean temperature	temp	Co	month temperature average in the camera trap location	Jácomo et al. 2004	Ferraz et al. 2010
	water area	wa	Co	proportion of water surface in the focal landscape	-	-
Puma	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Dotta and Verdade 2011	-
	native forest	vnf	Co	proportion of vnf in the focal landscape	Dotta and Verdade 2011	Vynne et al. 2012
	urban distance	ud	Co	distance of the sampling point from a urban settlement	Pônzio unpublished data	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-
	silviculture	silv	Co	proportion of silv in the focal landscape	Dotta and Verdade 2011	Ponzio unpublished data
	edge	bor	Co	proportion of edge (30m of width in vnf) in the landscape	Lyra-Jorge et al. 2010	-
Ocelot	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Massara et al. 2017	Ferreira et al. 2017
	native forest	vnf	Co	proportion of vnf in the focal landscape	Massara et al. 2016	Lyra-Jorge et al. 2010
	native forest distance	nd	Co	distance from sampling point to natural remnant	Naggy-Reis et al. 2017	-
	silvilculture	silv	Co	proportion of silv in the focal landscape	Massara et al. 2017	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-

Table S2. Complete *post hoc* modelling results for maned wolf, giant anteater and brown brocket deer at FCP+FEC landscape. Model(s) highlighted in bold was (were) considered for biological interpretation.

Species	AICc	ΔAICc	wAICc	L	K	deviance
Maned wolf						
p(road)Ψ(can)	**467.64**	**0.00**	**0.27**	**1.00**	**4.00**	**459.24**
p(road)Ψ(vna62)	**467.91**	**0.26**	**0.24**	**0.88**	**4.00**	**459.50**
p(road)Ψ(can+silv)	469.49	1.84	0.11	0.40	5.00	458.87
p(road)Ψ(silv)	469.50	1.85	0.11	0.40	4.00	461.09
p(road)Ψ(.)	470.61	2.96	0.06	0.23	3.00	464.37
p(road)Ψ(can+silv+vna10)	471.17	3.52	0.05	0.17	6.00	458.29
p(road)Ψ(vnf10)	471.18	3.54	0.05	0.17	4.00	462.78
p(road)Ψ(can+silv+vnf10)	471.21	3.56	0.05	0.17	6.00	458.33
p(road)Ψ(vna10)	472.43	4.78	0.03	0.09	4.00	464.02
p(road)Ψ(can+silv+vna10+vnf10)	472.82	5.18	0.02	0.08	7.00	457.64
p(road)Ψ(vna10+vnf10)	472.97	5.32	0.02	0.07	5.00	462.35
p(.)Ψ(.)	489.08	21.43	0.00	0.00	2.00	484.96
Giant anteater						
p(protec+road+wa)Ψ(vna62)	**440.84**	**0.00**	**0.51**	**1.00**	**6.00**	**427.97**
p(protec+road+wa)Ψ(.)	444.11	3.27	0.10	0.20	5.00	433.49
p(protec+road+wa)Ψ(silv10)	444.64	3.80	0.08	0.15	6.00	431.77
p(protec+road+wa)Ψ(can)	444.82	3.98	0.07	0.14	6.00	431.95
p(protec+road+wa)Ψ(silv+vna10)	445.84	5.00	0.04	0.08	7.00	430.66
p(protec+road+wa)Ψ(vnf10)	445.88	5.04	0.04	0.08	6.00	433.01
p(protec+road+wa)Ψ(vnf10+vna10)	446.24	5.40	0.03	0.07	7.00	431.06
p(protec+road+wa)Ψ(silv+can)	446.32	5.48	0.03	0.06	7.00	431.14
p(protec+road+wa)Ψ(vna10)	446.32	5.48	0.03	0.06	6.00	433.45
p(protec+road+wa)Ψ(silv+vnf10)	446.88	6.04	0.03	0.05	7.00	431.70
p(protec+road+wa)Ψ(silv+can+vna10)	448.06	7.22	0.01	0.03	8.00	430.53
p(protec+road+wa)Ψ(silv+can+vnf10)	448.61	7.76	0.01	0.02	8.00	431.07
p(protec+road+wa)Ψ(silv+can+vnf10+vna10)	450.40	9.56	0.00	0.01	9.00	430.46
p(.)Ψ(.)	466.57	25.73	0.00	0.00	2.00	462.45
Brown brocket deer						
p(road+wd+vaa+vna10)Ψ(vna62)	**328.46**	**0.00**	**0.57**	**1.00**	**7.00**	**313.29**
p(road+wd+vaa+vna10)Ψ(.)	332.19	3.73	0.09	0.16	6.00	319.32
p(road+wd+vaa+vna10)Ψ(can)	332.90	4.43	0.06	0.11	7.00	317.72
p(road+wd+vaa+vna10)Ψ(silv)	333.01	4.55	0.06	0.10	7.00	317.83
p(road+wd+vaa+vna10)Ψ(vnf10)	333.43	4.97	0.05	0.08	7.00	318.25
p(road+wd+vaa+vna10)Ψ(vna10)	334.29	5.82	0.03	0.05	7.00	319.11
p(road+wd+vaa+vna10)Ψ(can+vnf10)	334.56	6.09	0.03	0.05	8.00	317.02
p(road+wd+vaa+vna10)Ψ(silv+can)	334.79	6.33	0.02	0.04	8.00	317.26
p(road+wd+vaa+vna10)Ψ(vna10+silv)	334.98	6.52	0.02	0.04	8.00	317.45
p(road+wd+vaa+vna10)Ψ(silv+vnf10)	335.08	6.62	0.02	0.04	8.00	317.55
p(road+wd+vaa+vna10)Ψ(vna10+vnf10)	335.57	7.10	0.02	0.03	8.00	318.04
p(road+wd+vna10)Ψ(can+vnf10)	336.21	7.75	0.01	0.02	7.00	321.04
p(road+wd+vaa+vna10)Ψ(silv+can+vnf10)	336.84	8.38	0.01	0.02	9.00	316.91
p(.)Ψ(.)	338.33	9.87	0.00	0.01	2.00	334.21
p(road+wd+vaa+vna10)Ψ(silv+can+vnf10+vna10)	339.13	10.66	0.00	0.00	10.00	316.74

Chapter 3

Critical threshold responses of medium and large-sized mammals to natural and agricultural environments

Authors: Victor G Krepschi[1]*, Larissa L Bailey[2], Nielson AS Pasqualotto[4], Thiago F Rodrigues[4], Natalia F Versiani[3], Roberta M Paolino[4], Milton C Ribeiro[1] & Adriano G Chiarello[3]

[1] Universidade Estadual Paulista (Unesp), Rua 24ª 1515, Rio Claro, São Paulo, Brasil. Instituto de Biociências, Departamento de Ecologia

[2] Colorado State University (CSU), Fish and Wildlife Conservation Biology Department, Fort Collins, Colorado, United States of America

[3] Universidade de São Paulo (USP), Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Ribeirão Preto, São Paulo, Brasil

[4] Universidade de São Paulo (USP), Escola Superior de Agricultura Luiz de Queiroz (ESALQ), Piracicaba, São Paulo, Brasil

**corresponding author: vkrepschi@gmail.com*

Abstract

In ecology, the tipping-point of non-linear species responses to habitat loss is known as critical threshold. The most accepted explanation for this sudden change in species response is the summed effects of fragmentation (loss of connectivity) to the effect of habitat loss. Critical threshold studies are commonly associated to human-modified landscapes, a context in which the replacement of primary habitat by anthropogenic environments result in distinct responses among taxonomic groups. The wide consensus in critical threshold theory predicts that the cut-off value of biological responses occurs around 30% of habitat in the landscape. However, this turning point varies among taxonomic groups and regarding that, the medium and large-sized mammal community is a few studied group in the critical threshold arena. This scarcity is mainly due to the difficulty in detecting precise responses at the community level, what in turn requires both an individualized species approach and more accurate analytical methods for detection of species responses. Given this, the present study aimed in detecting critical threshold responses of medium and large-sized mammal species to both native and anthropogenic environments free from time-delayed responses in human-modified landscapes, using the analytical framework of species occupancy estimates modelling accounting for imperfect detection. Mammal recordings were obtained through camera-trap sampling of 206 randomly chosen focal landscapes, equally distributed inside and outside (buffer zone) Protected Areas, of three study areas of the same region, which are mostly covered by native vegetation, sugar cane crops and silviculture stands. The occupancy modelling resulted in detection of non-linear response only for the collared peccary at the proportion of 50% of native forest in the landscape. This empirical cut-off value of critical threshold response points to an approximated proportion of habitat in which species demonstrate a steep decline in using the landscape. Thus, we infer that the maintenance of slight higher amount of primary habitat is necessary in order to assure the persistence of collared peccary in human-modified landscapes. Notwithstanding, the study area where this threshold response was found harbors only half of the habitat amount required for the collared peccary persistence. Thus, we suspect that this location has a small collared peccary population, which is being benefited from the presence of a large and continuous protected remnant of Cerrado forest in the landscape. This in turn, reinforces the need of conserving large and protected areas in agricultural landscapes, especially in cases where the locality doesn’t provide the amount of primary habitat above the critical threshold level to assure the persistence of habitat sensitive medium and large-sized mammal species.

Keywords: Ecological threshold, collared peccary, Protected Area, Cerrado, savanna

Introduction

The search for patterns in species distribution and occurrence according to environmental variation is one ancient arenas in ecological science (McArthur and Wilson 1965, Whitaker 1967, Turner 1980, Fahrig 2013). Over the years, the advances of this approach resulted in many accurate statistical modelling and new ecological knowledge, improving the detection of species responses according to environmental factors. Such valuable background both deepened the knowledge and widened the awareness of other new ecological processes acting in species responses. One emerging arena is the critical habitat threshold concept (Andrén 1994), which nowadays strongly influences ecological studies (Swift and Hannon 2010) and has become an important issue in applied ecology at supporting environmental and biological conservationist strategies (Banks-Leite et al. 2014, Roque et al. 2018)

Ecological Thresholds has its original concept accrued from Percolation of Fluids Theory (Stauffer 1985) and was first demonstrated to ecological communities on Andrén’s (1994) mini review, in which the author found sudden and steep changes on response of bird community responses below certain level of habitat loss (percentage of habitat in the landscape) rather than linear responses. Analogous to the behavior of fluids percolation through a grid of squares (using the four neighborhood rule), non-linear response in ecological community occurs below 60% of habitat in the landscape. At this level of habitat loss in the landscape, it was observed that sensitive species start declining due to lack of habitat contiguity, regardless of habitat patches configuration. However, more drastic changes in community composition and resilience occurs below 30% of habitat amount, affecting even the persistence of species more tolerant to habitat loss. Up to date, the most plausible explanation for this steep decline in biological response around 30% of habitat is the added effect of fragmentation (decreased patch size and isolation of remnants) in species responses to habitat loss (Swift and Hannon 2010). In this manner, this tipping-point in species responses to habitat proportion became an important warning of biological and environmental collapse known as “critical threshold” (or extinction threshold).

