

UNIVERSIDADE FEDERAL DE ALFENAS

LUCAS GOULART DA SILVA

**INFLUÊNCIA DE PARÂMETROS DA PAISAGEM NA OCORRÊNCIA DE PRIMATAS
EM FRAGMENTOS FLORESTAIS NO SUL DE MINAS GERAIS**

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Dissertação apresentada para obtenção do título de Mestre no Programa de Pós-Graduação em Ecologia e Tecnologia Ambiental na Universidade Federal de Alfenas.

Área de concentração: Meio Ambiente, Sociedade e Diversidade Biológica

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LUCAS GOULART DA SILVA

**“INFLUÊNCIA DE PARÂMETROS DA PAISAGEM NA OCORRÊNCIA DE PRIMATAS
EM FRAGMENTOS FLORESTAIS NO SUL DO ESTADO DE MINAS GERAIS”**

A Banca examinadora, abaixo assinada, aprova a Dissertação apresentada como parte dos requisitos para a obtenção do título de Mestre em Ecologia e Tecnologia Ambiental pela Universidade Federal de Alfenas. Área de Pesquisa: Meio Ambiente, Sociedade e Diversidade Biológica.

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“Prefiro errar crendo num Deus que não existe, a errar não crendo num Deus que existe... pois, se depois não há nada, evidentemente nunca o saberei, quando me afundar no nada eterno; mas se existe alguma coisa, se existe Alguém, terei que prestar contas da minha atitude de rejeição.”

Pascal

RESUMO

A fragmentação florestal e a perda de habitats estão entre as principais causas de extinções de espécies na atualidade. Os fragmentos remanescentes são, em sua maioria, pequenos, isolados e de baixa qualidade. Por serem predominantemente arborícolas, os primatas neotropicais, em geral, são sensíveis aos efeitos da fragmentação. E, uma vez que os primatas estão envolvidos em complexos processos ecológicos, mudanças na paisagem que alterem negativamente a dinâmica de suas populações afetam, conseqüentemente, a estrutura, a composição e a viabilidade de toda comunidade. Com base nisso, nosso objetivo foi avaliar se a área, o isolamento e a visibilidade dos fragmentos e a permeabilidade das matrizes são importantes para explicar a ocorrência de três espécies de primatas. Utilizando a metodologia de playback, analisamos a presença de *Callicebus nigrifrons*, *Callithrix aurita* e *Sapajus nigritus* em 45 fragmentos florestais ao redor do município de Alfenas-Brasil. Com auxílio de ferramentas de geoprocessamento, classificamos a paisagem e analisamos as métricas propostas através de modelos preditivos de ocorrência. Selecionamos os melhores através do Critério de Seleção de Akaike e aplicamos esses modelos plausíveis à outra região (20 fragmentos pertencentes ao município de Poço Fundo-Brasil), com o objetivo de validarmos nossos resultados. Doze modelos foram plausíveis e três foram validados: dois para *Sapajus nigritus* (“Área” e “Área+Visibilidade”) e um para *Callicebus nigrifrons* (“Área+Matrizes”). Nossos resultados reforçaram o valor do tamanho dos fragmentos em habitat muito degradados e evidenciou a importância de incluirmos a visibilidade e a permeabilidade das matrizes em estudos de paisagem. Esses parâmetros propostos poderão auxiliar muito estudos de conservação pelo seu fácil manuseio e ótima resposta.

Palavra-chave: Ecologia, Proteção Ambiental, Primatas, Mata Atlântica, Paisagens Fragmentadas.

ABSTRACT

Forest fragmentation and habitat loss are among the major current extinction causes. Remaining fragments are mostly small, isolated and of a poor quality. Being primarily arboreal, Neotropical primates are generally sensitive to fragmentation effects. Besides, primates are involved in complex ecological process. Thus, landscape changes that negatively interfere with primate population dynamics affect the structure, composition, and ultimately the viability of the whole community. We evaluated if fragment size, isolation and visibility and matrix permeability are important for explaining the occurrence of three Neotropical primate species. Employing playback, we verified the presence of *Callicebus nigrifrons*, *Callithrix aurita* and *Sapajus nigrurus* at 45 forest fragments around the municipality of Alfenas, Brazil. We classified the landscape and evaluated the metrics through predictive models of occurrence. We selected the best models through Akaike Selection Criterion. Aiming at validating our results, we applied the plausible models to another region (20 fragments at the neighbor municipality of Poço Fundo, Brazil). Twelve models were plausible, and three were validated, two for *Sapajus nigrurus* ("Area" and "Area+Visibility") and one for *Callicebus nigrifrons* ("Area+Matrix"). Our results reinforce the value of fragment size in highly degraded habitats, and stress the importance of including novel, biologically relevant metrics in landscape studies, such as visibility and matrix permeability. Such parameters can provide invaluable help for conservation studies, given their easiness for handling and excellent response.

Key words: Ecology, Environmental Protection, Primates, Atlantic Forest, Fragmented Landscapes.

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1. INTRODUÇÃO

1.1 REFERENCIAL TEÓRICO

Processo de fragmentação

A Mata Atlântica é o terceiro bioma em extensão do Brasil, atrás apenas da Amazônia e do Cerrado. Ocupava originalmente 150 milhões de hectares e abrange 17 estados brasileiros (RIBEIRO et al., 2009). Apresenta a segunda maior riqueza de espécies do país, além de altíssimos níveis de endemismo (MYERS et al., 2000). Porém, o grau de devastação é o maior dentre os biomas brasileiros, com seus remanescentes ocupando atualmente entre 11,4% e 16% da sua área original, grande parte desses menores que 100 ha (RIBEIRO et al., 2009). A maioria dos remanescentes corresponde a florestas degradadas, que sofreram muitas alterações em sua estrutura e composição devido à atividades de expansão e de uso da terra pelo homem (FONSECA et al., 2009; METZGER et al., 2009). Esses ainda estão distribuídos de forma não homogênea em pequenos e isolados remanescentes florestais, compostos por florestas secundárias em estágios iniciais ou médios de sucessão, resultado de um processo denominado fragmentação (FAHRIG, 2003; PARDINI et al., 2009).

A fragmentação é o processo onde ocorrem perda e subdivisão de uma extensão relativamente contínua de habitat, transformando-o em uma série de pequenas manchas de tamanhos menores, isoladas, de baixa qualidade e imersas em matrizes de origem antrópica (WILCOVE et al., 1986; GASCON et al., 1993; PRUGH, 2008). Os remanescentes que persistem são, em sua maioria, isolados, pequenos e próximos de rodovias e cidades, geralmente em áreas íngremes e dissecadas, em solos pobres e com altas elevações (FAHRIG, 2003). Com isso, as características abióticas desses habitats, como temperatura, radiação, umidade e velocidade do vento, são drasticamente alteradas (SAUNDERS et al., 1991).

