Paula Koeler Lira

EFEITOS DO HISTÓRICO DE ALTERAÇÕES DA PAISAGEM SOBRE
AVES E PEQUENOS MAMÍFEROS NA MATA ATLÂNTICA

EFFECTS OF LANDSCAPE CHANGE HISTORY ON BIRDS AND SMALL MAMMALS IN THE ATLANTIC FOREST

São Paulo

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Tese apresentada ao Instituto de
Biociências da Universidade de São
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Orientador: Dr. Jean Paul Metzger
Co-orientador: Dra. Renata Pardini

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ÍNDICE

Capítulo 1. Introdução geral	01
1.1. Introdução	02
1.2. Objetivos	07
1.3. Área de estudo	09
1.4. Coleta de dados	11
Capítulo 2. Land-use and land-cover change in Atlantic Forest landscapes	27
Resumo/Abstract	28
2.1. Introduction	31
2.2. Methods	32
2.3. Results	36
2.4. Discussion	38
2.5. Conclusions	43
Capítulo 3. Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest	62
Resumo/Abstract	63
3.1. Introduction	65
3.2. Methods	68
3.3. Results	72
3.4. Discussion	74
Capítulo 4. Importance of considering forest age for modelling bird species distribution in highly dynamic Atlantic Forest landscapes	97
Resumo/Abstract	98
4.1. Introduction	100
4.2. Methods	102
4.3. Results	105
4.4. Discussion	107
Capítulo 5. Considerações finais	131
Resumo/Abstract	141

CAPÍTULO 1

INTRODUÇÃO GERAL

1.1. Introdução

O processo de perda e fragmentação de habitats naturais é considerado uma das maiores ameaças à biodiversidade global (Tilman et al. 2001). No entanto, a taxa de extinção de espécies também vem sendo acelerada por outros distúrbios ambientais, tais como invasão de espécies exóticas, superexploração, mudanças climáticas, degradação do habitat e extinções em cascata, que podem interagir aditivamente ou de forma sinérgica com a perda e fragmentação de habitats (Thomas et al. 2004, Ewers & Didham 2006, Bradshaw et al. 2009, Gardner et al. 2009). Em alguns casos, a perda e fragmentação de habitats naturais leva à perda imediata de várias espécies (Stouffer & Bierregaard Jr. 1995, Stouffer et al. 2009), mas em outras situações, o intervalo entre a alteração do habitat e a extinção das espécies pode ser bastante prolongado (Brooks et al. 1999a, b, Hanski & Ovaskainen 2002, Lindborg & Eriksson 2004, Helm et al. 2006, Vellend et al. 2006), resultando em um débito de extinção. Em outras palavras, o débito de extinção é o número de espécies presentes atualmente em uma área, mas destinadas à extinção em função da perda e fragmentação pretérita do habitat (Tilman et al. 1994). O tempo necessário para que a riqueza de uma comunidade possa se adequar às novas condições estruturais do habitat e atingir um novo equilíbrio, ou seja, o tempo para que o débito de extinção seja pago, é denominado tempo de relaxamento (Diamond, 1972).

Os estudos realizados até hoje investigando o intervalo de tempo entre a alteração de habitats e a resposta das espécies sugerem três hipóteses sobre os fatores que determinam a probabilidade e a magnitude de um débito de extinção (Kuussaari et al. 2009): (1) débitos de extinção devem declinar ao longo do tempo após a alteração do habitat; (2) a magnitude de um débito de extinção deve apresentar uma relação não-linear com a intensidade da alteração do habitat; e (3) débitos de extinção devem variar de acordo com as características biológicas das espécies envolvidas.