Critical threshold studies are commonly conducted at community level (Andrén 1994; Pardini et al. 2010; Estavillo et al. 2013; Martensen et al. 2012; Lima and Mariano-Neto 2014; Banks-Leite et al. 2014; Muylaert et al. 2016; Ochoa-Quintero et al. 2015; Brito et al. 2016; Roque et al. 2018; Pardo et al. 2018), using species richness as the state variable. Notwithstanding, critical thresholds have also been investigated and detected in a wide array of approaches and other ecological levels, such as landscape land use and land cover dynamics (Ferraz et al. 2005, Rocha-Santos et al. 2016), functional ecology (Magiolli et al. 2015, Boesing et al. 2018), phylogenetic diversity (Boesing et al. 2018) and populational level (Beca et al. 2017; Pardo et al. 2018). The consistent achievements on critical thresholds research backgrounded important studies aiming conservation planning, as presented by Banks-Leite and colaborators (2014) which developed a multi-taxon vertebrate threshold model to set the key areas of Atlantic Forest restoration in this biome. Another example is the recently published metanalyse study of Roque and colaborators (2018) working with multi-taxon dataset. They demonstrated that early sings of amphibian community collapse could be predicted through the heterokedasticity of regression residuals close to the critical threshold value, anticipating community collapse. Notwhitstanding, the limitation of this study (Roque et al. 2018) was the lack of critical threshold studies with other biological groups, what indicates that limitations on critical threshold literature are the frontier for future research development.

The general consensus of critical threshold predicts that it occurs due to species responses to habitat loss (Swift and Hannon 2010). Thus, there are biological and ecological factors modulating the cut-off value of species responses to habitat loss. According to Swift and Hannon (2010) review, species mobility and delay in species response to habitat change (time-lagged responses) are among the main factors involved in critical threshold responses. Species mobility is dependent on species tolerance on habitat loss and in species vagility through the intervenient matrix. Studies considering the environment as a binary system, for example forest and non-forest, found good responses classifying species of the biological community in assemblages of specialists and generalists (Pardini et al. 2010; Lira et al. 2012). In this classification, forest specialists species are those presenting less tolerance to habitat loss and dependent on specific traits of this type of habitat. As a consequence, they will respond earlier to habitat loss, probably facing isolation and lack of mobility in anthropogenic disturbed landscapes (Boscolo and Metzger 2009; Uezu and Metger 2016). The same type of response is expected from species dependent on the matrix environment and which do not tolerate high amounts of forested environment in the landscape, the open area specialists (Estavillo et al. 2013). Opposite to these two types of response are the generalist species, which have more ecological plasticity and resilience to habitat change and might tolerate better both forest habitat and the anthropogenic matrix and thus, present higher mobility on matrix environment until a certain level of anthropogenic disturbance in habitat (Andrén 1994; Pardini et al. 2010; Estavillo et al. 2013; Martesen et al. 2012; Pardo et al. 2018). Grouping species in assemblages according to habitat specialization, however, has its limitations for certain taxonomic groups, which require a more specific approach based on their biology.

Detecting responses at the community level may be harder for less-speciose taxonomic groups with distinct biological and ecological traits, such as medium and large-sized mammals (Jorge et al. 2013; Magioli et al. 2015). Better predictions at this group requires populational species level approach and the use of more accurate state variables (Beca et al. 2017; Pardo et al. 2018). Beca and colaborators (2017), for example, found that medium and large-sized mammals richness was unresponsive to the predictor covariates chosen in human-modified landscape, but evidences of threshold responses to forest amount were detected when individual species of forest dwellers were analyzed separately. A similar finding in species response detection was reported by Pardo and colaborators (2018) studying medium and large-sized mammal community threshold responses in palm oil plantations at Colombia. At the community level threshold responses were not detected, while at species level, distinct threshold responses could be found. Pardo and collaborators's (2018) study was also a step forward onto the understanding of medium and large-sized mammal species tolerance to the dominant intervenient matrix environment, given the novel evidences that the cut-off value of the threshold response is affected by the quality of distinct matrix cover types (Boesing et al. 2018).

The second factor for critical threshold responses detection is time-lagged responses. Even though this aspect is highly relevant in detecting species responses at the landscape level, it has been neglected in most threshold studies. If ongoing delayed species responses to past disturbances in the landscape remain unnoticed by the researchers, critical threshold might be underestimated (Hanski and Ovaskainen 2002; Swift and Hannon 2010). In this manner, assuming that there are no species time-delayed responses in a landscape, rather than empirically testing them when conducting a study (Beca et al. 2017, Boesing et al. 2018) is an important decision, which will probably lead to a harmful and misleading conclusion if this assumption is wrong. Time-delayed responses may last over a century to take place at long-lived organisms, such as in trees (Metzger et al. 2009; Vellend et al. 2006), 15 years in small-bodied vertebrates (Metzger et al. 2009; Pardini et al. 2010; Lira et al. 2012; Uezu and Metzger; 2016) and intermediary time spans for neotropical medium and large-sized mammals, whose delayed responses might range from 15 to 50 years (Semper-Pascual et al. 2018; Krepschi et al. *in prep*).

In this manner, taking into consideration the biological specific traits of species and preventing species time-lagged responses, the present study aimed at detecting critical threshold responses of medium and large-sized mammal species at agricultural landscapes harboring both native vegetation cover and agricultural cover and where important remnants of the Cerrado (the Brazilian savannah) and Atlantic Rainforest biomes still remain.

Material and Methods

Study areas

Our three study areas are located in the Northeastern region of São Paulo State, Brazil (21º02' – 21º43'S and 47º54' – 47º16'W; Figure 1). This region harbors important protected remnants of Cerrado forest (also called "Cerradão"), open Cerrado (also called "Cerrado stricto sensu") and Areas of Permanent Protection (APP), enforced as Conservation Units. We included a 5km buffer zone around them, which comprises remnants of native vegetation immersed in matrix of anthropogenic use. Sugar cane plantations and forestry (eucalyptus and pinus) are the main agricultural activities and, in a less extent, pasture and orange plantations. Due the presence of a large river (Mogi-Guaçu River) and the flat relief, marshlands occur in the landscape. Climate varies from a warm and wet season (October – March) to a cold and a dry season (April – September), with most of annual precipitation (1470mm) concentrated in the former and an average temperature of 21.6ºC (annual range: 14 – 28ºC; CEPAGRI, 2014).

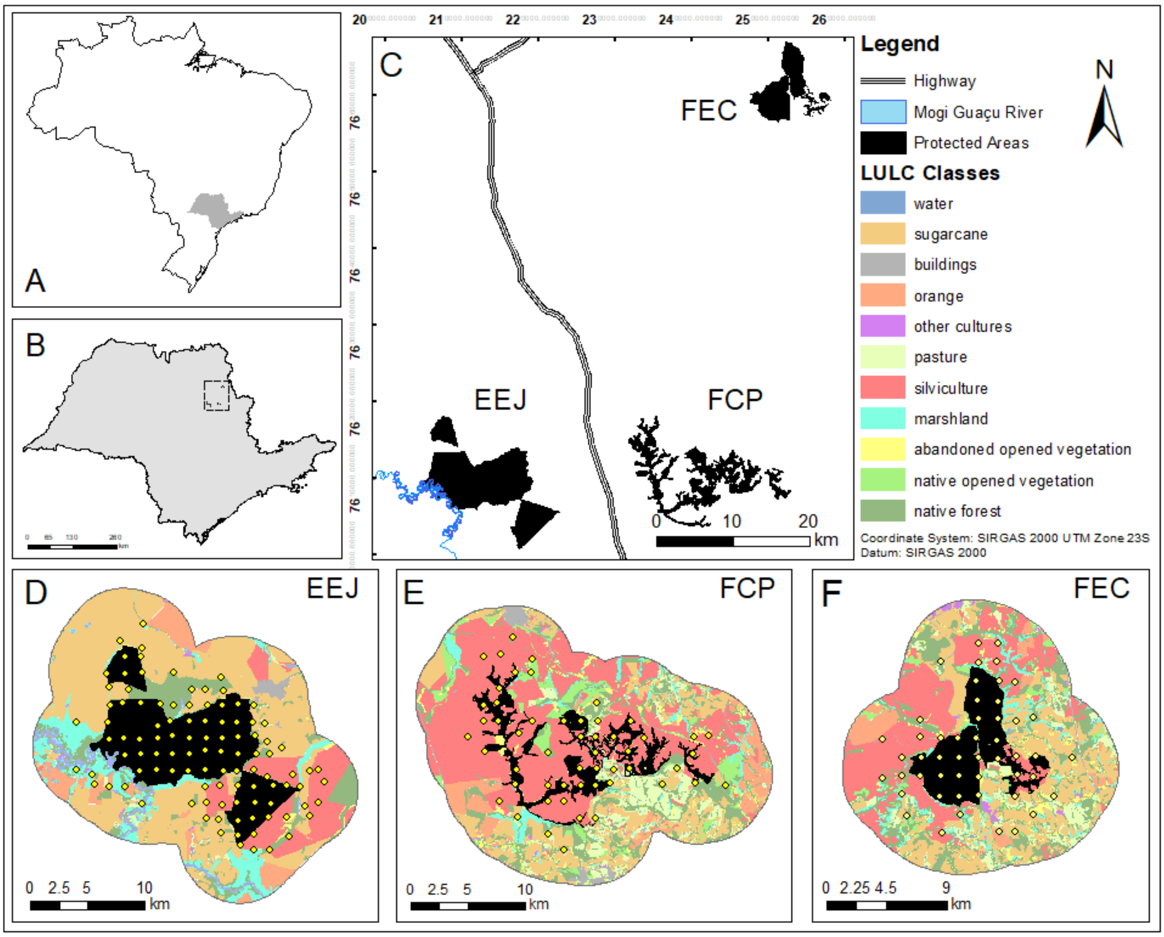

Figure 1. Location of São Paulo State (grey shaded) in Brazilian geopolitical map (A), location of studied landscapes evidenced inside the dashed square at São Paulo State geopolitical map (B) and studied landscapes protected areas (in black) in the regional context (C). Figure D to F show each studied landscape individually, comprised by the PA (in black) and their buffer zone, determined by a 5 km radius from the PA's edge, including main current land use and land cover classes (distinct colors) and the yellow dots the location of camera-trap station settlement. Abbreviation of landscape names: EEJ: "Jataí" Ecological Station, FCP: "Cara Preta" Farm and FEC: "Cajuru" State Forest.

Land use and land cover characterization and landscape covariates

We classified land use and land cover (lulc) of the areas in 2010 by visual identification of aerial photographs in a 1:10,000 scale (for detailed description, see mapping procedure section in Chapter 1). The mapping procedure resulted in eleven lulc classes (native forest (vnf), native open vegetation (vna), marshlands (var), sugarcane (can), managed forests (silv), orange plantations (lar), pasturelands (pas), open abandoned vegetation (vaa), urban area (ua), water and others (out)). For each lulc class we generated one landscape covariate calculating its proportion on the focal landscape (200 ha circular landscape around sampling point) through moving window procedure in GrassGIS (Grass Development Team, 2015). In addition, we included distance measurements from the sampling point as site covariates (urban distance (ud), native forest distance (nd) and water distance (wd), mean temperature (temp), edge (30 m of width from interface inward native forest), area of water surface (wa) and density of rivers (dens). All covariates used in mammals modelling were selected based on mammal species literature (Table S1; Supplementary Material).

Sampling design

For each study area, we overlaid a squared grid of 200 ha cells (to maximize independency between sampling points on the basis of giant anteater ranging (see Paolino et al. 2016 and Rodrigues et al. 2017). Cell centers were assigned as potential sampling points, of which we randomly selected 206 (102 in EEJ, 52 in FCP and 52 in FEC). Half of the selected points occurred inside protected areas and half of them outside protect area (buffer zone). We assumed that this sampling design satisfied the independence assumption among adjacent sampling points (about 1400m of distance between) and assured a balanced effort inside and outside protected areas. Some selected points were replaced due to logistic limitations (inaccessibility) and those located within sugar cane crops were relocated, for safety purposes, to the nearest native vegetation fragment, but were aimed at sugar cane environment.