As populações que persistem ficam mais vulneráveis a fatores que agem com mais força nessa paisagem fragmentada, como deriva genética, variações demográficas e endogamia, além de ameaças por eventos estocásticos ambientais (HILL, CURRAN, 2003; UMETSU et al., 2008; VIEIRA et al., 2009; HOBBS, YATES, 2003). Com isso, aspectos de distribuição, dieta, área de vida, tamanho da população e organização social das espécies animais são negativamente alterados (CHAPMAN et al., 2006; ARROYO-RODRÍGUEZ et al., 2009). Em última análise,

esses fatores podem até mesmo aumentar a probabilidade de extinções locais (YOUNG, CLARKE, 2000; FAHRIG, 2002).

Primatas em habitats fragmentados

Dentro desse contexto, os primatas neotropicais são intensamente afetados pelos efeitos derivados do processo de fragmentação e perda de habitat (COWLISHAW, DUNBAR, 2000), como, por exemplo, a redução de área de habitats (CHIARELLO, 1999), a redução da densidade e do tamanho médio das árvores (SAUDERS et al., 1991; CHAPMAN, ONDERDONK, 1998), a sobrevivência e a germinação de sementes (LAURENCE, YENSEN, 1991), a formação de copas e a mortalidade das árvores (LOVEJOY, 1986; MESQUITA, 1999). Por mais que os primatas ocupem diferentes micro-habitats florestais, todos os primatas neotropicais são exclusivamente dependentes de ecossistemas arborícolas (POZO-MONTUY et al., 2011). É nas árvores que encontram locais específicos de alimentação, refúgio, locais para dormir e reproduzir (MENDES-PONTES, SOARES, 2005). E, alterando-se a estrutura dessa paisagem, a dinâmica desses animais também é alterada (ARROYO-RODRIGUEZ et al., 2007).

Essa paisagem alterada, contudo, implica consequências negativas não só aos primatas, mas a toda comunidade que esteja ligada direta ou indiretamente aos primatas (CHAPMAN, 1996; TABARELLI et al., 2004). Isso porque os primatas têm uma importância ecológica crucial na manutenção da estrutura e função de seus ecossistemas (CHAPMAN, ONDERDONK 1998; STONER et al., 2007) por estarem envolvidos em complexos processos ecológicos, como dispersão, frugivoria e predação (DEW, WRIGHT, 1998; ALBERT et al., 2013). Assim, mudanças na paisagem que alterem negativamente a dinâmica de suas populações afetam, conseqüentemente, a estrutura, a composição e a viabilidade da comunidade (CRUMPACKER, 1998; COWLISHAW, DUNBAR, 2000).

Ecologia de paisagem e modelagem ecológica

A paisagem é definida como um “mosaico heterogêneo formado por unidades interativas” sendo que essa heterogeneidade “existe para pelo menos um fator, segundo um observador e numa determinada escala” (METZGER, 2001). Ainda segundo Metzger (2001), no campo ecológico, esse mosaico é considerado como sendo um conjunto de habitats significativos para a espécie ou comunidade estudada e, da mesma forma que o habitat, o espaço que será estudado e o

tempo do estudo serão definidos de acordo com a espécie/comunidade do estudo. Diferentemente das ecologias de ecossistemas e de comunidades, a ecologia em escala de paisagem seria uma junção da análise espacial de uma área com a interação entre a espécie/comunidade alvo do estudo e esse ambiente (METZGER, 2008). Em outras palavras, seria a relação entre os padrões espaciais e os processos ecológicos de determinada área. Como a fragmentação florestal ocorre ao nível de paisagem, é essencial adotarmos essa escala de paisagem para estudos que tratem do tema (FAHRIG, 2003).

As análises no campo da ecologia ao nível de paisagem são realizadas utilizando “métricas” ou “índices” de paisagem, que nada mais são do que quantificações de funções, parâmetros ou estruturas da paisagem que serão abordados (TURNER, 1989; MCGARIGAL et al., 2002; TRISURAT et al., 2012). Essas métricas de paisagem podem ser utilizadas com diversos objetivos, entre eles quantificar as mudanças da paisagem ao longo do tempo (O’NEIL et al., 1997), realizar análises de metapopulações (KAREIVA E WENNERGREN, 1995) e avaliar os efeitos de perda e fragmentação do habitat sobre parte da comunidade de animais (FAHRIG, 1998; RIITTERS et al., 2000).

Um grande número de métricas foi desenvolvido nas últimas duas décadas (TRISURAT et al., 2012) sendo que, de acordo com McGarigal e Cushman, em 2002 já existiam na literatura mais de 40 dessas métricas. Porém, com tantas opções, a escolha de qual conjunto de métricas é apropriado para determinado estudo torna-se uma tarefa complexa (MARGULES, PRESSEY, 2000). A seleção das métricas deve basear-se em determinados aspectos do estudo, como as hipóteses que serão testadas, as características da estrutura da paisagem que são relevantes para o organismo ou o processo de interesse e as características da paisagem em si (MCGARIGAL, MARKS, 1995). Segundo Bonilla-Sanchez et al. (2010), as métricas escolhidas devem ser previamente selecionadas, considerando quais fatores podem afetar direta ou indiretamente os padrões de distribuição das espécies alvo e incluindo nos critérios de escolha não somente os parâmetros do local estudado, mas também características específicas do grupo ou espécies estudados.

Definidos os índices de paisagem, precisamos incorporá-los, juntamente com os dados biológicos, aos modelos adequados aos objetivos da pesquisa em questão, processo esse denominado modelagem ecológica. Modelos são uma representação simplificada de sistemas e processos reais, devendo ter, porém, um mínimo de detalhamento para que possam ser

consideradas representações válidas (CAMARGO, 2009). Analisando esses modelos podemos traçar ligações entre os componentes envolvidos, evidenciando quais parâmetros foram importantes ou não para alcançar os objetivos propostos (ANGELINI, 1999) e, assim, fornecer as informações necessárias para que sejam tomadas ações mitigadoras correspondentes.

A modelagem ecológica é composta basicamente por duas etapas: primeiramente, verificam-se as relações entre organismos e paisagem, elaborando um modelo específico que supostamente possa descrever o ecossistema modelado; na segunda etapa, avalia-se a qualidade do modelo criado através de técnicas de validação (GOMES, VARRIALE, 2004).

Entre os tipos de modelos ecológicos que podem ser empregados para se estudar os efeitos da fragmentação sobre as espécies, temos os modelos preditivos de ocorrência. Modelos preditivos de ocorrência são aqueles que objetivam prever a distribuição de espécies nas paisagens, estimando a relação entre as ocorrências destas e as características biofísicas da paisagem (GUISAN, ZIMMERMANN 2000; YOST et al., 2008). Através da junção entre os dados de presença/ausência da espécie alvo, coletados sistematicamente em vários locais, e as métricas estruturais/funcionais de interesse, podemos criar modelos que nos indicarão padrões de ocorrência do organismo estudado na paisagem (TRISURAT et al., 2010). Esse tipo de modelo tem ganhado um lugar de destaque como ferramenta de conservação em paisagens fragmentadas, permitindo aos pesquisadores elaborar planos de conservação, mapear padrões de biodiversidade ou quantificar como a variação de um parâmetro da paisagem pode alterar a distribuição de espécies (MARGULES, AUSTIN, 1994; JEDRZEJEWSKI et al., 2008; GRAY 2009).