A probabilidade de débito de extinção é maior em paisagens onde a alteração do habitat ocorreu recentemente do que em paisagens que foram alteradas há muito tempo atrás e onde, possivelmente, o débito de extinção já foi pago (Vellend et al. 2006). Adicionalmente, débitos de extinção também são mais prováveis em paisagens que sofreram uma perda intermediária de habitat (~20-30% de habitat remanescente) do que em paisagens que perderam muito ou pouco habitat. Esta expectativa não-linear existe porque em paisagens onde a perda de habitat foi intermediária, muitas espécies ainda podem persistir por um razoável período de tempo perto de seus limiares de extinção, i.e. das condições mínimas de quantidade de habitat para manutenção da população (Hanski & Ovaskainen 2002). Ao contrário, em uma paisagem onde a perda de habitat foi muito intensa é mais provável que as extinções ocorram rapidamente, e em uma paisagem pouco modificada (pouca perda de habitat), muitas espécies são capazes de persistir em longo prazo sem nenhum impacto adverso. Cousins (2009) compilou os resultados de estudos sobre os efeitos da fragmentação de campos semi-naturais da Europa sobre a diversidade de espécies de plantas e constatou que débitos de extinção só foram detectados em paisagens com mais de 10% de habitat remanescente. Finalmente, a probabilidade de débito de extinção difere entre grupos taxonômicos ou grupos de espécies devido, em parte, a um efeito da longevidade na persistência de populações em longo prazo (Brook et al 2003, Krauss et al 2010, Lindborg 2007). Espécies com ciclo de vida curto já passaram por várias gerações desde a alteração do habitat e provavelmente apresentam uma taxa de relaxamento mais rápida (mas veja Burel 1992, Petit & Burel 1998), enquanto que as espécies que têm ciclo de vida longo e, portanto, passaram menos gerações perto de um limiar de extinção crítico, podem persistir por mais tempo (Brook et al 2003, Lindborg 2007, Metzger 1998).

A existência de um débito de extinção indica que algumas espécies estão destinadas à extinção e que somente a manutenção da cobertura remanescente de habitat não será suficiente

para garantir a persistência dessas espécies em longo prazo. Como consequência, a restauração de habitats naturais vem sendo apontada, cada vez mais, como uma opção importante para evitar a perda destas espécies.

Providencialmente, os danos ambientais em alguns países do mundo vêm sendo reduzidos como resultado do desenvolvimento sócio-econômico destes. Na década de 1990, alguns pesquisadores começaram a perceber que muitos países desenvolvidos apresentavam um histórico semelhante de mudanças na cobertura florestal em função do processo de desenvolvimento (Perz 2007). Inicialmente, o desenvolvimento desses países estava associado ao uso indiscriminado dos recursos florestais, com o predomínio do desmatamento, mas a partir de um dado momento – denominado transição florestal – esta tendência foi revertida e tais países começaram a apresentar ganhos líquidos em sua cobertura florestal (Rudel et al. 2005). A transição florestal, i.e. inversão na dinâmica florestal a partir da qual a área florestal começa a expandir ao invés de diminuir, está associada principalmente ao aumento da industrialização e da urbanização (Rudel et al., 2002), mas outras condições que também levam ao abandono de terras agrícolas (como, por exemplo, guerras, escassez de madeira, catástrofes ambientais e mudanças de políticas públicas) já foram apontadas como causas importantes (Perz & Skole 2003, Lambin & Meyfroidt 2010). O processo de transição florestal foi inicialmente identificado com maior frequência em países da Europa e da América do Norte (Mather et al. 1999, Rudel et al. 2005), mas estudos recentes têm relatado a ocorrência desse processo em algumas regiões tropicais (Rudel et al. 2000, Rudel et al. 2002, Lugo & Helmer 2004).

Com o aumento da cobertura florestal, as taxas de imigração devem aumentar em toda a paisagem e, desta forma, permitir tanto o resgate de populações em declínio nos fragmentos florestais (Brown & Kodric-Brown 1977, Hanski 2000, Pardini et al. 2010, Puettker et al. submetido) como a re-colonização de fragmentos florestais por espécies que já haviam sido