Mammal surveying

We surveyed medium and large-sized mammals through camera-trapping during two consecutive dry seasons (April through September of years 2013 and 2014, totaling 12 months). At each selected sampling point, one camera-trap station (Reconyx HC500 HyperFire®) was deployed in tree trunks (~ 40cm above the ground); vegetation that could interfere in camera view was cleared and cameras were tested for triggering. Each camera operated for 30 consecutive days, and at the end of this period, the camera-trap device was recovered for batteries replacement, to substitute the memory card and to be settled in the next sampling point. Eighteen camera-trap stations operated simultaneously every month, resulting in a total sampling effort of 6,240 camera-trap days during the entire mammal survey.

Mammal species

We tested critical threshold responses for species of our data set with the highest number of camera trap recordings. Thus, six species were included: manned wolf (*Chrysocyon brachyurus*, recorded in 72 camera-traps), collared peccary (*Pecary tajacu*, recorded in 31 camera-traps), giant anteater (*Myrmecophaga tridactyla*, recorded in 82 camera-traps), brown brocket deer (*Mazama gouazoubira*, recorded in 72 camera-traps), puma (*Puma concolor*, recorded in 59 camera-traps) and crab-eating fox (*Cerdocyon thous*, recorded in 31 camera-traps). Besides this criterion, these species are representative of distinct feeding guilds and play distinct roles in ecosystem services, such as seed dispersion and predation of seeds, invertebrates and vertebrates.

Statistical Analysis

Occupancy estimation models

We adopted occupancy estimation models accounting for imperfect detection, using a single-season/single-species approach (MacKenzie et al. 2017) incorporated in MARK (White and Burnham 1999). Our primary goal was to determine if species occupancy to both natural and anthropogenic covariates was better fitted in a non-linear (the threshold response) or in a linear adjustment. Based on the 30 days of monitoring at each camera trap, we generated a detection history (detection/non-detection data) consisting of six independent occasions of 5 days (e.g., 100101). The set of detection histories for each species was joined with species-specific covariates thought to influence detection (Table S1 of Supplementary Material for detailed description of the covariates used for each species; we only included covariates that were not correlated - Pearson correlation coefficient < 0.6) in order to perform the threshold analysis (described in the section below). We developed balanced model sets, attending multi-model inference assumptions (Burnham and Anderson 2002), which allows comparing multiple hypothesis (models) to determine which best explains our data. Akaike Information Criterion (AIC) corrected for small samples (AICc) was used to rank models and those with ΔAICc < 2 were considered equally plausible. The importance of each model was accessed through cumulative model weights (Burnham and Anderson, 2002). Even though the top ranked model represent the most parsimonious model, given our data, in some cases, equally plausible models (ΔAICc < 2) were also interpreted regarding their biological meaningfulness. We evaluated the precision of covariates effects (betas) by reporting/examining upper and lower confidence intervals (95%) from selected models and reporting if these confidence intervals overlapped zero, in which case the estimated betas were considered imprecise.

Threshold Analysis

We analyzed species threshold responses for native forest (vnf) and silviculture (silv). Even though open native vegetation (vna) and sugarcane (can) are important environments in our landscapes, we didn’t analyze these land cover types here. We based this decision on three main arguments: first, we found that three species presented time-lagged responses (giant anteater, brown brocket deer and maned wolf), so they shouldn’t be investigated in current vna environment, assuming that they are not responding to current levels of vna in the landscape (see Chapter 2). Additionally, collared peccary didn’t occur in the areas were vna is predominant (FEC landscape), and the remaining species (puma and crab eating fox) showed imprecise responses for this covariate (vna). Thirdly, the decision of not including sugar cane in this analysis is due to a possible bias in camera-trap location, which likely resulted in under sampling of sugar cane (see description in *Sampling Design* section).

Before performing the critical threshold analysis itself, we ran two occupancy model sets for each species to find the best structure of detection on vnf and silv. This procedure allowed us to establish simultaneously the best structure of covariates of detection and precise species response to the covariate of occupancy being tested (vnf or silv). If species presented a precise response (upper and lower confidence intervals of the estimated beta did not overlapping 0) to the occupancy covariate, then we performed a threshold analysis for that covariate. We selected the right function on MARK to fit the data based on the trend of beta estimates of occupancy covariate. If the beta estimate was positive, we used minimum function (MIN) to constrain the data and, if negative, we used instead the maximum function (MAX). Each threshold model set consisted of eleven competing hypothesis (concurrent models): the null model, nine models with distinct percentages of occupancy covariate (each increasing by 10%) and the linear model (or 100%). Two types of responses were expected *a priori* in our threshold model set: a threshold response, when a threshold model explain better species occupancy than the linear model, and a linear response, when the linear model explains better or similarly the threshold models. The threshold response was considered only if the linear model isn´t positioned among top ranked models (delta AICc < 2). If the linear model was among the best ranked models, we didn’t consider the threshold response as meaningful.

Results

We found threshold response only for the species with the strongest association with forest, the collared peccary (table S2 in Supplementary Material). This relationship of peccary occupancy with native forest (vnf) was positive and precise (figure 2A). The threshold modelling revealed a sudden decrease in this species occupancy below the threshold of 50% of native forest in the surrounding landscape (table 1 and figure 2B). Top ranked models (equally plausible models) included thresholds ranging from 30% to 60% of vnf (table 1). We didn't find a precise response of collared peccary to silviculture (confidence interval overlapped 0), thus, no threshold modelling for this environment was developed.

Table 1. Peccary threshold model set for native forest percentage (vnf) in the landscape. Model in bold correspond to the linear model.

Model	AICc	ΔAICc	wAICc	L	K	deviance
p(road+temp+dens)Ψ(vnf_50)	339.20	0.00	0.22	1.00	6	326.32
p(road+temp+dens)Ψ(vnf_40)	339.30	0.09	0.21	0.95	6	326.41
p(road+temp+dens)Ψ(vnf_30)	339.46	0.25	0.20	0.88	6	326.57
p(road+temp+dens)Ψ(vnf_60)	339.81	0.61	0.16	0.74	6	326.93
p(road+temp+dens)Ψ(vnf_20)	341.43	2.22	0.07	0.33	6	328.54
p(road+temp+dens)Ψ(vnf_70)	341.43	2.22	0.07	0.33	6	328.54
p(road+temp+dens)Ψ(vnf_80)	343.26	4.06	0.03	0.13	6	330.38
p(road+temp+dens)Ψ(vnf_90)	344.44	5.23	0.02	0.07	6	331.55
p(road+temp+dens)Ψ(vnf_100)	**345.27**	**6.07**	**0.01**	**0.05**	**6**	**332.39**
p(road+temp+dens)Ψ(vnf_10)	346.67	7.47	0.01	0.02	6	333.79
p(.)Ψ(.)	355.24	16.04	0.00	0.00	2	351.12

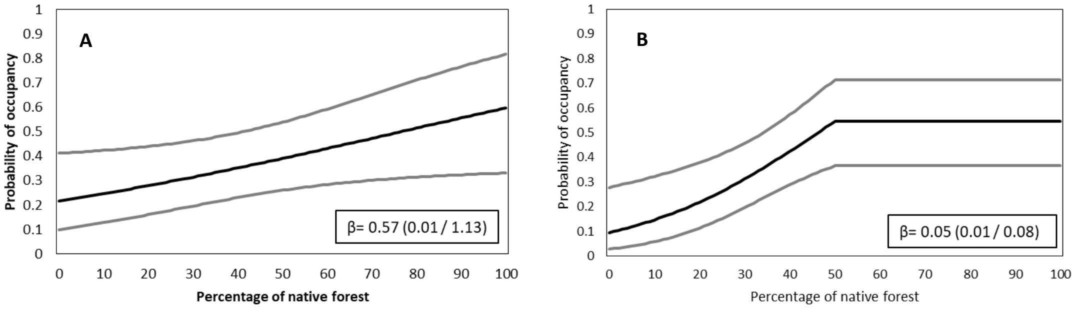

Figure 2. (A) Collared peccary's probability of occupancy as a function of native forest cover and (B) collared peccary critical threshold response to the percentage of native forest in the landscape. Dark lines represent the occupancy estimates and grey lines theirs upper and lower 95% confidence intervals. Estimated betas are displayed followed by their lower and upper 95% confidence intervals inside brackets.

Occupancy models of maned wolf and crab-eating fox to native forest (table S2 in the Supplementary Material section) showed a precise and negative response to this environment (figure 3A and 3B, respectively). However, after performing threshold modelling, the linear model appeared among the top ranked models (table 2). In these cases, therefore, we didn't assume the threshold hypothesis better represents the data than the linear model hypothesis, which means that no threshold was found for vnf in both species. The effect of silviculture for the crab-eating fox occupancy was negative and imprecise, while for the maned-wolf the effect was precise and positive (figure 4A). However, similarly to vnf response for this species, threshold response in silviculture wasn't detected due the top ranking position of the linear model in the model set (table 3).

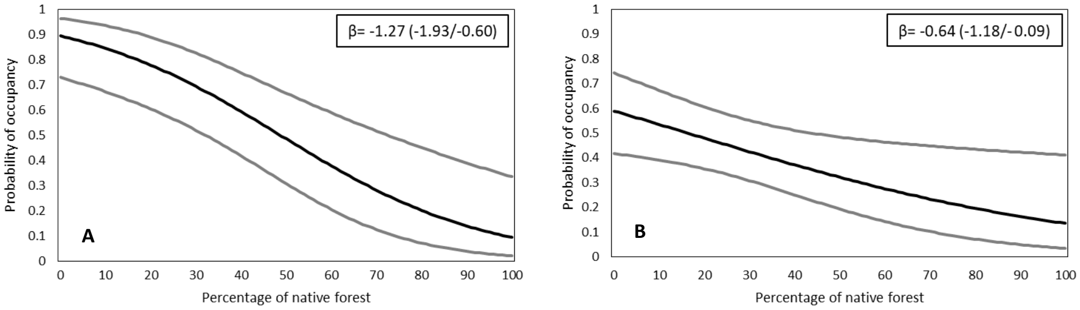

Figure 3. (A) Manned wolf and (B) crab-eating fox probability of occupancy at continuous gradient of native forest percentage. Dark lines represent the occupancy estimates and grey lines their upper and lower 95% confidence intervals. Estimated betas are displayed followed by their lower and upper 95% confidence interval inside brackets.

Table 2. Maned wolf and crab-eating fox threshold model set to native forest at the landscape. Models in bold correspond to the linear model.