Métricas de possível interesse para primatas

Entre as várias métricas de paisagem empregadas em modelagem ecológica, abordaremos a seguir aquelas que foram empregadas nesse trabalho por apresentar um possível potencial para explicar a ocorrência/ausência dos primatas em paisagens fragmentadas.

Área

O aspecto da paisagem considerado mais importante para a conservação das espécies é o tamanho dos habitats, com vários estudos apontando uma relação positiva entre a área e tanto a riqueza de espécies quanto o tamanho das populações (ROSENZWEIG, 1995; HILL, CURRAN, 2003). Segundo a Teoria da Biogeografia de Ilhas (MACARTHUR, WILSON, 1963), alterações

nos fatores influenciados pela área, como, por exemplo, a redução na quantidade dos recursos disponíveis, podem reduzir as populações e torná-las mais vulneráveis a estocasticidades ambientais, demográficas e genéticas. A riqueza de espécies também é afetada, uma vez que em áreas menores geralmente encontramos uma baixa heterogeneidade de habitats, possibilitando que menos espécies especialistas se estabeleçam (CONNOR, MCCOY, 2001). A conjunção desses fatores tende a elevar as taxas de extinção em pequenos habitats (HOBBS, YATES, 2003; MATTHIES et al., 2004)

A maioria dos estudos de primatas evidencia os efeitos negativos da redução do tamanho dos fragmentos sobre as comunidades desses animais (CHIARELLO, DE MELO, 2001). Somente para algumas espécies muito plásticas ou em hipóteses que seus predadores estão ausentes a redução do tamanho dos fragmentos resultou em aumento de suas populações (GONZÁLES-SOLÍS et al., 2001; BONILLA-SÁNCHEZ, SERIO-SILVA, 2010). Em nenhum desses estudos, contudo, a paisagem era tão fragmentada como em Alfenas-MG. O tamanho dos maiores fragmentos desse município equivale, na melhor das hipóteses, ao tamanho dos pequenos fragmentos de outros estudos semelhantes (MARTINS, 2005). Assim, não temos informações se os resultados encontrados para a importância do tamanho dos fragmentos em outros estudos com primatas também se aplicam a uma paisagem altamente fragmentada.

Isolamento

A fragmentação não causa apenas a perda de habitat, mas gera também um isolamento entre as manchas remanescentes, anteriormente contínuas (VAN DEN BERG et al., 2001). Quanto mais isolado é um fragmento, menos habitat existe na paisagem que o rodeia (FAHRIG, 2003). As espécies restritas a esses remanescentes, por serem incapazes de se locomover no ambiente externo, têm o tamanho das suas populações ainda mais reduzidas (SISK et al., 1997). Dessa forma, o isolamento pode influenciar diretamente na estrutura gênica de uma população em determinado fragmento. Em última análise, toda a viabilidade de uma população pode ser comprometida pelo aumento dos níveis de endogamia e de deriva genética aleatória (YOUNG et al., 1996).

Alguns estudos com primatas mostraram que existe uma relação negativa entre o isolamento entre os fragmentos e a abundância de espécies, ou seja, quanto maior a distância entre os fragmentos, menor a abundância de primatas (ESTRADA, COATES-ESTRADA, 1996;

POZO-MONTUY et al., 2011). Esses estudos, contudo, geralmente abordam o isolamento através da “distância euclidiana” (menor distância entre dois pontos) entre a unidade amostral e o fragmento florestal mais próximo (ESTRADA, COATES, 1996). Por mais essa seja uma técnica amplamente utilizada, ela ignora alguns elementos da paisagem que podem ser relevantes, como, por exemplo, as barreiras impostas por grandes corpos d’água. Além disso, o isolamento calculado através da distância euclidiana considera para cálculo o fragmento mais próximo, independente do tamanho ou do quanto esse fragmento será importante para a espécie em questão.

A área e o isolamento dos fragmentos, por serem aspectos clássicos derivados da Teoria da Biogeografia de Ilhas, são os parâmetros da paisagem historicamente considerados mais críticos para descrever a dinâmica de espécies em regiões fragmentadas (HANSKI, GAGGIOTTI, 2004). Somente essas métricas, contudo, podem não ser suficientes para explicar toda a variabilidade na probabilidade de ocorrência das espécies, uma vez que cada uma dessas apresenta necessidades biológicas específicas (MCGARIGAL, MARKS, 1995; BONILLA-SÁNCHEZ et al., 2010). Além disto, os estudos normalmente têm se restringido a métricas de paisagem clássicas e fixas entre os trabalhos, sem considerar a realidade biológica dos objetos de estudo. Assim, faz-se necessário considerar também parâmetros ligados a singularidade de cada grupo, elaborando modelos específicos e mais eficientes (MCGARIGAL et al., 2002; NEEL et al., 2004; ARROYO-RODRÍGUES, MANDUJANO, 2009).

Permeabilidade das Matrizes

A matriz é definida como a porção da paisagem que sofreu, em algum momento, uma intensa perturbação antropogênica (corte, queimadas etc) (ANTOGIOVANNI, METZGER, 2005). Esse novo ambiente, geralmente composto por cultivos agrícolas ou pastagens, se torna uma área heterogênea quando comparada ao habitat original (EWERS, DIDHAM, 2006). Por representar todo habitat presente ao redor do fragmento florestal, a matriz está diretamente ligada a sua dinâmica (GASCON et al., 1999), influenciando, por exemplo, os efeitos de borda dos fragmentos: quanto mais similar a matriz é do habitat original, menores as variações físicas e biológicas sofridas pelos fragmentos na região de contato com a matriz. Neste caso, a matriz atuaria como uma zona de amortecimento, reduzindo os efeitos de borda (MESQUITTA et al., 1999).

Dependendo da sua estrutura e composição, a matriz pode ainda atuar como um habitat secundário para espécies que sejam capazes de explorá-la (JOKIMAKI, HUHTA, 1996; GASCON et al., 1999), oferecendo recursos alimentares e até mesmo territórios de menor qualidade para os animais (ROCHA et al., 2007). Nesse sentido, ela pode suprir parte dos recursos da mata, desempenhando um papel crucial para sobrevivência dessas espécies (POZO-MONTUY et al., 2011). Por exemplo, alguns cultivos agrícolas, como a cana-de-açúcar (que possui altos valores energéticos), podem atrair indivíduos para além dos fragmentos florestais, complementando suas dietas (ROCHA, 2007).

Além disso, por ser um ambiente transitório e heterogêneo que separa os habitats animais, a matriz está diretamente relacionada ao isolamento dos remanescentes florestais (ARROYO-RODRÍGUEZ, MANDUJANO, 2009). A matriz atua como um filtro seletor para o movimento das espécies: matrizes com estruturas similares aos habitats florestais seriam mais permeáveis para espécies de interior, enquanto as menos similares (como as áreas de pastagens) seriam mais resistentes à movimentação de espécies florestais (RICKETTS, 2011; CRONIM, 2003). Muitas espécies florestais de pássaros, por exemplo, preferem colonizar porções da matriz que sejam estruturalmente semelhantes às florestas primárias (STOUFFER, BORGES, 2001). Porém, além dos altos custos energéticos para se movimentar através do não-habitat, essas espécies ainda ficam mais susceptíveis à predação (SELMAN, DOAR, 1992).