localmente extintas (Hanski 2000, Nagelkerke et al. 2002, Cristofoli et al. 2010). Sendo assim, a dinâmica da imigração pode cancelar parte do débito de extinção. No entanto, assim como no caso das extinções após o desmatamento, os efeitos positivos da regeneração florestal sobre a biodiversidade podem levar algum tempo para se tornarem evidentes, resultando em um crédito de espécies (Hanski 2000). É importante notar, entretanto, que a re-colonização de fragmentos florestais por espécies que já haviam sido localmente extintas só poderá acontecer naturalmente após o aumento da cobertura florestal se populações dessas espécies tiverem persistido em fragmentos florestais próximos (Hanski 2000, Pardini et al. 2010). Desta forma, o crédito de espécies só deve ser pago no futuro se a quantidade total de habitat na paisagem não está (ou não esteve durante sua história) abaixo de um limiar crítico para a extinção regional de espécies (Hanski 2000, Pardini et al. 2010).

Com o processo de transição florestal ocorrendo em muitas paisagens ao redor do mundo (e.g. Rudel et al. 2005), precisamos entender como variam tanto os débito de extinção quanto os créditos de espécies para que estratégias de conservação e restauração sejam implementadas com sucesso. Apesar do crescente número de estudos sobre o débito de extinção causado pela destruição dos habitats (ver referências em Kuussaari et al. 2009), pouco se sabe ainda sobre o crédito de espécies gerado pelo incremento de habitat (mas veja Cristofoli et al. 2010 e Piqueray et al. 2011).

Igualmente importante é o entendimento de como a fauna se recupera ao longo do processo de sucessão florestal (Prach & Walker 2011) e o quão adequada são as florestas mais jovens para a persistência de espécies florestais (Gardner et al. 2007), já que o processo de transição florestal também implica na redução da idade média da floresta em uma paisagem. Na realidade, independentemente da transição florestal, paisagens dominadas pelo homem já são, em geral, muito dinâmicas, o que significa que uma área desmatada pode vir a ser floresta novamente

para ser desmatada subsequentemente e, isso, obviamente, já faz com que essas paisagens sejam progressivamente dominadas por florestas em estádios mais iniciais de sucessão. Como a estrutura e a composição vegetal são drasticamente alteradas ao longo do processo de sucessão vegetal (Clark 1996, Brown & Lugo 1990, Guariguata & Ostertag 2001, DeWalt et al. 2003), algumas consequências importantes podem ser observadas já que muitos animais dependem de recursos florestais que variam em abundância entre florestas de diferentes idades.

Apesar da vasta literatura sobre os efeitos da perda e fragmentação florestal sobre a biodiversidade (ver referências em Fahrig 2003 e Ewers & Didham 2006), somente alguns estudos incorporaram o aspecto temporal, ou seja, a história da paisagem, em suas análises (ver referências em Kuussaari et al. 2009). No entanto, de acordo com Ewers & Didham (2006), a história da paisagem é um dos fatores que, ao ser ignorado, pode mascarar a detecção ou impedir a manifestação dos reais efeitos da perda e fragmentação florestal sobre as espécies. De fato, alguns estudos já deixaram clara a existência de um atraso entre as mudanças da estrutura da paisagem e a resposta das espécies (e.g. Lindborg & Eriksson 2004, Krauss et al. 2010), o que em alguns casos pode justificar a ausência de relação entre os padrões de riqueza de espécies e as características atuais da paisagem. Adicionalmente, ao considerar o histórico de alteração da paisagem, outro aspecto, não menos importante, pode emergir: áreas florestais podem ser, na verdade, um mosaico de florestas com diferentes idades de regeneração. Como mencionado anteriormente, florestas com diferentes idades de regeneração devem apresentar estrutura e composição vegetal bastante distintas. Portanto, como as características internas do habitat podem ser mais importantes do que a quantidade ou configuração espacial deste para a persistência das espécies em paisagens fragmentadas (Fleishman et al. 2002, Franken & Hik 2004, Summerville & Crist 2004), este aspecto, quando possível, também deve ser considerado. No entanto, a maioria dos estudos investigando os efeitos da estrutura da paisagem sobre as

espécies consideram uma situação binária de floresta e não-floresta (e.g. Uezu et al. 2005, Boscolo & Metzger 2009, Pardini et al. 2010). A última década foi marcada por um grande esforço feito no sentido de mostrar a importância de considerar a qualidade da matriz não-florestal ao avaliar a vulnerabilidade das espécies em paisagens fragmentadas (Gascon et al. 1999, Ricketts 2001, Pires et al. 2002, Henle et al. 2004, Viveiros de Castro & Fernandez 2004, Antongiovanni & Metzger 2005, Prugh et al. 2008, Umetsu et al. 2008), no entanto, a importância de considerar a idade de regeneração das florestas (ou seja, a estrutura da floresta) foi muito pouco investigada.