Species	AICc	ΔAICc	wAICc	L	K	deviance
Maned wolf						
p(road)Ψ(vnf_100)	**725.60**	**0.00**	**0.36**	**1.00**	**4**	**717.40**
p(road)Ψ(vnf_10)	726.23	0.63	0.26	0.73	4	718.03
p(road)Ψ(vnf_20)	727.30	1.70	0.15	0.43	4	719.10
p(road)Ψ(vnf_30)	728.17	2.56	0.10	0.28	4	719.97
p(road)Ψ(vnf_40)	729.00	3.40	0.07	0.18	4	720.80
p(road)Ψ(vnf_50)	729.85	4.24	0.04	0.12	4	721.65
p(road)Ψ(vnf_60)	732.40	6.80	0.01	0.03	4	724.20
p(road)Ψ(vnf_70)	735.63	10.03	0.00	0.01	4	727.43
p(road)Ψ(vnf_80)	737.45	11.85	0.00	0.00	4	729.25
p(road)Ψ(vnf_90)	739.42	13.82	0.00	0.00	4	731.22
p(.)Ψ(.)	789.71	64.11	0.00	0.00	2	785.65
Crab-eating fox						
p(road+protec)Ψ(vnf_20)	551.48	0.00	0.23	1.00	5	541.18
p(road+protec)Ψ(vnf_30)	551.83	0.35	0.19	0.84	5	541.53
p(road+protec)Ψ(vnf_10)	552.16	0.68	0.16	0.71	5	541.86
p(road+protec)Ψ(vnf_100)	**552.46**	**0.98**	**0.14**	**0.61**	**5**	**542.16**
p(road+protec)Ψ(vnf_40)	553.32	1.84	0.09	0.40	5	543.02
p(road+protec)Ψ(vnf_50)	553.54	2.06	0.08	0.36	5	543.24
p(road+protec)Ψ(vnf_60)	554.53	3.05	0.05	0.22	5	544.23
p(road+protec)Ψ(vnf_70)	555.71	4.23	0.03	0.12	5	545.41
p(road+protec)Ψ(vnf_80)	557.07	5.59	0.01	0.06	5	546.77
p(road+protec)Ψ(vnf_90)	557.83	6.35	0.01	0.04	5	547.53
p(.)Ψ(.)	600.20	48.72	0.00	0.00	2	596.14

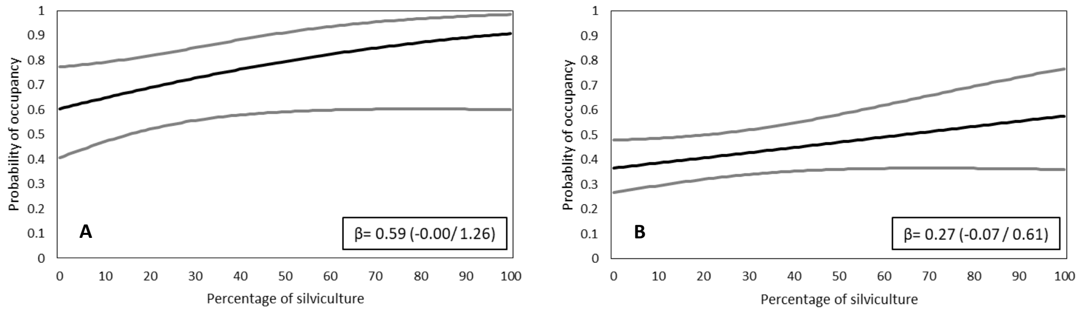

Figure 4. (A) Maned wolf and (B) brown brocket deer probability of occupancy as a function of silviculture in the landscape. Dark lines represent the occupancy estimates and grey lines their upper and lower 95% confidence interval. Estimated betas are displayed followed by their lower and upper 95% confidence interval inside brackets.

Table 3. Maned wolf threshold model set for silviculture proportion at the landscape. Model in bold correspond to the linear model.

Model	AICc	ΔAICc	wAICc	L	K	deviance
p(road)Ψ(silv_100)	**738.45**	**0.00**	**0.11**	**1.00**	**4**	**730.25**
p(road)Ψ(silv_20)	738.48	0.03	0.11	0.99	4	730.28
p(road)Ψ(silv_30)	738.48	0.03	0.11	0.98	4	730.28
p(road)Ψ(silv_90)	738.54	0.09	0.11	0.96	4	730.34
p(road)Ψ(silv_80)	738.64	0.19	0.10	0.91	4	730.44
p(road)Ψ(silv_40)	738.77	0.32	0.10	0.85	4	730.57
p(road)Ψ(silv_70)	738.82	0.37	0.10	0.83	4	730.62
p(road)Ψ(silv_60)	738.98	0.53	0.09	0.77	4	730.78
p(road)Ψ(silv_10)	739.08	0.63	0.08	0.73	4	730.88
p(road)Ψ(silv_50)	739.19	0.74	0.08	0.69	4	730.99
p(.)Ψ(.)	789.71	51.26	0.00	0.00	2	785.65

The remaining three species (brown brocket deer, giant anteater and puma) showed imprecise responses to native forest (figure S1 in Supplementary Material section), thus, no threshold modelling was performed for these species. The effect of silviculture on occupancy was precise (and positive) only for the brown brocket deer (figure 4B above), but the threshold hypothesis were not well supported (linear model with ΔAICc < 2; table 4).

Table 4. Brown brocket deer threshold model set for silviculture at the landscape. Model in bold correspond to the linear model.

Model	AICc	ΔAICc	wAICc	L	K	deviance
p(road+wd+vna)Ψ(silv_80)	745.02	0.00	0.13	1.00	6	732.60
p(road+wd+vna)Ψ(silv_70)	745.09	0.07	0.13	0.97	6	732.67
p(road+ wd +vna)Ψ(silv_90)	745.11	0.08	0.13	0.96	6	732.69
p(road+wd+vna)Ψ(silv_100)	**745.16**	**0.14**	**0.13**	**0.93**	**6**	**732.74**
p(road+ wd +vna)Ψ(silv_60)	745.35	0.33	0.11	0.85	6	732.93
p(road+ wd +vna)Ψ(silv_50)	745.76	0.73	0.09	0.69	6	733.33
p(road+ wd +vna)Ψ(silv_40)	745.95	0.92	0.08	0.63	6	733.52
p(road+ wd +vna)Ψ(silv_30)	746.48	1.46	0.06	0.48	6	734.06
p(road+ wd +vna)Ψ(silv_10)	746.67	1.65	0.06	0.44	6	734.25
p(road+ wd +vna)Ψ(silv_20)	746.94	1.91	0.05	0.38	6	734.51
p(.)Ψ(.)	749.49	4.46	0.01	0.11	2	745.43

Discussion

The non-linear response detected in the occupancy of the collared peccary is an empirical evidence of critical threshold responses to habitat loss in medium and large-sized mammal species. The cut-off value found for this species in this Cerrado landscape is similar to the previous evidences of non-linear responses for the species in Atlantic forest patches distributed in São Paulo State (Beca et al. 2017), which demonstrated a steeper decline in collared peccary detection in patches with less than 45% of native forest cover. This critical threshold is also similar to that found for bats in EEJ (around 48%, Muylaert et al. 2016) and specialized birds of Atlantic forest remnants (50%, Martensen et al. 2012), but higher than most threshold values reported for most biological groups (Andrén 1994; Pardini et al. 2010; Banks-Leite et al. 2014; Roque et al. 2018). Although this amount of habitat in the landscape indicates the lower limit of ecological requirement for the collared peccary population, it is intriguing that the proportion of native forest cover in EEJ landscape (around 27%) is far below the cut-off value of critical threshold found. This is an indicative that collared peccary population is small (Swift and Hannon 2010) in this locality and suggests that the presence of large and continuous forest remnants in EEJ landscape exerts a positive effect on the permanence of collared peccaries in this region. This is even more supported if we consider the low number of records of collared peccary obtained in FCP landscape, and the absence of records at FEC landscape (Vitor Breda unpublished monography). These two landscapes harbor less continuous forest and smaller-sized remnants than EEJ, landscape traits that, in turn, decrease the carrying capacity of the regional landscape in sustaining specialized species populations (Swift and Hannon 2010). Additionally, most of collared peccary records was obtained inside EEJ landscape Protected Area (Paolino et al. 2016), strengthening the idea that large and protected native forest patches are important in the maintenance of collared peccary's ecological resources at agricultural landscapes.

The interpretation of the top ranked model of the model set represent the best adjustment of the response variable to the structure of covariates. However, the three equally plausible ranked models (ΔAICc < 2) of collared peccary model set provides the cautionary message that the sudden changes in this species response might also occur between the range of 30% and 60% of native forest in this landscape. In this manner, when aiming the conservation purposes of safeguarding species in the long term, it is recommended that the availability of habitat to be retained in the landscape might be kept slightly above the critical threshold value (Banks-Leite et al. 2014), preventing undesirable and unexpected effects of stochastic events and genetic erosion (Pflüger et al 2018), which in our case, should be more than 60% of native forest in the landscape. Moreover, it was demonstrated that critical threshold cut-off value vary (up to 58% in simulation studies) in a landscape according to the risks (Swift and Hannon 2010) and type (Boesing et al 2018) of the intervenient matrix. This influence is related to biological traits of specialist species, such as elevated mobility (which is the case of collared peccary, Neri unpublished dissertation), which might bring on early extinctions in population, even in landscapes with proportions of 50% of habitat amount (based on a simulation study of Pflüger et al. 2018).

The adopted procedures of excluding environments in which species presented time-lagged responses (native open vegetation), using individual-based approach (to avoid generalizations of community level approach, Semper-Pascual et al. 2018) and adopting occupancy models accounting for imperfect detection (Mackenzie et al. 2017), all seemed to contribute to the desired objective in our analysis: improving the detection of species responses both to native and human-modified environments. Based on that, this analytical framework is highly recommend in studying medium and large-sized mammal responses in human-modified landscapes. However, it still remains unclear the specific reasons why the detection of critical threshold responses weren't obtained for the remaining mammal species of the present study, considering that recent findings reported success in detecting non-linear species response to the matrix environment (Pardo et al. 2018). We suspect this is due to the interaction of species with the distinct environments of the heterogeneous landscape, which adds complexity in the interpretation of species responses, differing from patterns found in landscapes of binary land cover (e.g., forest and non-forest), where evidences of non-linear responses of medium and large-sized mammals were found (Ochoa-Quintero et al. 2015; Pardo et al. 2018).

Besides the high mobility of collared peccary (Fernanda Maria Neri, unpublished dissertation), this species is highly dependent on native forest resources (Keuroghlian et al. 2004). This dependence is probably the main reason for both the non-linear response found for this species to native forest and the imprecise responses to silviculture, an environment where this species is indeed rarely recorded (Timo et al. 2015). Following this rationale, our interpretation for the absence of non-linear response in the remaining medium and large-sized mammal species is that they are not dependent (in case of linear positive responses) or impacted (in cases of linear negative responses) by the environments analyzed in our landscapes, but rather, they shift the use of environments according to their ecological needs and the temporal availability of resources which these environments provide (Timo et al. 2015). The brown brocket deer, for example, shows a strong response to silviculture (Andrade-Nuñes and Aide 2010; Dotta and Verdade 2011; Rodrigues et al. 2017; the present study), but lacks non-linear response to this environment, suggesting the non-dependence on it. Furthermore, it was also reported that the brown brocket deer was unresponsive to traits of pristine Atlantic forest (Ferregueti et al. 2015) and that this species uses several types of environment, such as the interface of sugar cane and native forest, native forest (Rodrigues et al. 2017) and pastures (Nanni et al. 2015).

The responses of crab-eating fox also exemplify this lack of specificity in using the environments of the heterogeneous landscape. Based on literature of the species in both pristine (Jácomo et al. 2004) and human-modified areas (Andrade-Nuñes and Aide 2010; Ferraz et al. 2010; Dotta and Verdade 2011), the negative response found for this species to native forest means, rather than a harmful effect, that it prefers landscapes with low proportions of this native environment. The above mentioned interpretations also seems to reflect the maned-wolf responses to human-modified landscapes (Vynne et al 2014). This species has proved resilient in persisting at the surrounding of Protected Areas (Vynne et al. 2011, Massara et al. 2012) or in human modified landscapes (Dotta and Verdade et al. 2011; Beca et al. 2017), besides the previous findings of temporal association to native open vegetation (Chapter 2) evidencing its specialization on it (Jácomo et al. 2004).