Em relação aos primatas arbóreos, há alguns estudos que demonstraram a importância das matrizes na dinâmica desses animais (POZO-MONTUY et al., 2011). Porém não há, até o momento, estudos que explorem a influência que a matriz exerce sobre a movimentação dos primatas. Não temos informações se diferentes tipos de matrizes geram respostas diferentes na movimentação. Ou até mesmo quais tipos de matrizes são mais ou menos favoráveis/desfavoráveis para a locomoção desses animais.

Visibilidade dos fragmentos florestais

Pensando na singularidade do grupo, exploramos a influência do relevo da paisagem sobre a ocorrência de primatas. Esse parâmetro da paisagem é pouco explorado para fauna em geral (STONE et al., 1997; GREENBERG, MCCLINTOCK, 2008) e nunca para os primatas. Uma qualidade característica dos primatas neotropicais é a sua aguçada visão, amplamente utilizada na locomoção, obtenção de alimentos e atividades sociais (COIMBRA-FILHO, 1982

DOMINY, LUCAS, 2001; SURRIDGE et al., 2003).. Considerando que esses animais tomam conhecimento de outros fragmentos florestais principalmente através da visão, por mais que os outros parâmetros sejam favoráveis, se o indivíduo não tiver conhecimento da existência desses outros fragmentos eles podem nem mesmo ser considerados como potenciais locais para dispersão/migração. Com base nessa nisso, a visibilidade das manchas que estão ao redor do fragmento principal pode estar relacionada à ocorrência dos primatas. Assim, fragmentos visíveis poderiam ser mais acessados pelos primatas, enquanto fragmentos “escondidos” pela distância, por variações do relevo ou por barreiras naturais e artificiais não seriam tão acessados.

1.2 OBJETIVOS

Dentro desse contexto, o objetivo desse estudo é responder as seguintes questões centrais: O tamanho dos fragmentos florestais em uma região altamente fragmentada é um parâmetro importante para prever a ocorrência de primatas? Nossa métrica refinada de isolamento é plausível para explicar as ocorrências das espécies estudadas? Diferenças estruturais entre as matrizes, analisadas com foco na permeabilidade animal, influenciam na ocorrência de primatas em fragmentos florestais? Se sim, há um tipo de matriz que seja mais benéfico? Fragmentos florestais “escondidos” por barreiras físicas naturais são menos acessados que fragmentos visíveis? Para responder essas perguntas, analisamos 45 fragmentos florestais na região de Alfenas-MG, a fim de avaliar se os parâmetros da paisagem “área”, “isolamento”, “permeabilidade das matrizes” e “visibilidade dos fragmentos vizinhos” influenciam na ocorrência de três espécies de primatas (*Callicebus nigrifrons*, *Callithrix aurita* e *Sapajus nigrurus*) em fragmentos florestais.

1.3 REFERÊNCIAS

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2. DESENVOLVIMENTO E CONCLUSÃO

ARTIGO

Patch size, isolation, visibility and matrix permeability influence Neotropical primate occurrence within highly fragmented landscapes

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Abstract

Forest fragmentation and habitat loss are among the major current extinction causes. Remaining fragments are mostly small, isolated and of a poor quality. Being primarily arboreal, Neotropical primates are generally sensitive to fragmentation effects. Besides, primates are involved in complex ecological process. Thus, landscape changes that negatively interfere with primate population dynamics affect the structure, composition, and ultimately the viability of the whole community. We evaluated if fragment size, isolation and visibility and matrix permeability are important for explaining the occurrence of three Neotropical primate species. Employing playback, we verified the presence of *Callicebus nigrifrons*, *Callithrix aurita* and *Sapajus nigrurus* at 45 forest fragments around the municipality of Alfenas, Brazil. We classified the landscape and evaluated the metrics through predictive models of occurrence. We selected the best models through Akaike Selection Criterion. Aiming at validating our results, we applied the plausible models to another region (20 fragments at the neighbor municipality of Poço Fundo, Brazil). Twelve models were plausible, and three were validated, two for *Sapajus nigrurus* ("Area" and "Area+Visibility") and one for *Callicebus nigrifrons* ("Area+Matrix"). Our results reinforce the value of fragment size in highly degraded habitats, and stress the importance of including novel, biologically relevant metrics in landscape studies, such as visibility and matrix

permeability. Such parameters can provide invaluable help for conservation studies, given their easiness for handling and excellent response.

1. Introduction

Human actions, such as rapid urbanization and intense land use for agriculture and animal ranching, modify the original landscape, reducing the quantity, quality and spatial configuration of essential resources for the maintenance of the local and regional biodiversity (Fonseca et al., 2009; Metzger et al., 2009; Ellis et al., 2010). As a consequence of such anthropic interference, an intensification of the habitat fragmentation process takes place (Fahrig, 2003), usually with negative effects for various taxa (Pardini et al., 2009). Neotropical primates, being primarily arboreal, are strongly affected (Cowlshaw and Dunbar, 2000; Pozo-Montuy and Serio-Silva, 2011). They find food, shelter and reproductive sites in the trees, being thus very sensitive to changes in the vertical structure of the vegetation, as well as to the availability of such sites in the landscape (Chapman and Peres, 2001; Mendes-Pontes and Soares, 2005). Given that primates are involved in complex ecological processes, such as dispersion, frugivory and predation (Chapman and Onderdonk, 1998; Dew and Wright, 1998; Albert et al., 2013), landscape changes negatively affecting their population dynamics consequently influence the structure, composition and viability of the whole community that is directly or indirectly related to the primates (Chapman, 1996; Cowlshaw and Dunbar, 2000). However, few studies are able to predict primate occurrence (Chapman and Peres, 2001). Most studies relate primate presence to common landscape parameters only (e.g. fragment size and Euclidian isolation), also not taking into consideration structural peculiarities of the animals (Wieczkowski, 2004; Anzures-Dadda and Manson, 2007; Bonilla-Sánchez et al., 2010). To understand how different landscape features influence primates directly and ecological processes indirectly, is therefore essential for defining more effective strategies for landscape and resource management. We aimed at estimating the relative contribution of fragment size, isolation, visibility between neighbor fragments and matrix permeability on the occurrence of three Neotropical primate species at an Atlantic forest region.

Forest fragmentation is the process by which a former continuous habitat suffers loss and subdivision into patches that are smaller, isolated, of a lower quality and under a stronger influence of the border with anthropic matrixes (i.e. non-habitat, such as sugar cane, pasture, forestry etc. Gascon et al, 1993; Ricketts, 2001; Tabarelli et al, 2005; Prugh, 2008). Populations

living in those landscapes are more vulnerable not only to environmental, demographic and genetic stochastic events (Hill and Curran, 2003; Umetsu et al., 2008; Vieira et al., 2009), but also to several other negative factors, such as endogamy (Fahrig, 2003; Hobbs and Yates, 2003). As a result, the distribution, diet, home range, population size and social organization are also negatively changed (Chapman et al., 2006; Arroyo-Rodríguez et al., 2009). Ultimately, all those factors increase the likelihood of local extinctions (Young and Clarke, 2000; Fahrig, 2002).