Assim, para o pleno entendimento das relações entre a estrutura de paisagens fragmentadas e as comunidades que elas sustentam, precisamos incorporar em nossas análises a história dessas paisagens. Desta forma, o principal objetivo dessa tese de doutorado foi investigar os efeitos da dinâmica temporal de três paisagens fragmentadas de Mata Atlântica – localizadas no Planalto Atlântico de São Paulo – sobre a comunidade de aves e pequenos mamíferos.

Esta tese de doutorado está organizada em cinco capítulos. O primeiro é esta introdução geral que apresenta resumidamente os assuntos que serão abordados nos capítulos 2 a 4, o objetivo geral da tese e os objetivos específicos de cada capítulo, uma breve descrição das áreas de estudo e da metodologia de coleta dos dados. Os capítulos 2 a 4 são apresentados em formato de manuscritos a serem publicados em revistas científicas internacionais. Finalmente, no último capítulo, todos os resultados são discutidos de forma integrada.

1.2. Objetivos

O objetivo desta tese de doutorado foi investigar os efeitos do histórico de mudanças de três paisagens de Mata Atlântica do Planalto Atlântico de São Paulo (SP, Brasil) sobre a comunidade

de aves e pequenos mamíferos. Para tanto, foram realizados três estudos individuais cujos objetivos específicos estão descritos a seguir.

Capítulo 2: Land-use and land-cover change in Atlantic Forest landscapes

Capítulo 2: Mudanças no uso e cobertura das terras em paisagens de Mata Atlântica – O objetivo deste capítulo foi descrever a dinâmica de três paisagens fragmentadas de Mata Atlântica (São Paulo, Brasil) entre 1960–1980 e entre 1980–2000, e analisar se as alterações de uso e cobertura das terras são aleatórias, constantes ao longo do tempo (em uma determinada paisagem) e constantes no espaço (em um determinado período de tempo). Adicionalmente, também foi possível investigar os efeitos das mudanças no uso e cobertura das terras na estrutura das paisagens (tamanho, forma e isolamento de fragmentos florestais) e os efeitos da dinâmica das paisagens na atual proporção e distribuição espacial de florestas com diferentes idades de regeneração.

Capítulo 3: Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest

Capítulo 3: Avaliando a herança do histórico da paisagem: débito de extinção e crédito de espécies em assembleias de aves e pequenos mamíferos na Mata Atlântica Brasileira – Neste capítulo, o objetivo principal foi investigar a herança do histórico de mudança de paisagens fragmentadas de Mata Atlântica, localizadas no Planalto Atlântico de São Paulo, sobre as comunidades de aves e pequenos mamíferos. Foi investigada a existência de débito de extinção e de crédito de espécies em três paisagens com diferentes históricos de mudança e diferentes proporções atuais de cobertura florestal.

Capítulo 4: Importance of considering forest age for modelling bird species distribution in highly dynamic Atlantic Forest landscapes

Capítulo 4: Importância de considerar a idade da floresta para modelar a distribuição de aves em paisagens de Mata Atlântica altamente dinâmicas – O principal objetivo deste capítulo foi verificar se a plausibilidade de modelos descrevendo riqueza e abundância de aves em fragmentos florestais é maior quando a disponibilidade de vegetação nativa é calculada considerando a idade de regeneração das florestas. Essa análise considerou grupos com diferentes preferências de habitat e paisagens com diferentes históricos de mudança e diferentes proporções atuais de cobertura florestal.