For the last two species investigated in this study, the giant anteater and puma, we interpreted their responses as the absence of a specific response to the environments studied. This doesn’t mean these two environments might not provide ecological resources to these species (Suguituru et al. 2011; Gheler-Costa et al. 2012), but, that we didn’t detected consistence in their use by these two the species. The puma is a species with high behavioral plasticity in human modified landscapes (Magioli et al. 2014; Gheler-Costa et al. 2018) and known to occupy both inside and outside Protected Areas inserted in anthropic landscapes (Paolino et al. 2016). Additionally, another explanation for our finding is that puma responses are better detected in larger scales (Lyra-Jorge et al. 2010) than the one used in the experimental design of the present study (200 ha rounded shape focal landscape). The giant anteater, by the other hand, is the species by which this design of this study was developed for. Thus, the lack of detection in the response of this mammal species is accurate and reflects its ecological interaction with the two environments tested.

According to the previous study conducted in the same landscapes of the present study which describes the occupancy of the giant anteater (Natalia F Versiani unpublished dissertation), the landscape traits that explained this species occupancy were unpaved roads, protected areas and distance from urban areas. In addition, among the covariates that influenced its detection, a positive effect was found for open native vegetation (Natalia F Versiani, unpublished dissertation). Based on that, our results indicate two possibilities. First, feeding resources are scattered in the remnants of the landscape and, as consequence, the giant anteater is using unpaved roads for moving farther in order to find them, resulting in little interaction with native forests and silviculture environments, similarly to the suggestioned by Andrade-Nuñes and Aide (2010) for other medium and large-sized mammals. The second possibility is that there are time-lagged responses occurring in the landscape (Zimbres et al. 2013), making difficult the detection of such responses. Indeed, a time-lagged response of giant anteater was found for the open savanna in these same landscapes of the present study (Chapter 2) and, although other studies report this species present in silvicultural stands (Timo et al. 2015, Ferreira et al. 2017), the detected responses lack precision (Ferreira et al. 2017).

The main contribution of the present study is the application of occupancy estimates in critical threshold approach, providing a reliable framework of testing the existence of ecological threshold in species with responses associate both to native and human-modified environments. The responses found seem to resemble the ecology of species reported in literature, but it is here described through a more accurate state variable, the occupancy estimate. This perspective is promising for medium and large-sized mammal studies, of which responses are difficult to obtain, particularly in human modified landscapes. This in turn has an applicable usefulness in guiding decisions of conservationist concern, which most of times are surpassed by agribusiness lobby interests.

This positive effect of large proportions of continuous primary habitat on mammals (even in landscapes where the total native vegetation proportion below the detected critical threshold level) provides enough background to counteract the recently proposed Law Project (number 2362/2019) processing in Brazilian National Congress, which intend to revoke the category of environmental protection “Legal Reserves” (a fixed set-aside portion of land of native environment in private lands) from the Brazilian Forest Code (Law number 12.651/2012) in favor of agricultural expansion all over the country. Losing such large set-asides of Protected Areas in private lands jeopardize the possibility of retaining the minimum amount of habitat for maintaining forest structure (Rocha-Santos et al. 2016) and biodiversity persistence, especially at imperiled biomes such as the Atlantic Forest (Ribeiro et al 2009) and the Cerrado (Ribeiro and Walter 2008).

Further, we reinforce that the cut-off value represent a critical turning point in species responses, meaning that sudden loss in biodiversity might occur if slightly higher amounts of primary habitat is not kept in the landscape. Otherwise, impacts might not only be immediate on population, but affect their genetic parameters. As future directions of critical threshold studies using single-species occupancy estimates, we recommend the development of additive models to stablish the contribution of distinct proportions of each land cover type in species response to find the consolidation of the ecological niche for each species based on landscape level traits. Finally, there is strong evidences that time-delayed responses still occurs in the landscape and influences the detection of species responses to current human-modified landscape traits, thus, this aspect should always be taken into consideration before associating species to their actual environment.

Acknowledgements

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Supplementary Material

Table S1. Detection covariates selected for occupancy modeling of mammal species based on literature search. Abbreviation of covariate types “Ca” and “Co” correspond to Categorical or Continuous data. The full references are available at Reference section of the manuscript.

Mammal species	Covariates of detection	Abreviature	Type	Description	References	
Manned wolf	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Vinny et al 2012	Ferreira et al. 2017
	protected area	protec	Ca	camera placement (0 inside of protected area)	Massara et al 2012	Paolino et al. 2016
Collared peccary	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Breda unpublished data	-
	density of rivers	dens	Co	linear measurement of rivers inside focal landscape	Breda unpublished data	-
	mean temperature	temp	Co	month temperature average in the camera trap location	Breda unpublished data	-
Giant anteater	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-
	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Ferreira et al. 2017	-
	water area	wa	Co	proportion of water surface in the focal landscape	Versiani unpublished data	-
	urban area	ua	Co	proportion of buildings in the landscape	Versiani unpublished data	-
Brown brocket deer	silviculture	silv	Co	proportion of silv in the focal landscape	Rodrigues et al. 2017	-
	pasture	pas	Co	proportion of pas in the focal landscape	Nanni et al. 2015	Dotta and Verdade 2011
	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Rodrigues et al 2017	-
	open abandoned vegetation	vaa	Co	proportion of vaa in the focal landscape	Ferreira et al 2017	-
	water distance	wd	Co	distance from sampling point to a source of water	Rodrigues et al. 2014	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Rodrigues et al. 2014	-
	sugarcane	can	Co	proportion of can in the focal landscape	Rodrigues et al. 2014	-
	urban distance	ud	Co	distance of the sampling point from a urban settlement	Rodrigues et al. 2014	-
	open native vegetation	vna	Co	proportion of vna in the focal landscape	Rodrigues et al. 2017	-
Crab-eating fox	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Dotta and Verdade 2011	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-
	mean temperature	temp	Co	month temperature average in the camera trap location	Jácomo et al. 2004	Ferraz et al. 2010
	water area	wa	Co	proportion of water surface in the focal landscape	-	-
Puma	unpaved road	road	Ca	camera placement (0 out of unpaved road)	Dotta and Verdade 2011	-
	native forest	vnf	Co	proportion of vnf in the focal landscape	Dotta and Verdade 2011	Vynne et al. 2011
	urban distance	ud	Co	distance of the sampling point from a urban settlement	Pônzio unpublished data	-
	protected area	protec	Ca	camera placement (0 inside of protected area)	Paolino et al. 2016	-
	silviculture	silv	Co	proportion of silv in the focal landscape	Dotta and Verdade 2011	Pônzio unpublished data
	edge	bor	Co	proportion of edge (30m of width in vnf) in the landscape	Lyra-Jorge et al. 2010	-

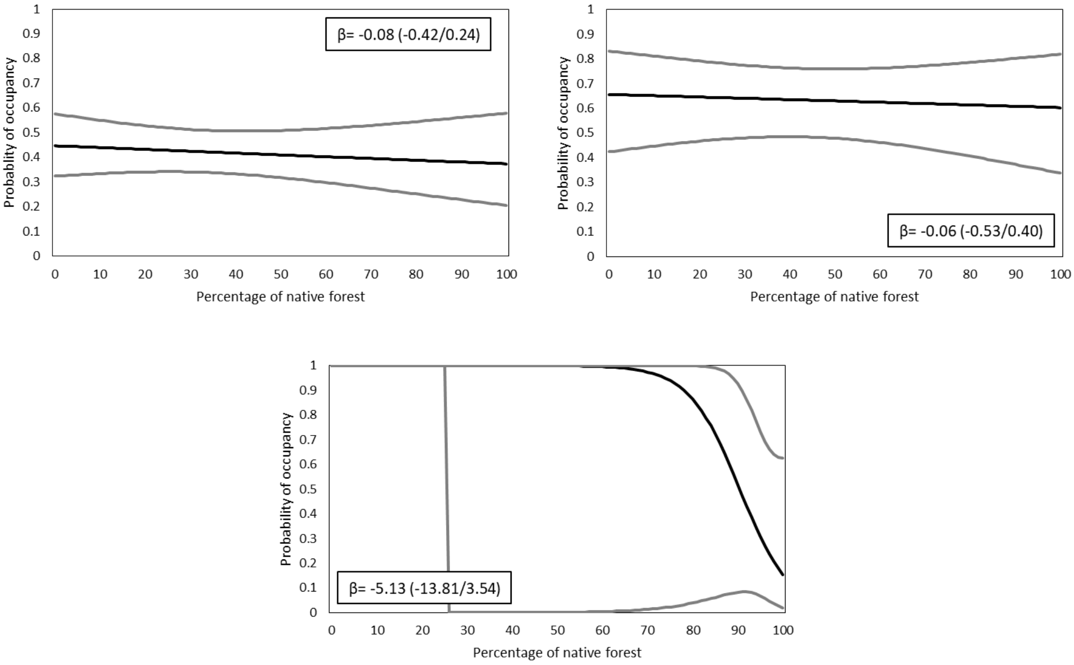
Table S2. Top ranked occupancy models (ΔAICc < 2) of all species in response to native forest (vnf) with model set parameters described in each column.

Species	AICc	ΔAICc	wAICc	L	K	deviance
Collared peccary						
p(road+temp+dens)Ψ(vnf)	344.89	0.00	0.26	1.00	6	332.00
p(road+temp)Ψ(vnf)	345.04	0.15	0.24	0.93	5	334.42
p(road)Ψ(vnf)	346.89	2.00	0.09	0.37	4	338.48
Maned wolf						
p(road)Ψ(vnf10)	725.60	0.00	0.72	1.00	4	717.403
p(road+protec)Ψ(vnf)	727.48	1.88	0.28	0.39	5	717.183
Crab-eating fox						
p(road+protec)Ψ(vnf)	552.46	0.00	0.28	1.00	5	542.16
p(road)Ψ(vnf)	553.62	1.16	0.15	0.56	4	545.42
p(road+protec+wa)Ψ(vnf)	553.92	1.46	0.13	0.48	6	541.49
p(road+protec+temp)Ψ(vnf)	554.38	1.92	0.11	0.38	6	541.96
Brown brocket deer						
p(protec+road+vaa+wd)Ψ(.)	736.99	0.00	0.27	1.00	6	724.56
p(protec+road+vaa)Ψ(.)	738.73	1.74	0.11	0.42	5	728.43
p(protec+road+vaa+wd)Ψ(vnf)	738.87	1.88	0.11	0.39	7	724.30
Giant anteater						
p(protec+road)Ψ(.)	833.27	0.00	0.26	1.00	4	825.07
p(protec+road+wa)Ψ(.)	834.62	1.35	0.13	0.51	5	824.32
p(protec+road+ua)Ψ(.)	834.69	1.42	0.13	0.49	5	824.38
Puma						
p(road+protec+vnf+ud+egde)Ψ(vnf)	559.64	0.00	0.28	1.00	8	542.90
p(road+protec+egde)Ψ(.)	561.49	1.85	0.11	0.40	5	551.19

Table S3. Top ranked occupancy models (ΔAICc < 2) of all species in response to silviculture (silv) with model set parameters description in each column.