Primates are no exception, and several authors have related negative effects of fragmented landscape parameters on arboreal primates (Estrada and Coates-Estrada, 1996; Chapman and Onderdonk, 1998; Arroyo-Rodríguez and Mandujano, 2009). The negative effects of fragment size are the most commonly studied issue (Chiarello and Melo, 2001; Arroyo-Rodríguez and Mandujano, 2006). The effects resulting from patch isolation is another usual study topic (Estrada and Coates, 1996). Such isolation, however, is usually measured via Euclidian distance, a metric which ignores several landscape elements, such as physical barriers, stepping stones, matrix types and human edifications. Besides, the usual approach is to include in the analyses all fragments surrounding the focal ones, irrespective of their characteristics, thus not taking into consideration their real usefulness for the animals. In our study we have refined the isolation metric, by taking into consideration the size of the surrounding fragments, and also the presence of insurmountable barriers (e.g. reservoirs and cities). We therefore attempted to bring the parameter closer to the biological reality of the study species.

Moving to other metrics, some studies have attempted to clarify the influence of matrix features on the population of arboreal primates (Pozo-Montuy and Serio-Silva, 2011). However, to our knowledge, no study has focused on the permeability of the matrix for primate movement. We do not know, for example, if distinct matrix types influence primate movement differently. However, movement is a primary factor in the establishment and maintenance of metapopulations, and it must be considered when discussing the isolation of forest fragments (Arroyo-Rodríguez and Mandujano, 2009).

Landscape relief is another likely relevant, yet poorly explored, parameter for animals as a whole (Stone et al., 1997; Greenberg and McClintock, 2008), and not considered for primates so far. Primates most likely acquire knowledge about other forest fragments mostly through their vision, highly developed and largely employed in locomotion, foraging and social activities (Dominy and Lucas, 2001; Surridge et al., 2003). Thus, how can a primate know about the

existence of a neighbor fragment, if it is not visible to it? Therefore, taking into consideration the biological reality of primates facing a rugged topography can help elucidating part of their distribution in the landscape, by revealing the existence of “hidden” forest fragments.

Within the context above, the objective of the current study was to answer the following questions: Is the size of forest fragments in a highly fragmented region an important parameter for predicting primate occurrence? Is our refined isolation metric plausible for explaining the occurrence of the studied species? Do structural differences among matrix types, considered with a focus on animal permeability, influence primate occurrence on forest fragments? If so, is there a matrix type which is more favorable to primates? Are forest fragments which are “hidden” by natural physical barriers less accessed than visible ones?

2. Material and Methods

2.1 Study area and fragment selection

We carried out the study in forest fragments around the municipality of Alfenas, Minas Gerais, Brasil (Figure 1). The region is in a transition zone between the Atlantic Forest (seasonal or semideciduous type) and Cerrado biomes, the first being dominant. The original vegetation is highly degraded and fragmented, with circa 4% remaining (Ribeiro et al., 2009). The remaining fragments have an average size of 10ha (0.1-182ha). We selected 45 fragments for the study, showing a gradient of size, isolation and shape (more circular to more irregular).

2.2 Primate species

We studied the three primate species naturally occurring in the region *Callicebus nigrifrons* (black-fronted titi monkeys), (buffy-tufted-ear marmosets) e *Sapajus nigritus* (black capuchin monkeys):

- *Callicebus nigrifrons* is a medium-sized primate (1050-1650g; Hershkovitz, 1990) and its diet is composed basically by fruits (Norconk, 2007). It is endemic to the Atlantic forest, and found in primary as well as secondary forests, being well-adapted to the last (Hershkovitz, 1990; Trevelin et al., 2007);
- *Callithrix aurita* is a small-bodied primate (400-450g; Garber, 1992), also endemic to the Atlantic forest. It inhabits upland evergreen and semideciduous forest at altitudes varying from 600 to 1200 m (Rylands and Faria, 1993).

Differently from the more generalist species of the genus, such as *C. jacchus* and *C. penicillata*, *C. aurita* is more sensitive to fragmented habitats, given it is not so well-adapted to exsudate consumption, insects being the main component of their diet (Muskin, 1984). Threatened with extinction, the species is listed as “vulnerable” (IUCN, 2013);

- *Sapajus nigritus* is a medium-sized primate (1.3 a 4.8kg; Ford and Davis, 1992) and its distribution encompasses a large region mostly within the Atlantic Forest biome (states of Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul), extending up the northernmost tip of the Argentinean province of Misiones (Fragaszy et al., 2004). It is characterized by its destructive foraging in the canopy (Garber et al., 2012). It is an omnivorous species, with a diet basically composed by fruits, seeds, nectar and animal prey, besides other items. There are reports that the species is capable of employing crops for complementing its diet (Rocha et al., 2007).

Given their occurrence in the Atlantic forest, a highly fragmented biome, *Callicebus nigrifrons* and *Sapajus nigritus* are listed as “near threatened” by the Red List of Threatened Species (IUCN, 2013).

2.3 Survey of primate occurrence

For detecting primate species we employed a playback sampling technique (Falls, 1981). Sampling scheme involved emitting calls of the study species separately, both inside and at the border of each study fragment, aiming at acoustically covering all or most of fragment surface. Inside the fragments we reproduced calls in three different directions (120° from each other) at each sampling point, thus covering 360° around it; from fragment borders, we broadcasted calls towards two directions, each one at a 45° angle in relation to the border line. We waited one minute in silence after each playback (adapted from Boscolo et al. 2006). If there was no response (vocal or approach) after the emissions at a given point, we repeated the procedure at another point, and consecutively so. We sampled each fragment as many times as necessary to cover its whole area or until we obtained a positive response. Distance between sampling points was always smaller than the estimated hearing range. If we did not obtain a positive response, we carried out two other visits to a given fragment, at different dates, before considering a given

species as being absent from it. We carried out playbacks preferably during mornings (7:00-10:30), from July, 2010 until January, 2013. For each species, we selected the call type to be reproduced based on the behavior of each species, choosing the one most likely to elicit responses. Such calls are those usually related to resource defense, group protection, or related to the maintenance of contact between group members. Thus, we chose the long phee calls (Bezerra and Souto, 2008) for *Callithrix aurita*, duets (Robinson, 1981) for *Callicebus nigrifrons* and contact whistles (Wheeler, 2008) for *Sapajus nigrurus*. The recordings played back to survey *Callithrix aurita* were actually from *C. flaviceps*, a procedure successfully adopted in our research group. The calls for detecting *Sapajus nigrurus* came from *S. apella* (Emmons et al., 1997), following the procedure recommended in Pereira et al. (2010). Note that former *Sapajus apella* was lately split in several species, *S. nigrurus* being one of them.