1.3. Área de estudo

Mata Atlântica

A Mata Atlântica apresenta um dos mais altos graus de riqueza de espécies e taxas de endemismo do planeta (Myers et al. 2000, Mittermeier et al. 2005). No entanto, recentemente, um estudo quantificou a cobertura e configuração florestal de toda região da Mata Atlântica brasileira (Ribeiro et al. 2009) e os resultados revelaram uma situação bastante alarmante: mais de 80% dos fragmentos de Mata Atlântica possuem menos de 50 ha, quase metade da floresta remanescente está a menos de 100 m de uma borda de floresta e a distância média entre os fragmentos florestais é 1.440 m. Adicionalmente, grande parte dos remanescentes de Mata Atlântica é composta por florestas secundárias e não por florestas maduras (Ribeiro et al. 2009).

A devastação da Mata Atlântica é um reflexo da ocupação territorial e da exploração desordenada dos recursos naturais desde o início da colonização européia, no século XVI, e mesmo antes da chegada dos portugueses, em menor escala, pelos povos indígenas (Fonseca 1985, Dean 1996). Os sucessivos impactos resultantes de diferentes ciclos de exploração, da

concentração da população (aproximadamente 70% da população brasileira, cerca de 120 milhões de pessoas, se concentra nesta região) e dos maiores núcleos urbanos e industriais levaram a uma drástica redução na cobertura vegetal natural, resultando em paisagens, hoje, fortemente dominadas pelo homem (Fonseca 1985, Dean 1996).

Recentemente, no entanto, uma queda nas taxas de desmatamento da Mata Atlântica vem sendo observada (SOS Mata Atlântica & INPE 2008, 2009), ao contrário do que vem ocorrendo na Amazônia, onde cada vez mais florestas são derrubadas (http://www.obt.inpe.br/prodes/sisprodes2000_2010.htm). Segundo levantamentos recentes, o processo de desmatamento no estado de São Paulo caiu drasticamente nos últimos anos (SOS Mata Atlântica & INPE 2008, 2009) e, segundo o último inventário florestal houve um acréscimo de cobertura florestal no estado (Kronka et al. 2005), o que pode estar indicando o início de um processo de transição florestal como já sugerido para os estados de Santa Catarina e Rio Grande do Sul (Becker et al. 2004, Baptista & Rudel 2006).

O início de um processo de transição florestal no estado de São Paulo ainda é controverso (Melges et al. 2011), mas independentemente da ocorrência ou não deste fenômeno, a Mata Atlântica vem sendo progressivamente dominada por florestas mais novas. Teixeira et al. (2009), por exemplo, mostraram que uma paisagem de Mata Atlântica do Planalto Atlântico Paulista é bastante dinâmica e, mesmo em períodos onde houve ganho de cobertura florestal, as florestas mais antigas foram convertidas em áreas de uso antrópico ocasionando uma diminuição da idade média das florestas ao longo da paisagem.

Paisagens estudadas

Esta tese foi desenvolvida usando dados provenientes de três paisagens fragmentadas de Mata Atlântica localizadas no Planalto Atlântico de São Paulo, sudeste do Brasil (Figura 1).

Originalmente, toda a região do Planalto Atlântico era coberta por Mata Atlântica classificada como floresta ombrófila densa montana ou sub-montana (Oliveira-Filho & Fontes, 2000), mas atualmente uma grande parte da vegetação dessa região está reduzida a remanescentes florestais em diferentes estágios de regeneração (Ribeiro et al. 2009, Teixeira 2009). A altitude no Planalto Atlântico de São Paulo varia de 700 a 1.100 metros acima do nível do mar, a precipitação média anual é de cerca de 1.350-2.000 mm e a temperatura média anual varia de 15°C a 22°C (www.cpa.unicamp.br).