Species	AICc	ΔAICc	wAICc	L	K	deviance
Collared peccary						
p(temp+protec)Ψ(.)	342.94	0.00	0.39	1.00	4	334.53
p(temp+protec)Ψ(silv)	345.00	2.06	0.14	0.36	5	334.38
Maned wolf						
p(road)Ψ(silv)	738.45	0.00	0.34	1.00	4	730.25
p(road+protec)Ψ(silv)	738.48	0.03	0.34	0.98	5	728.18
p(road+protec)Ψ(.)	739.61	1.16	0.19	0.56	4	731.41
p(road)Ψ(.)	740.36	1.90	0.13	0.39	3	734.24
Crab-eating fox						
p(road+protec)Ψ(.)	555.82	0.00	0.22	1.00	4	547.62
p(road+protec)Ψ(silv)	556.75	0.94	0.14	0.63	5	546.45
p(road+protec+wa)Ψ(.)	556.86	1.04	0.13	0.60	5	546.55
p(road+protec+temp)Ψ(.)	556.97	1.15	0.13	0.56	5	546.67
p(road+protec+temp)Ψ(silv)	557.76	1.94	0.09	0.38	6	545.33
Brown brocket deer						
p(road+wd+vna150)Ψ(silv)	745.16	0.00	0.29	1.00	6	732.74
p(road+wd)Ψ(silv)	745.54	0.38	0.24	0.83	5	735.24
p(road)Ψ(silv)	746.32	1.16	0.16	0.56	4	738.12
p(road+vna150)Ψ(silv)	746.79	1.63	0.13	0.44	5	736.49
Giant anteater						
p(protec+road)Ψ(.)	833.266	0.00	0.25	1.00	4	825.07
p(protec+road+wa)Ψ(.)	834.6183	1.35	0.13	0.51	5	824.32
p(protec+road+ud)Ψ(.)	834.6856	1.42	0.13	0.49	5	824.38
p(protec+road)Ψ(silv)	835.1846	1.92	0.10	0.38	5	824.88
Puma						
p(road+protec+edge)Ψ(.)	561.4889	0.00	0.23	1.00	5	551.19
p(road+protec+silv+edge)Ψ(.)	562.7418	1.25	0.12	0.53	6	550.32
p(road+protec+vnf+edge)Ψ(.)	562.8398	1.35	0.12	0.51	6	550.42
p(road+protec+ud+silv+edge)Ψ(.)	563.3086	1.82	0.09	0.40	7	548.74
p(road+protec+edge)Ψ(silv)	563.3648	1.88	0.09	0.39	6	550.94
p(road+protec+vnf+ud+edge)Ψ(.)	563.3676	1.88	0.09	0.39	7	548.80

Figure S1. (A) Brown brocket deer, (B) giant anteater and (C) puma probability of occupancy according to the percentage of native forest in the landscape. Dark lines represent the occupancy estimates and grey lines their upper and lower 95% confidence interval. Estimated betas are displayed followed by their lower and upper 95% confidence intervals inside brackets.



Conclusão

A conclusão geral desse estudo é de que as respostas biológicas aferidas em áreas de uso humano não estão sendo moldadas somente pelas características atuais da paisagem, mas são também influenciadas por processos ecológicos que atuam espacial e temporalmente nas paisagens. A detecção da ocorrência desses processos ecológicos foi possível, principalmente, devido à incorporação da idiossincrasia ecológica das espécies nas metodologias e nas análises empregadas no estudo. Nesse sentido, três recomendações podem ser sugeridas para futuros estudos: primeiro, a de investigar o histórico e a trajetória do habitat primário usado pelas espécies, o que revelou em nosso estudo a forma correta de agrupar as paisagens previamente à análise de respostas dos mamíferos; segundo, o emprego de modelos de estimativa de ocupação de espécie única considerando detecção imperfeita, o qual demonstrou ser um método adequado para inferir com precisão a existência de respostas temporais e de limiares ecológicos nas paisagens; e por fim, a importância de se excluírem das análises os ambientes em que foram encontrados evidências de respostas atrasadas, o que diminui as chances de encontrar respostas imprecisas e de interpretar erroneamente as respostas dos mamíferos aos ambientes estudados.

Especificamente em relação às respostas atrasadas de mamíferos de médio e grande porte, conclui-se que o tempo de relaxamento seja maior do que o constatado previamente para esse e outros grupos taxonômicos de vertebrados. Isso significa que a quantidade de Cerrado aberto existente nas paisagens atuais pode não ser suficiente para garantir a persistência populacional de três espécies de mamíferos em duas das áreas de estudo. Dessa forma, considerando que nossas inferências foram feitas baseando-se na resposta da espécie pela proporção de habitat primário, a principal medida de conservação recomendada para essas localidade é o aumento da quantidade de Cerrado aberto nas paisagens, o que envolve medidas de restauração e o manejo adequado das fisionomias abertas do Cerrado já existentes na paisagem, que por sua vez, vêm sendo afetadas pelo fenômeno de encolhimento de savanas, que apesar de não causar a diminuição da quantidade de vegetação nativa da paisagem, substitui as feições abertas do Cerrado pela fisionomia florestal, colocando em risco a heterogeneidade desse bioma.

As conclusões a respeito dos limiares críticos na paisagem, corroboraram a importância da influência da especialização e da sensibilidade da espécie em relação ao seu habitat primário na detecção precisa de respostas não lineares. O valor de inflexão da resposta não linear do cateto à quantidade de floresta nativa demonstra que se faz necessário manter proporções desse ambiente acima de 50% da cobertura total da paisagem, a fim de diminuir o risco de ocorrer respostas negativas abruptas da população. Contudo, considerando que a quantidade de floresta na paisagem de estudo é menor do que a encontrada para a espécie, ficou implícito que a população local esteja sendo positivamente influenciada pela presença de um grande e contínuo remanescente de Cerrado protegido, fato que reforça a necessidade de se manterem as áreas protegidas de maior tamanho nas paisagens agrícolas para a manutenção da biodiversidade. Ademais, constatou-se que várias espécies de mamíferos de médio e grande porte interagem com os ambientes da paisagem modificada, mas o fazem sem dependência, isso é, de acordo com sua necessidade ecológica e disponibilidade temporal de recursos. Para entender a resposta limiares dessas espécies que possuem maior resiliência e plasticidade, se faz necessário mais estudos buscando entender o conjunto de relações que moldam seu uso do ambiente.

Por fim, mediante o conhecimento de que processos ecológicos temporais (respostas atrasadas) e não-lineares (limiares críticos de paisagem) atuam na resposta de espécies de mamíferos de médio e grande porte inseridos em paisagens modificadas pelo homem, as medidas de conservação a serem tomadas para as espécies desse grupo biológico dependem do olhar cuidadoso dos pesquisadores, dos tomadores de decisão e dos propositores de políticas públicas sobre os parâmetros ambientais obtidos no tempo presente, considerando a possibilidade de que eles não traduzem um estado ecológico estacionário da população, mas transitório, que pode estar sob influência de eventos ocorridos no passado e que são detectáveis ao nível de paisagem. Isso por sua vez, mesmo baseado em fatos empíricos, pode induzir a conclusões espúrias.

Referências

Abreu RCR, Hoffmann WA, Vasconcelos HL, et al (2017) The biodiversity cost of carbon sequestration in tropical savanna. Sci Adv 3:e1701284. doi: 10.1126/sciadv.1701284

Alofs KM, González AV, Fowler NL (2014) Local native plant diversity responds to habitat loss and fragmentation over different time spans and spatial scales. Plant Ecol 215:1139–1151. doi: 10.1007/s11258-014-0372-5

Andrade-Núñez MJ, Aide TM (2010) Effects of habitat and landscape characteristics on medium and large mammal species richness and composition in northern Uruguay. Zool 27:909–917. doi: 10.1590/S1984-46702010000600012

Andrén H (1994) Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat : A Review. Nordic Society Oikos 71:355–366.

Banks-Leite C, Pardini R, Tambosi LR, et al (2014) Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345(6200):1041-1045.

Beca G, Vancine MH, Carvalho CS, et al. (2017) High mammal species turnover in forest patches immersed in biofuel plantations. Biol Conserv 210:352–359. doi: 10.1016/j.biocon.2017.02.033

Bertassoni A, Mourão G, Ribeiro RC, et al. (2017) Movement patterns and space use of the first giant anteater (Myrmecophaga tridactyla) monitored in São Paulo State, Brazil. Stud Neotrop Fauna Environ 52:68–74. doi: 10.1080/01650521.2016.1272167

Boesing AL, Nichols E, Metzger JP (2018) Biodiversity extinction thresholds are modulated by matrix type. Ecography (Cop) 41:1520–1533. doi: 10.1111/ecog.03365

Bommarco R, Lindborg R, Marini L, Öckinger E (2014) Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. Diversity and Distributions 20:591-599.

Bond WJ, Parr CL (2010) Beyond the forest edge : Ecology , diversity and conservation of the grassy biomes. Biol Conserv 143:2395–2404. doi: 10.1016/j.biocon.2009.12.012

Boscolo D, Metzger JP (2009) Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? Landsc Ecol 24:907–918. doi: 10.1007/s10980-009-9370-8

Brancalion PHS, Garcia LC, Loyola R, et al (2016) Análise crítica da Lei de Proteção da Vegetação Nativa (2012), que substitui o antigo Código Florestal: atualizações e ações em curso. Natureza e Conservação 14(1):e1-e16. doi: 10.1016/j.ncon2016.03.004

Brasil (1965) Código Florestal. Available at http://www2.planalto.gov.br, website accessed in January, 28th 2019

Breda VA. Ocorrência do caititu, *Pecari tajacu* (Mammalia, Artiodactyla), no interior e entorno do maior remanescente de Cerrado de São Paulo. Monography, University of São Paulo, 2017.

Bressan PM, Kierulff MCM, Sugieda AM (org.). Fauna ameaçada de extinção no Estado de São Paulo: Vertebrados. São Paulo, Fundação Parque Zoológico de São Paulo, 648 pp, São Paulo: Secretaria de Meio Ambiente, 2009.

Brito, J. G. Comunidade de invertebrados aquáticos como ferramenta para avaliar o efeito do uso da terra sobre riachos da Amazônia Oriental, Brasil. PhD dissertation, Instituto Nacional de Pesquisas da Amazônia, Manaus,AM (2016).

Brooks TM, Pimm SL, Oyugi JO (1999) Time Lag between Deforestation and Bird Extinction in Tropical Forest Fragments. Cons Biol 13(5):1140-1150.

Burnham KP, Anderson DR. Model selection and multimodel inference: A practical information-theoretic approach, second ed., Springer, New York, USA, 2002.

Cava MGB, Pilon NAL, Ribeiro MC, Durigan G (2018) Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas. J Appl Ecol 55:1164–1172. doi: 10.1111/1365-2664.13046

Chen Y, Peng S (2017) Evidence and mapping of extinction debts for global forest-dwelling reptiles, amphibians and mammals. Sci Rep 7:1–10. doi: 10.1038/srep44305

Cowlishaw G (1999) Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conserv Biol 13:1183–1193.

de Rezende CL, Uezu A, Scarano FR, Araujo DSD (2015) Atlantic Forest spontaneous regeneration at landscape scale. Biodivers Conserv 24:2255–2272. doi: 10.1007/s10531-015-0980-y

Diamond JM (1972) Biogeographic Kinects: Estimation of Relaxation Times for Avifaunas of Southwest Pacific Islands. Proceedings of Natural Academy of Science 69(11):3199-3203.

Dietz JM (1985) Chrysocyon brachyurus. Mammalian Species 234:1–4.