2.3 Land cover and use and landscape metrics

For selecting the study fragments, we employed both Landsat satellite images from 2011 and 2012, and also a map of land use and cover available at a 1:50.000 scale. Later, for each landscape surrounding the study fragments we produced a new land use and vegetation cover map. We generated such map by manual vectorization, at a 1:10.000 scale, followed by visual classification of high resolution (1m) Google Earth images in the program QGIS 1.8, with the help of the OpenLayer plugin. We also employed ArcGis®10.0 software at several stages of the study. For building the occurrence models, we calculated or estimated the following parameters for each fragment (Table 1):

- Area: size of the forest fragment, in ha;
- Isolation: we attempted to calculate an isolation metric which had a higher biological significance than the mere Euclidian distance between the study fragments and their nearest neighboring fragment. Thus, we created a metric which simultaneously takes into consideration the presence of possible stepping stones, the size of the neighboring fragments (potential source or targets for dispersion) and the limiting distance in the path between the sampling fragment and its neighbors. Firstly, based on the sizes of the studied fragments and on the presence/absence data, we calculated the area which corresponds to a 50% chance of occurrence (p50) of each study species. We thus restricted the set of neighboring fragments to those with a higher probability of

harboring the primate species. Then, for each species we drew links between each of the 45 sampling fragments and its nearest fragment with a size equal or larger than p50 for that species. The path, however, was not the shortest linear distance between the fragments (Euclidian distance). Instead, we chose broken routes which had the shortest distances over open areas (for example, paths with stepping stones). Besides, we also included unavoidable detours, such as going round water bodies. We then considered our isolation metric to be the largest distance (among the sequences of segments for each route) over an open area in a path between the focal fragment and its nearest p50 neighbor. We believe this segment is the limiting factor in the movement between these neighboring fragments;

- Visibility, in ha: we created this metric in order to quantify the total area of visible forest remnants surrounding the study fragments. The first step in its calculation was to insert a topography map of the region (IBGE; 1:50.000) on top of the classification of the study fragments. Next, we traced “lines of sight” from the border of each study fragment to the border of each of its neighboring forest patches (commonly more than one line between each fragment pair) within a 500m buffer. For that end we employed the “3D Analyst - Interpolate Line” tool from the ArcGis®10.0 software. We then retrieved the topographic profile of such line. If at least one of the profiles showed that there was a clear line of sight from a focal fragment towards a neighboring one, the last was deemed visible. We considered a clear line of sight if, from a virtual tree, 10m high, at the border of the study fragment a monkey could have a direct view of a similar tree standing at the border of the target fragment. The size of all visible fragments around a study fragment was added to calculate its ‘visibility’. We chose the 500m buffer criterion as a rough estimate of the maximum distance a primate would travel in an open area. Such information is extremely rare in the literature, and we based our criterion in the few available values (Estrada and Coates, 1996; Heiduck, 2002; Jerusalinsky, 2013);
- Matrix permeability: we find three main matrix types in the study region, coffee, sugar cane and pastures. These types can be ranked from the most structurally similar to the original habitats (coffee plantations) to the more dissimilar one (pastures), sugar cane being intermediary (Figure 2). Broadly, we aimed at identifying if coffee plantations

are considered more permeable to movement than sugar cane plantations, and if both are more permeable than pastures, given their structural differences. However, information regarding the influence or permeability of each of these types on Neotropical primate movement are basically non-existent, and difficult to obtain at first-hand. We then resorted to a methodology based on the knowledge of experts (adapted from Lima 2012). We sent forms to researchers familiar with one or more of the study species and with field experience, asking them to attribute a permeability value (PV) for each of several land use types for each species. Such values varied from 0 to 100, in increments of 10 units, 0 being the least and 100 the most permeable. Then, the PV for a given matrix type was the average of the values attributed to it by several researchers. Next, for each fragment we attributed a Matrix Permeability Index (MPI). The higher this index, the more permeable is the set of matrix types surrounding a focal fragment. The MPI was calculated according to the formula:

$$\text{MPI}_b = \frac{\sum(PVs \cdot As)}{Ab}$$

Where: MPI_b = Matrix Permeability Index at point b; PVs = Permeability Value of land use type s; A_s = Area occupied by land use type s; A_b = Total area of the buffer at point b; b = focal fragments; s = Land use type (coffee, sugar cane or pasture).

2.4 Competing models

To evaluate the influence of different environmental parameters on the occurrence of the study species, we generated a set of a priori competing models. Each model included a combination of the study metrics which were considered relevant for the species, based on their biological characteristics (Table 2). Such an approach has been considered preferable to testing all possible combinations of parameters.

2.5 Data analysis

We employed simple and multiple logistic regression models to evaluate the relation between presence/absence of the three species (*Callicebus nigrifrons*, *Callithrix aurita* and *Sapajus nigritus*). The four independent variables which were selected to build the models were

fragment size, isolation, visibility and matrix permeability. We selected the plausible models based on the Akaike Criterion Information, corrected for small samples (AICc) (Akaike, 1974). Independent variables with more than 70% of correlation were not included in the models (Pearson's correlation). We conducted all analysis in the software R 2.15.3 (R Core Team, 2013).

We considered as the more plausible models the ones with the lower AICc values. We considered models with wAICc higher than 0.1 (i.e. > 10%) also to be plausible ones. The wAICc index allows estimating the relative efficiency of a given model, given a list of competing models attempting to explain the patterns in the data (Zuur et al., 2009).

2.6 Model validation

After selecting the plausible predictive models of occurrence (wAICc>0.1), we tested their effectiveness at a different landscape (20 forest fragments in the municipality of Poço Fundo/Brasil), a process labeled validation (Jørgensen and Bendoricchio, 2001). First, we collected primate occurrence data on those fragments, employing the same methodology as above. We then calculated their metrics, as we did for the first 45 fragments. However, instead of comparing the competing models in these 20 new fragments, we applied on them the plausible models generated in the previous phase with the 45 original fragments. The result was a set of values of probability of occurrence, for each species and fragment. We adopted 80% as the threshold probability value for distinguishing presence from absence. Thus, fragments with a probability of occurrence of a given species equal or higher than 80% were predicted to harbor that species. We then compared such predictions with the field data, thus verifying which models successfully explained primate occurrence, and which did not. We employed the confusion matrix technique (Pearson, 2010) and the Kappa test (Cohen, 1960) for such comparisons, and thus to estimate the precision of each model.

3. Results

Among the 45 surveyed fragments, we registered the occurrence of *Callicebus nigrifrons* in 28, of *Callithrix aurita* in 15, and of *Sapajus nigritus* in 9 of them.

When evaluating competing predictive models for each species, fragment size appeared as the main parameter explaining presence patterns (Table 3). However, for all study species, visibility, matrix permeability and isolation were also important.

When validating the models with the additional 20 fragments at a neighboring locality, three of the plausible models produced significant results, with $Kappa > 0.4$ and $p < 0.05$ (Table 4).