Nas três paisagens estudadas, os fragmentos florestais, compostos por florestas em estádios médios e avançados de sucessão, são circundados por uma matriz de pastos e agricultura. Todas as três paisagens estão a uma distância semelhante da Serra do Mar, que contém a maior extensão contínua de Mata Atlântica (1.109.546 ha) existente atualmente no Brasil (Ribeiro et al. 2009), e são separadas entre si por distâncias inferiores de 120 km. Embora similares em termos de topografia, relevo, clima, tipo de floresta e uso antrópico, as três paisagens estudadas, com cerca de 10.000 ha, diferem na quantidade de cobertura florestal atual: a paisagem denominada Ribeirão Grande situa-se na região oeste do estado de São Paulo e apresenta 11% de cobertura florestal; a paisagem denominada Caucaia está mais ao leste do estado e apresenta 31% de cobertura florestal; e a paisagem denominada Tapiraí apresenta 49% de cobertura florestal e está localizada entre as duas paisagens anteriormente citadas (Figura 1).

1.5. Coleta de dados

Dinâmica das paisagens

A dinâmica das três paisagens estudadas – descritas no capítulo 2 e fonte de dados para a realização dos capítulos 3 e 4 – foi baseada em fotografias aéreas e imagens de satélite (SPOT) de três datas distintas. As fotografias aéreas foram adquiridas da empresa privada BASE

Aerofotogrametria S. A. e cedidas pelo Laboratório Aerofotogeografia e Sensoriamento Remoto (LASERE) do Departamento de Geografia da Universidade de São Paulo. Para a análise da dinâmica da paisagem de Ribeirão Grande foram usadas fotografias aéreas de 1962 (1:25.000; 30 fotos), 1980 (1:35.000, 10 fotos) e uma imagem SPOT de 2005 (10 m de resolução). Para Caucaia, foram utilizadas fotografias aéreas de 1962 (1:25.000, 12 fotos), 1981 (1:35.000, 5 fotos) e 2000 (1:10.000, 61 fotos), e para Tapiraí, fotografias aéreas de 1962 (1:25.000; 23 fotos), 1978 (1:35.000; 15 fotos) e uma imagem SPOT de 2005 (10 m de resolução). A escolha das datas foi baseada na disponibilidade das imagens e na possibilidade de se obter intervalos regulares entre os anos estudados.

Os mapeamentos foram realizados somente por quatro pessoas para evitar erros relacionados a diferentes habilidades de interpretação. A Dra. Cristina Simonetti foi responsável pelo mapeamento da paisagem de Caucaia no ano de 2000 e a MSc. Ana Maria Teixeira mapeou as demais datas dessa paisagem como parte de sua tese de mestrado (Teixeira 2005, Teixeira et al. 2009). O Dr. Milton Ribeiro fez o mapeamento das paisagens de Ribeirão Grande e Tapiraí no ano de 2005 e a BSc. Thaís Olitta, sob minha supervisão, mapeou essas duas paisagens nas demais datas estudadas. A seguir descrevo brevemente o protocolo adotado para classificação das imagens.

As fotografias aéreas foram digitalizadas gerando imagens de resoluções equivalentes a 1,5 m e, a seguir, georreferenciadas utilizando cerca de 30 pontos de controle bem distribuídos em cada fotografia. O georreferenciamento foi feito com base em cartas topográficas do Instituto Cartográfico Geográfico (ICG) e do Instituto Brasileiro de Estatística e Geografia (IBGE), e apresentou erro médio inferior a 5 m. Após o georreferenciamento, as fotografias aéreas correspondentes a cada paisagem e data foram sobrepostas dando origem a fotomosaicos distintos.

Figura 1: Localização das áreas de estudo no estado de São Paulo, Brasil. (a) Ribeirão Grande com 11% de cobertura florestal, (b) Caucaia com 31% de cobertura florestal, e (c) Tapiraí com 49% de cobertura florestal.