Dirzo R, Young HS, Galetti M, et al. (2014) Defaunation in the Anthropocene. Science 345(6195):401-406. doi: 10.1126/science.1251817

Dotta G, Verdade LM (2011) Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil. Mammalia 75:345–352. doi: 10.1515/MAMM.2011.049

Durigan G, Ratter JA (2016). The need for a consistent fire policy for Cerrado conservation. Journal of Applied Ecology 53:11-15. doi: 10.1111/1365-2664.12559

Essl F, Dullinger S, Rabitsch W, et al. (2015) Delayed biodiversity change: No time to waste. Trends Ecol Evol 30:375–378. doi: 10.1016/j.tree.2015.05.002

Estavillo C, Pardini R, Da Rocha PLB (2013) Forest loss and the biodiversity threshold: An evaluation considering species habitat requirements and the use of matrix habitats. PLoS One 8:1–10. doi: 10.1371/journal.pone.0082369

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Evol Syst 34:487–515. doi: 10.1146/annurev.ecolsys.34.011802.132419

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40:1649-1663. doi: 10.1111/jbi.12130

Ferraz G, Russell GJ, Stouffer PC, et al. (2003) Rates of species loss from Amazonian forest fragments. Proceedings of the National Academy of Sciences 100(24):14069-14073. doi: 10.1073/pnas.2336195100

Ferraz KMPMB, Siqueira MF, Martin JÁ, et al. (2010) Assessment of Cerdocyon thous distribution in an agricultural mosaic, southeastern Brazil. Mammalia 74:275–280. doi: 10.1515/MAMM.2010.036

Ferraz SFB, Vettorazzi CA, Theobald DM, Ballester MVR (2005) Landscape dynamics of Amazonian deforestation between 1984 and 2002 in central Rondônia, Brazil: Assessment and future scenarios. For Ecol Manage 204:67–83. doi: 10.1016/j.foreco.2004.07.073

Ferraz SFB, Vettorazzi CA, Theobald DM (2009) Using indicators of deforestation and land-use dynamics to support conservation strategies: A case study of central Rondônia, Brazil. For Ecol Manage 257:1586–1595. doi: 10.1016/j.foreco.2009.01.013

Ferraz SFB, Ferraz KMPMB, Cassiano CC, et al (2014) How good are tropical forest patches for ecosystem services provisioning? Landsc Ecol 29:187–200. doi: 10.1007/s10980-014-9988-z

Ferreguetti ÁC, Tomás WM, Bergallo HG (2015) Density, occupancy, and activity pattern of two sympatric deer (Mazama) in the Atlantic Forest, Brazil. J Mammal 96:1245–1254. doi: 10.1093/jmammal/gyv132

Ferreira GB, Ahumada JÁ, Oliveira MJR, et al. (2017) Assessing the conservation value of secondary savanna for large mammals in the Brazilian Cerrado. Biotropica 49:734–744. doi: 10.1111/btp.12450

Gheler-Costa C, Vettorazzi CA, Pardini R, et al. (2012) The distribution and abundance of small mammals in agroecosystems of southeastern Brazil. Mammalia 76:185-191. doi: 10.1515/mammalia-2011-0109

Gheler-Costa C, Botero GP, Reia L, et al. (2018) Ecologia trófica de onça-parda (*Puma concolor*) em paisagem agrícola. Ver Agro Amb 11(1):203-225.

GRASS Development Team (2015) Geographic Resources Analysis Support System (GRASS) Software, Version 6.4. Open Source Geospatial Foundation. Electronic document: http://grass.osgeo.org

Grecchi RC, Gwyn QHJ, Bénié GB (2014) Land use and land cover changes in the Brazilian Cerrado : A multidisciplinary approach to assess the impacts of agricultural expansion. Applied Geography 55:300–312. doi: 10.1016/j.apgeog.2014.09.014

Halley JM, Monokrousos N, Mazaris AD, et al. (2016) Dynamics of extinction debt across five taxonomic groups. Nat Commun 7:1–6. doi: 10.1038/ncomms12283

Halstead BJ, Wylie GD, Casazza ML (2014) Ghost of habitat past: Historic habitat affects the contemporary distribution of giant garter snakes in a modified landscape. Anim Conserv 17:144–153. doi: 10.1111/acv.12073

Hanski I (2015) Habitat fragmentation and species richness. J Biogeogr 42:989–993. Doi: 10.1111/jbi.12478

Hanski I, Ovaskainen O (2002) Extinction debt at extinction threshold. Conserv Biol 16:666–673. doi: 10.1046/j.1523-1739.2002.00342.x

Heim N, Fisher JT, Clevenger A, et al. (2017) Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine (Gulo gulo L.). Ecol Evol 1–12. doi: 10.1002/ece3.3337

Hylander K, Ehrlén J (2013) The mechanisms causing extinction debts. Trends Ecol Evol 28:341–346. doi: 10.1016/j.tree.2013.01.010

ICMBio. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume 2 – Mamíferos, 1ª Edição, Brasília: ICMBio/MMA, 2018.

Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology and Evolution 25(3):153-160. doi: 10.1016/j.tree.2009.10.001

Jácomo ATA, Silveira L, Diniz-Filho JAF (2004) Niche separation between the maned wolf (Chrysocyon brachyurus), the crab-eating fox (Dusicyon thous) and the hoary fox (Dusicyon vetulus) in central Brazil. J Zool 262:99–106. doi: 10.1017/S0952836903004473

Jorge MLSP, Galetti M, Ribeiro MC, et al. (2013) Mammal defaunation as surrogate of trophic cascades in biodiversity hotspot. Biological Conservation 163:49-57. doi: 10.1016/j.biocon.2013.04.018

Keuroghlian A, Eaton DP, Longland WS (2004) Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biological Conservation 120(3):411-425. doi: 10.1016/j.biocon.2004.03.016

Kitzes J, Harte J (2015) Predicting extinction debt from community patterns. Ecology 96:2127–2136. doi: 10.1890/14-1594.1

Koyanagi TF, Akasaka M, Oguma H, et al (2017) Evaluating the local habitat history deepens the understanding of the extinction debt for endangered plant species in semi-natural grasslands. Plant Ecol 218:725–735. doi: 10.1007/s11258-017-0724-z

Kuussaari M, Bommarco R, Heikkinen RK, et al. (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 24:564–571. doi: 10.1016/j.tree.2009.04.011

Lima MM, Mariano-Neto E (2014) Extinction thresholds for Sapotaceae due to forest cover in Atlantic Forest landscapes. For Ecol Manage 312:260–270. doi: 10.1016/j.foreco.2013.09.003

Lindborg R, Eriksson O (2004) Historical landscape connectivity affects present plant species diversity. Ecology 85(7):1840-1845.

Lira PK, Ewers RM, Banks-Leite C, et al (2012a) Evaluating the legacy of landscape history: Extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest. J Appl Ecol 49:1325–1333. doi: 10.1111/j.1365-2664.2012.02214.x

Lira PK, Tambosi LR, Ewers RM, et al (2012b) Forest Ecology and Management Land-use and land-cover change in Atlantic Forest landscapes. For Ecol Manage 278:80–89. doi: 10.1016/j.foreco.2012.05.008

Livingston AC, Varner JM, Jules ES, et al (2016) Prescribed fire and conifer removal promote positive understorey vegetation responses in oak woodlands. J Appl Ecol 53:1604–1612. doi: 10.1111/1365-2664.12703

Lyra-Jorge MC, Ciocheti G, Tambosi L, et al. Carnivorous mammals in a mosaic landscape in southeastern Brazil: Is it possible to keep them in an agro-silvicultural landscape? In: Runas J and Dahlgren T, Grassland Biodiversity-Habitat Types, 317–332p, 2009. doi: 10.1007/s10531-008-9366-8

Lyra-Jorge MC, Ribeiro MC, Ciocheti G, et al. (2010) Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. Eur J Wild Res 56:359-368. doi: 10.1007/s10344-009-0324-x

Mackenzie DI (2006) Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. Journal of Wildlife Management 70:367-374.

Mackenzie DI, Nichols JD, Royle JA, et al. Occupancy Estimation and Modelling: inferring patterns and dynamics of species occurrence, second edition, Elsevier Academic Press, 641 pp., 2017.

Magioli M, Moreira MZ, Ferraz KMB, et al. (2014) Stable isotope evidence of *Puma concolor* (Felidae) feeding patterns in agricultural landscapes in southeastern Brazil. Biotorpica 46(4):451-460. doi: 10.1111/btp.12115

Magioli M, Ribeiro MC, Ferraz KMPMB, Rodrigues MG (2015) Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Anim Conserv 18:499–511. doi: 10.1111/acv.12201

Magioli M, Ferraz KMPMB, Setz EZF, et al. (2016) Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. Eur J Wildl Res 62:431–446. doi: 10.1007/s10344-016-1017-x

Martensen AC, Ribeiro MC, Banks-Leite C, et al (2012) Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. Conserv Biol 26:1100–1111. doi: 10.1111/j.1523-1739.2012.01940.x

Massara RL, Paschoal AM de O, Bayle LL, et al. (2016) Ecological interactions between ocelots and sympatric mesocarnivores in protected areas of the Atlantic Forest, southeastern Brazil. Journal of Mammalogy 97(6):1634-1644. doi:10.1093/jmammal/gyw129

Massara RL, Paschoal AM de O, Hirsch A, Chiarello AG (2012) Diet and habitat use by maned wolf outside protected areas in eastern Brazil. Trop Conserv Sci 5:284–300.

Massara RL, Paschoal AM de O, L. Bailey L, et al. (2017) Factors influencing ocelot occupancy in Brazilian Atlantic Forest reserves. Biotropica 50:125–134. doi: 10.1111/btp.12481

McArthur RH and Wilson EO. The Theory of Island Biogeography. Monographs in population biology. I. Princeton University Press, Princeton, 1967.

Metzger JP, Martensen AC, Dixo M, et al (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biol Conserv 142:1166–1177. doi: 10.1016/j.biocon.2009.01.033

Michalski F, Peres C (2005) Anthropogenic determinants of primate and carnivore local extinctions in fragmented forest landscape of southern Amazonia. Biological Conservation 124:383-396.

Moledo JC, Saad AR, Dalmas FB, et al (2016) Impactos ambientais relativos à silvicultura de eucalipto: uma análise comparativa do desenvolvimento e aplicação no plano de manejo florestal. Geociências 35:512–530.

Molin PG, Gergel SE, Soares-Filho BS, et al (2017) Spatial determinants of Atlantic Forest loss and recovery in Brazil. Landsc Ecol 32(4):857-870. doi: 10.1007/s10980-017-0490-2

Moraes MCP, Mello K, Toppa RH (2017) Protected areas and agricultural expansion: Biodiversity conservation versus economic growth in the Southeast of Brazil. J Environ Manage 188:73–84. doi: 10.1016/j.jenvman.2016.11.075

Muylaert RL, Stevens ED, Ribeiro MC (2016) Threshold effect of habitat loss on bat richness in cerrado-forest landscapes. Ecological Applications 26(6):1854-1867.

Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nagy-Reis MB, Nichols JD, Chiarello AG, et al. (2017) Landscape use and co-ocurrence patterns of neotropical spoted cats. Plos One 12(1): e0168441. doi: 10.1371/jornal.pone.0168441

Nanni AS (2015) Dissimilar responses of the Grey brocket deer (*Mazama gouazoubira*), Crab-eating fox (Cerdocyon thous) and Pampas fox (*Lycalopex gymnocercus*) to livestock frequency in subtropical forests of NW Argentina. Mammalian Biology 80:260-264. doi: 10.1016/j.mambio.2015.04.003

Neri FM. Ecologia e conservação de catetos, *Tayassu tajacu*, (Linnaeus, 1758) (ARTIODACTYLA, Tayassuidae) em áreas de Cerrado do estado de São Paulo. PhD Dissertation, Federal University of São Carlos, 2004.