4. Discussion

Fragment size was crucial for explaining primate occurrence. The smaller the fragment, the smaller the probability of species occurrence, a result also found at previous researches, both for mammals as a whole (Chiarello, 1999), and also for Neotropical primates (Estrada and Coates, 1996). However, in none of the previous studies, the field site was as degraded as ours. Around the municipality of Alfenas, there is only 4% of remaining forest cover (Ribeiro et al, 2009), and average fragment size is 30.29ha. The size of the largest fragments in our region is, at best, equal to the size of the small fragments of similar studies (Chiarello and Melo, 2001; Martins, 2005). Populations restricted to such small remnants are extremely vulnerable to the impact of demographic, genetic and environmental stochastic factors, thus increasing the risk of local extinction (Hobbs and Yates, 2003; Matthies, 2004). Hunting pressure can also have disastrous consequences in very small fragments (Chiarello, 1999). Besides, the smaller the fragment, the stronger are the border effects acting upon it. These factors affect, among other aspects, seed survival and germination, canopy formation and tree mortality, thus changing the structure and dynamics of the environment (Lovejoy, 1986; Laurence and Yensen, 1991; Mesquita, 1999). This set of impacts related to size probably explains its emergence as the most important parameter. Since Neotropical primates depend on arboreal habitats, their survival on very small fragments is unlikely (Pozo-Montuy et al., 2011). Since they provide relevant ecological services, such as predation, dispersion and frugivory, their absence may reflect in the whole fragment dynamics (Chapman, 1996; Dew and Wright, 1998).

Model validation

Sapajus nigritus was the only species for which the model with fragment size alone was validated (table 4). Among the study species, this is the largest bodied one, and its groups are composed by a larger number of individuals (Rowe, 1996). Those factors together result in the need of a larger home range for this species, thus explaining their need of larger areas. Being fragment size so important, why didn't the other species have their plausible models comprised by size alone validated? One possibility is related to the fact that the municipality of Poço Fundo,

where we validated the models, has a slightly larger vegetation cover than Alfenas. Thus, once fragment size and availability increased, the importance of fragment size decreased. Therefore, the non-validation of models including fragment size alone for the species *Callithrix aurita* and *Callicebus nigrifrons* may be related to the home range of these species, which are smaller than the one of *Sapajus nigritus* (Rylands and Faria, 1993; Bicca-Marques et al., 2006).

Among the study species *Sapajus nigritus* is also the one which travels more outside the fragments (Mittermeier et al., 1982; González-Solís et al., 2001). This is a possible reason for the validation of the model “area + matrix permeability” for this species. Such result stresses that different matrix types influence their movement, showing that matrix types which are structurally more similar to the original habitat are more permeable than structurally distinct matrix types. Since few patches in the region are large enough to provide the necessary home range even for a few groups (Rocha, 1995; Izar, 1999), the incorporation of permeable matrix types in their home range can be a crucial factor for their survival within forest fragments. Besides, such increase in permeability can even allow sporadic access even to other fragments, thus allowing the maintenance of a metapopulation (Anderson et al., 2007; Rocha et al, 2007).

Another interesting result from this study was the validation of the model “visibility + area” for *Callicebus nigrifrons* (table 4). Such result shows us that the perception of fragment surrounding a focal fragment can be positively influencing the occurrence/persistence of Neotropical primates. Such perception can be crucial for the establishment and maintenance of primate metapopulations, given the usually high philopatry degree, with dispersal events mostly related to migration (Estrada and Coates-Estrada, 1996; Pozo-Montuy et al, 2011). Besides, such results show us that the incorporation of a biologically relevant parameter in the study, reflecting the biological reality of the target species, produced interesting results.

We did not have any of the models for *Callithrix aurita* validated, even with the species showing four plausible models (table 3). Three non-mutually exclusive hypotheses may explain such result. First, since the validation region has a larger percentage of forest cover, and, out of the study species, this is the one with the smaller home range (Rowe, 1996), fragment size was not important for explaining its occurrence in the validation region. Second, of the three study species, *C. aurita* is the one showing the smaller drive or potential for locomotion outside the fragments. Alongside the larger forest cover at the Poço Fundo region, this possibility could explain the non-validation of models including the other three parameters. Last, since the species

is highly sensitive to this fragmented habitat (IUCN, 2013), some other parameter, not considered in this study, may be influencing its distribution in the landscape, such as some variable related to availability of feeding resources or the degree of degradation of forest patches.

Our study shows that the third dimension (as in the visibility parameter) and the permeability of the matrix are aspects that should be incorporated in landscape ecology studies aiming at animal conservation. The visibility methodology is simple to be implemented, since the necessary topographic data is easy to obtain, and the current GIS software packages are capable of working with the third dimension (Greenberg and McClintock, 2008). Besides, we believe that the parameters of visibility and matrix permeability will show even better results for species which move more and show a lesser degree of philopatry, not being restricted to primates whatsoever. We also reinforce the importance of forest fragment size in the occurrence/persistence of species at highly degraded regions, a scenario in which forest cover is greatly reduced, and species persistence is even more fragile.

We hope that the successful incorporation of novel, biologically relevant metrics will stimulate researchers working with similar topics to free themselves from the standard metrics, and to start thinking creatively in new, innovative metrics, which take into account the biology of their study species.

5. Implications for conservation

Landscape management is crucial for the maintenance of primate populations, with the incorporation of matrix types which are more structurally similar to the original habitat, being thus more permeable, something which indirectly contributes to the dynamics of the ecological processes in the community. It is also necessary for us to consider matrix management and the visibility component in the selection of areas both for the establishment of corridors and for ecological restoration.

Future studies with these animals must aim not only at testing some of the hypotheses proposed above, but also at studying these animals in regions with a larger variation of habitat cover, at larger spatial scales (e.g. considering larger radii, of 5 or 10 km), with more rugged terrain, and with a larger matrix heterogeneity. Besides, we strongly advocate the use of matrix permeability and visibility towards neighboring fragments in future studies with other species, particularly so from other groups.

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Tables:

Table 1 - Characteristics of the 45 studied fragments regarding the study metrics.

Metric		MIN	AVG	MAX
Area (ha)		0.92	30.29	96.21
Isolation (m)	<i>Callicebus nigrifrons</i>	2.90	367.74	1150.60
	<i>Callithrix aurita</i>	2.90	709.80	5500.00
	<i>Sapajus nigrinus</i>	2.90	963.04	5500.00
Visibility (ha)		1.19	49.65	281.10
Matrix	<i>Callicebus nigrifrons</i>	0.73	9.42	39.82
Permeability	<i>Callithrix aurita</i>	0.74	12.44	60.75
Index (MPI)	<i>Sapajus nigrinus</i>	1.18	25.46	94.97

MIN - minimum value, AVG –average value, MAX – maximum value. Note that although the fragments are the same for all species, the average and maximum values for isolation and MPI are different among the species. This result occurred because the metrics include values that are ecologically calibrated which are different among the species.

Table 2

Ecological hypotheses associated to the multiple logistic regression models which were tested to explain the occurrence of *Callicebus nigrifrons*, *Callithrix aurita* and *Sapajus nigritus* in forest remnants at a highly fragmented landscape.