Os sete fotomosaicos e as duas imagens SPOT foram classificados em cinco classes de uso e cobertura da terra definidas com base na imagem com a menor resolução (1:35.000): (1) instalações rurais e urbanas, (2) campos agrícolas e áreas de pastagem, (3) reflorestamento, (4) vegetação natural em estágio inicial de sucessão secundária e (5) floresta (Tabela 1). As

fotografias aéreas e as imagens SPOT foram visualmente interpretadas (a fotointerpretação foi realizada com o auxílio de estereoscópio) e os polígonos foram traçados diretamente sobre as imagens na tela do computador. Todo esse procedimento, desde o georreferenciamento das fotografias aéreas à classificação das imagens, foi feito no programa ArcGIS. Uma validação de campo intensa indicou uma alta precisão nos mapeamentos das datas mais recentes (2000 e 2005) (Silva et al., 2007; Ribeiro et al., 2009). Os mapas finais de uso e cobertura das terras (representação vetorial) foram transformados para uma resolução semelhante (15 m, representação matricial com pixels de 225 m² ou 0,0225 ha) de forma a evitar qualquer viés decorrente de diferenças na resolução das imagens de diferentes datas ou paisagens. Esta resolução foi definida em função das fotografias com menor resolução (1:35.000).

Amostragem de aves e pequenos mamíferos

O levantamento das comunidades de aves e de pequenos mamíferos nas paisagens estudadas foi realizado entre 2001 e 2007 durante o desenvolvimento do projeto “Conservação da biodiversidade em paisagens fragmentadas no Planalto Atlântico de São Paulo” (Processo Fapesp n° 99/05123-4, Processo CNPq n° 380435/2007-1), coordenado pelo Prof. Dr. Jean Paul Metzger. A amostragem de aves nas paisagens de Ribeirão Grande e Caucaia foi realizada pelo MSc. Alexandre Martensen e, na paisagem de Tapiraí, pela Dra. Cristina Banks-Leite. Já a amostragem de pequenos mamíferos em Caucaia foi executada pela Prof. Dra. Renata Pardini e, em Ribeirão Grande e Tapiraí, pela Dra. Adriana Bueno.

As aves foram amostradas em 53 fragmentos florestais, sendo 17 em Ribeirão Grande, 17 em Caucaia e 19 em Tapiraí. Em cada fragmento, 10 redes de neblina (12 m de comprimento, 2,5 m de altura e 31 mm de malha) foram dispostas em linha reta a pelo menos 50 m de distância da borda do fragmento. As redes eram checadas a cada hora e fechadas caso houvesse chuva. Todas

as aves capturadas foram identificadas no campo, marcadas com anilhas de alumínio numeradas (cedidas pelo Centro Nacional de Pesquisa para a Conservação de Aves Silvestres – CEMAVE, ICMBio) e liberadas próximas às redes.

Tabela 1: Classes utilizadas (e suas respectivas definições) para interpretação das fotografias aéreas e imagens de satélite de três paisagens fragmentadas do Planalto Atlântico de São Paulo, SP, Brasil, em três datas distintas.

Classes de uso e cobertura da terra	Definição
Instalações rurais e urbanas	Edificações isoladas, edificações agrupadas, loteamento, condomínios.
Campos agrícolas e áreas de pastagem	Agricultura anual, pastos limpo e sujo, vegetação herbácea rala a herbácea-arbustiva.
Reflorestamento	Florestas plantadas com espécies exóticas (<i>Pinus</i> spp. e <i>Eucalyptus</i> spp), cercas-vivas, bosques.
Vegetação natural inicial	Vegetação natural em estágio inicial de sucessão secundária; vegetação herbácea-arbustiva a arbórea com dossel de até 6 m de altura.
Floresta	Vegetação natural em estágio médio a avançado de sucessão secundária; vegetação arbórea-arbustiva a arbórea densa, com presença de espécies emergentes.