Ochoa-Quintero JM, Gardner TA, Rosa I, et al (2015) Thresholds of species loss in Amazonian deforestation frontier landscapes. Conserv Biol 29:440–451. doi: 10.1111/cobi.12446

Paolino RM, Royle JA, Versiani NF, et al. (2018) Importance of riparian forest corridors for the ocelot in agricultural landscapes. J Mammal 1–11. doi: 10.1093/jmammal/gyy075

Paolino RM, Versiani NF, Pasqualotto N, et al (2016) Buffer zone use by mammals in a Cerrado protected area. Biota Neotrop 16:1–13. doi: 10.1590/1676-0611-BN-2014-0117

Pardini R, de Bueno AA, Gardner TA, et al (2010) Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. PLoS One 5(10). doi: 10.1371/journal.pone.0013666

Pardo LE, Roque F de O, Campbell MJ, et al (2018) Identifying critical limits in oil palm cover for the conservation of terrestrial mammals in Colombia. Biol Conserv 227:65–73. doi: 10.1016/j.biocon.2018.08.026

Piha H, Luoto M, Merilä J (2007) Amphibian occurrence is influenced by current and historic landscape characteristics. Ecological Applications 17(8):2298-2309.

Pinheiro L, Kolb R, Rossatto D (2016) Changes in irradiance and soil properties explain why typical non-arboreal savanna species disappear under tree encroachment. Australian journal of Botany 64:333–341. doi: 10.1071/BT15283

Pflüger FJ, Signer J, Balkenhhol N (2018) Habitat loss causes non-linear genetic erosion in specialist species. Global Ecology and Conservation 17:e00507. doi: 10.1016/j.gecco.2018.e00507

Pinto FAS, Bager A, Clevenger AP, et al. (2018) Giant anteater (*Myrmecophaga tridactyla*) conservation in Brazil: Analysing the relative effects of fragmentation and mortality due to roads. Biological Conservation 228:148-157. doi: 10.1016/j.biocon.2018.10.023

Pônzio MC. Ocorrência de onça-parda (*Puma concolor*) e lobo-guará (*Chrysocyon brachyurus*) em paisagens agrosilviculturais e em remanescentes de Cerrado do Nordeste paulista. Master thesis, University of São Paulo, 2017.

Pütz S, Groeneveld J, Alves LF, et al (2011) Fragmentation drives tropical forest fragments to early successional states : A modelling study for Brazilian Atlantic forests. Ecological modelling 222:1986–1997. doi: 10.1016/j.ecolmodel.2011.03.038

Rappaport DI, Tambosi LR, Metzger JP (2015) A landscape triage approach: Combining spatial and temporal dynamics to prioritize restoration and conservation. J Appl Ecol 52:590–601. doi: 10.1111/1365-2664.12405

Ribeiro JF, Walter BM (2008). As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP and Ribeiro JF (edit.) Cerrado: ecologia e flora, 408p, Brasilia:Embrapa, 2008.

Ribeiro MC, Metzger JP, Martensen AC, et al (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142:1141–1153. doi: 10.1016/j.biocon.2009.02.021

Rocha-Santos L, Pessoa MS, Cassano CR, et al (2016) The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biol Conserv 196:1–9. doi: 10.1016/j.biocon.2016.01.028

Rodrigues TF, Kays R, Parsons A, et al. (2017) Managed forest as habitat for gray brocket deer (Mazama gouazoubira) in agricultural landscapes of southeastern Brazil. J Mammal 98:1301–1309. doi: 10.1093/jmammal/gyx099

Roque FDO, Menezes JFS, Northfield T, et al (2018) Warning signals of biodiversity collapse across gradients of tropical forest loss. Sci Rep 8:1–7. doi: 10.1038/s41598-018-19985-9

Sales LP, Hayward MW, Zambaldi L, et al. (2015) Time-lags in primate occupancy: A study case using dynamic models. Nat e Conserv 13:139–144. doi: 10.1016/j.ncon.2015.10.003

Semlitsch RD, Walls SC, Barichivich WJ, O’Donnell KM (2017) Extinction Debt as a Driver of Amphibian Declines: An Example with Imperiled Flatwoods Salamanders. J Herpetol 51:12–18. doi: 10.1670/16-090

Semper-Pascual A, Macchi L, Sabatini FM, et al (2018) Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. J Appl Ecol 55:1218–1229. doi: 10.1111/1365-2664.13074

Shida CN. Caracterização física do Cerrado Pé-de-gigante e uso das terras na região, 2.Evolução do Uso das Terras na Região. In: Pivello VR & Varanda EM (Orgs). O

Cerrado Pé de Gigante, Parque Estadual do Vassununga, 312p, São Paulo: Secretaria de Meio Ambiente, 2005.

Silva L, Sternberg L, Haridasans M, Hoffmann WA (2008) Expansion of gallery forests into central Brazilian savannas. Global Change Biology 14:2108–2118. doi: 10.1111/j.1365-2486.2008.01637.x

Silva RFB, Batistella M, Moran EF (2016) Drivers of land change: Human-environment interactions and the Atlantic forest transition in the Paraíba Valley, Brazil. Land Use Policy 58:133-144. doi:10.1016/j.landusepol.2016.07.021

Silva RFB, Batistella M, Moran EF, Lu D (2017) Land changes fostering Atlantic forest transition in Brazil: evidence from the Paraíba Valley. The Professional Geographer 69(1):80-93. doi: 10.1080/00330124.2016.1178151

SMA (2017) Secretaria do Meio Ambiente de São Paulo. Programa Etanol mais Verde. Avaliable at http://arquivo.ambiente.sp.gov.br/etanolverde/2011/10/88rotocol-etanol-mais-verde-2017-assinado.pdf, website accessed in Januray 28th.

SMA (2018) Secretaria do Meio Ambiente de São Paulo. Available at http://fflorestal.sp.gov.br/jatai/home, website accessed in Januray 28th.

Smith O, Wang J, Carbone C (2018) Evaluating the effect of forest loss and agricultural expansion on Sumatran tigers from scat surveys. Biol Conserv 221:270–278. doi: 10.1016/j.biocon.2018.03.014

Soto-Shoender JR, Mccleery RA, Monadjem A, Gwinn DC (2018) The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. Biol Conserv 221:127–136. doi: 10.1016/j.biocon.2018.02.028

Stanton-Jr RA, Boone-IV WW, Soto-Shoender J, et al. (2018) Shrub enchroachment and vertebrate diversity: A global meta-analysis. Global Ecology and Biogeography 27:368-379. doi: 10.1111/geb.12675.

Stauffer D. Introduction to Percolation Theory. Taylor & Francis Press, London, 1985.

Suguituru SS, Silva RR, Sousa DR, Munhae CB, et al (2011) Ant community richness and composition across a gradient from *Eucaliptus* plantations to secondary Atlantic Forest. Biota Neotropica 11(1):369-376.

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. Biological Reviews 85:35–53. doi: 10.1111/j.1469-185X.2009.00093.x

Targa MS, Batista GT, Almeida AA, et al (2017) Evaluation of soil water storage in native forest and eucalyptus areas. Ambiente & Agua – An Interdisciplinary Journal of Applied Science 12:873-984. doi: 10.4136/1980-993X

Tchabovsky AV, Savinetskaya LE, Surkova EN, et al. (2016) Delayed threshold response of a rodent population to human-induced landscape change. Oecologia 182:1075–1082. doi: 10.1007/s00442-016-3736-9

Teixeira MAG, Soares-filho BS, Freitas SR, et al (2009) Forest Ecology and Management Modeling landscape dynamics in an Atlantic Rainforest region: Implications for conservation. Forest Ecology and Management 257:1219–1230. doi: 10.1016/j.foreco.2008.10.011

Tilman D, May RM, Lehman CL, et al. (1994) Habitat destruction and the extinction debt. Nature 371:65-66.

Timo TPC, Lyra-Jorge MC, Gheler-Costa C, Verdade LM (2014) Effect of the plantation age on the use of eucalyptus stands by medium to large-sized wild mammals in south-eastern Brazil. IForest – Biogeosciences and Forestry 8:108–113. doi: 10.3832/ifor1237-008

Toppa RH. Estrutura e diversidade florística das diferentes fisionomias de Cerrado e suas correlações com o solo na Estação Ecológica do Jataí, Luiz Antônio, SP. PhD dissertation, São Carlos Federal University, São Carlos, 149p., 2004.

Tucker MA, Böhning-gaese K, Fagan WF, et al. (2018) Moving into the Anthropocene: Global reductions in terrestrial mammalian movements. Science 469(6374):466–469. doi: 10.1126/science.aam9712

Turner MG (1989) Landscape ecology: The effect of pattern and process. Annu. Rev. Ecol. Syst. 20: 171-197.

Uezu A, Metzger JP (2016) Time-lag in responses of birds to Atlantic forest fragmentation: Restoration opportunity and urgency. PloS One 11:1–16. doi: 10.1371/journal.pone.0147909

Valduga MO, Zenni RD, Vitule JRS (2016) Ecological impacts of non-native tree species plantations are broad and heterogeneous: a review of Brazilian research. Annals of the Brazilian Academy of Sciences 88(3):1675–1688. doi: 10.1590/0001-376520150575

Vellend M, Verheyen K, Jacquemyn H, et al (2006) Extinction debt of forest plants persist for more than a century following habitat fragmentation. Ecology 87(3):542-548.

Versiani NF. The giant anteater (*Myrmecophaga tridactyla*) in protected areas and its surroundings in Cerrado of São Paulo state. PhD Dissertation, University of São Paulo, 2016.

Victor MAM, Cavalli AC, Guillaumon JR, Serra-Filho R (2005) Cem anos de devastação: Revisitada 30 anos depois. Ministério do Meio Ambiente, Brasil.

Villard M, Metzger JP (2014) Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51:309-318.

Vynne C, Booth RK, Wasser SK (2014) Physiological implications of landscape use by free-ranging maned wolves (Chrysocyon brachyurus) in Brazil. Journal of Mammalogy 95:696–706. doi: 10.1644/12-mamm-a-247

Vynne C, Keim JL, Machado RB, et al. (2011) Resource selection and its implications for wide-ranging mammals of the Brazilian Cerrado. PloS One 6(12):e28939. doi: 10.1371/journal.pone.0028939

White GC, Burnham KP. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement: 120-138, 1999.

Whittaker RH (1967) Gradient analysis of vegetation (review). Biological reviews of the Cambridge Philosophical Society 42(2):207-264.

Xavier M, Paviolo A, Reverberi L, Pardini R (2018) Effectiveness of Protected Areas for biodiversity conservation: Mammal occupancy patterns in the Iguaçu National Park, Brazil. J Nat Conserv 41:51–62. doi: 10.1016/j.jnc.2017.11.001

Yamanaka S, Akasaka T, Yamaura Y, et al. (2015) Time-lagged responses of indicator taxa to temporal landscape changes in agricultural landscapes. Ecol Indic 48:593–598. doi: 10.1016/j.ecolind.2014.08.024

Zimbres B, Furtado MM, Jácomo ATA, et al. (2013) The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado. Landsc Ecol 28:259–269. doi: 10.1007/s10980-012-9832-2