Models	Hypotheses
Species~Area	Small forest fragments offer limited resources, negatively affecting population survival and making them more vulnerable to local extinction. ^{1,2}
Species~Isolation	Populations which are isolated from source patches (p50) have their long-term viability decreased due to genetic drift and increase in endogamy. ^{1,5}
Species~Matrix Permeability	More permeable matrix types increase the possibility of resource acquisition and favor movement between neighboring fragments, thus increasing chance of population survival. ^{3,4,5}
Species~Visibility	Visible fragments are more easily accessed and contribute to the establishment of metapopulations. The higher the total area of visible fragments, the higher is the likelihood of population survival, through metapopulations.
Species~Area + Visibility	Both fragment size and the amount of available habitat around it are important for the maintenance of populations/metapopulations.
Species~Area + Matrix Permeability	Both parameters considered together are better than each one in isolation in explaining primate presence. Small fragments surrounded by a more permeable matrix habitat offer additional areas for resource acquisition. On the other hand, large

			fragments surround by a more inhospitable matrix are more isolated, with a higher chance of local extinctions.
Species~Area + Isolation			Small fragments which are closer to larger remnants can be viable.
Species~Matrix Isolation	Permeability +		Matrix permeability partially compensate the effects of isolation. Thus, isolated fragments embedded in a permeable matrix are less functionally isolated.
Species~Matrix Visibility	Permeability +		Fragments which are visible and connected by a permeable matrix contribute for the establishment of metapopulations.
Species~Null			Species occurrence is not affected by any of the parameters, being determined at random.

1. Fahrig 2003, 2. Harcourt and Doherty 2005, 3. Antongiovanni and Metzger 2005, 4. Gascon et al 1999, 5. Pozo-Montuy and Serio-Silva 2011

Table 3

Comparison of competing predictive models of species occurrence for *Callicebus nigrifrons*, *Callithrix aurita* and *Sapajus nigritus*, through the Akaike Information Criterion, based on occurrence information at the region of Alfenas – Brasil. Plausible models are highlighted.

Models	<i>Callicebus nigrifrons</i>		<i>Callithrix aurita</i>		<i>Sapajus nigritus</i>	
	□AICc (a)	wAIC (b)	□AICc (a)	wAIC (b)	□AICc (a)	wAIC (b)
Area	0	0.476¹	0	0.3778¹	0	0.45376¹
Area + Visibility	1.6	0.218²	2.3	0.12019⁴	2.2	0.15315⁴
Area + Matrix	2.3	0.154³	1.6	0.17303²	2	0.1653³
Area + Isolation	2.3	0.151⁴	1.8	0.15195³	1.7	0.19586²
Visibility	14.5	<0.001	5	0.03129	8.4	0.00688
Isolation	15.6	<0.001	4.1	0.04978	8.1	0.00804
Matrix	15.9	<0.001	4.1	0.0478	8.5	0.00645
Matrix + Visibility	16.6	<0.001	6	0.01862	10.7	0.00218
Matrix + Isolation	17.8	<0.001	5.7	0.02157	10.2	0.00276

Null	18.8	<0.001	7.7	0.00796	8.8	0.00562
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(a) Difference between the AICc value of a given model and the lower AICc value among all models for a given species.

(b) Model weight.

Table 4

Validation of plausible models explaining the occurrence of three Neotropical primate species in the region of Alfenas, Brasil with the Kappa test, comparing prediction of species occurrence with real presence data at 20 fragments in the region of Poço Fundo, Brasil.

Kappa statistical test

Models	Kappa	(p)
<i>Callicebus nigrifrons</i> ~ Area + Visibility	0.41	0.03
<i>Sapajus nigritus</i> ~ Area	0.44	0.02
<i>Sapajus nigritus</i> ~ Area + Matrix	0.44	0.02

Figures

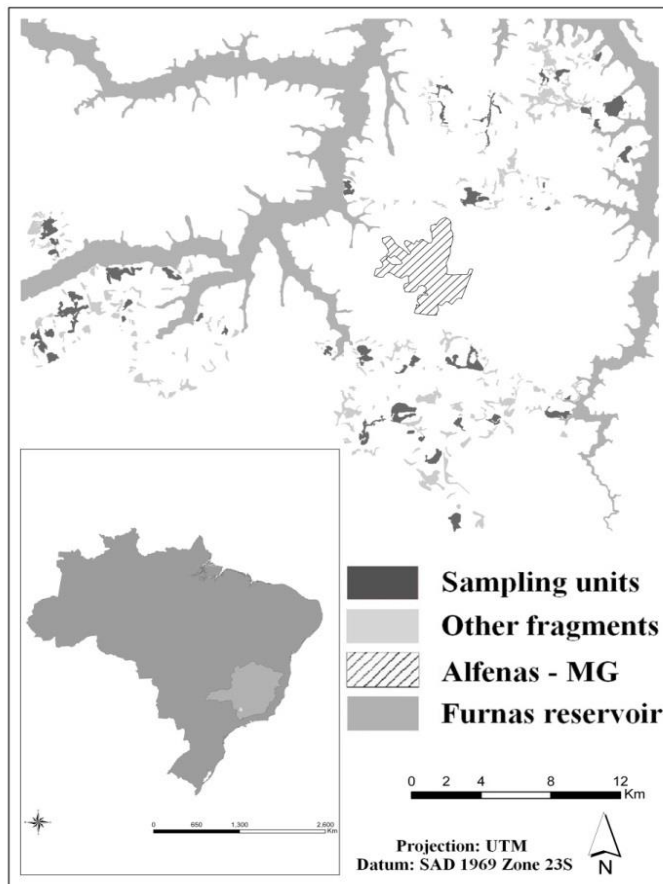


Figure 1 - Study area Alfenas - MG, Brazil. The Atlantic Forest remnants in the region are highly fragmented, with the vegetation reduced to 4% of the original area. The forest fragments were manually vectorized, scale 1:10,000, followed by visual.

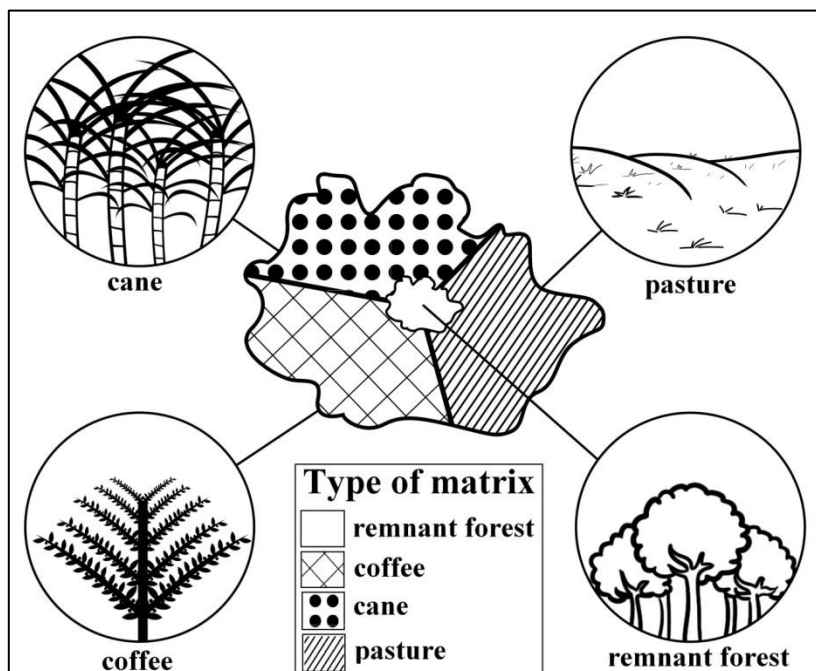


Figure 2 - Representation of the structure of the three main types of matrix (sugarcane plantations, coffee plantations and pastures) found in the region of Alfenas-MG. The structure of the sample unit (forest remnant) was also represented.