O protocolo de amostragem variou um pouco entre as paisagens estudadas. Nas paisagens de Ribeirão Grande e Tapiraí, cada fragmento florestal estudado foi amostrado duas vezes na estação seca e duas vezes na estação chuvosa, ou seja, foram realizadas, no total, quatro sessões de captura por fragmento florestal. Cada sessão de captura consistia em dois dias consecutivos de amostragem; no primeiro dia, as redes de neblina eram abertas com o nascer do sol e fechadas ao pôr-do-sol e, no segundo dia, as redes eram novamente abertas com o nascer do sol, mas eram fechadas seis horas depois. As sessões de captura foram conduzidas entre 2003 e 2004 em Ribeirão Grande, e entre 2005 e 2007 em Tapiraí (Martensen 2008, Banks-Leite 2009, Banks-Leite et al. 2011). Em Caucaia, foi usado um protocolo de amostragem diferente. Quatro dos 17 fragmentos florestais estudados nessa paisagem foram amostrados mensalmente entre Março e Novembro de 2001; as redes eram abertas com o nascer do sol e fechadas seis horas depois. Já os 13 fragmentos florestais restantes foram amostrados durante dois dias consecutivos em meses alternados entre Fevereiro e Julho de 2002; no primeiro dia, as redes de neblina eram abertas com o nascer do sol e fechadas ao pôr-do-sol e, no segundo dia, as redes eram novamente abertas com o nascer do sol e fechadas seis horas depois.

Da mesma forma, houve uma pequena variação no esforço amostral entre paisagens. O esforço amostral por fragmento florestal foi de 699 horas-rede ($DP = 21,7$) em Ribeirão Grande, 537 horas-rede ($DP = 6,2$) em Caucaia e 680 horas-rede em todos os fragmentos florestais estudados em Tapiraí. Apesar das diferenças no esforço amostral entre paisagens, Banks-Leite (2009) mostrou, analisando os dados provenientes de Tapiraí, que com apenas 340 horas-rede seriam obtidos os mesmo resultados e padrões ecológicos que foram obtidos com 680 horas-rede, sendo assim não há razão para esperar que estas diferenças amostrais resultem em estimativas incorretas da comunidade de aves.

Os pequenos mamíferos foram amostrados em 50 fragmentos florestais, sendo 15 na paisagem de Ribeirão Grande, 20 em Caucaia e 15 em Tapiraí. Foram instaladas 11 armadilhas de queda (balde plástico de 60 litros de volume, 40 cm de diâmetro e 53 cm de profundidade) em cada fragmento florestal estudado. As armadilhas, sem isca, foram dispostas de 10 em 10 m e conectadas por cercas-guia de plástico de aproximadamente 50 cm de altura. Em cada fragmento florestal estudado, foram realizadas quatro sessões de captura de oito dias cada, sendo duas por verão (dois verões consecutivos). Sendo assim, para cada fragmento, foram realizados, no total, 32 dias de amostragem com um esforço de 352 armadilhas-noite. As sessões de captura foram realizadas em Caucaia durante os verões de 2001-2002 e 2002-2003 (Pardini et al. 2005, Pardini et al. 2010) e em Ribeirão Grande e Tapiraí durante os verões de 2005-2006 e 2006-2007 (Bueno 2008, Pardini et al. 2010). Todos os indivíduos capturados foram marcados com brincos metálicos numerados.

As armadilhas de queda grandes são mais eficientes que as tradicionais armadilhas *Sherman* para captura de animais vivos, pois capturam um maior número de espécies, incluindo espécies raras, e um maior número de indivíduos (Umetsu et al. 2006). Adicionalmente, a amostragem foi concentrada na estação chuvosa, pois o número de capturas diárias em armadilhas de queda é maior nesta época do ano (Umetsu et al. 2006).

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CAPÍTULO 2

LAND-USE AND LAND-COVER CHANGE IN ATLANTIC FOREST LANDSCAPES

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Resumo

A Mata Atlântica é um dos biomas tropicais mais ameaçados do mundo porque grande parte de sua floresta remanescente encontra-se em fragmentos florestais pequenos (menos de 50 ha), isolados e perturbados pelo homem. Este cenário crítico é resultado da ainda pouco estudada dinâmica de uso e cobertura das terras da Mata Atlântica. Neste estudo, descrevemos a dinâmica de três paisagens fragmentadas de Mata Atlântica (São Paulo, Brasil) entre 1960-1980 e 1980-2000. As três paisagens apresentam atualmente diferentes proporções de cobertura florestal, com aproximadamente 10%, 30% e 50%. Entre os anos 1960 e 1980, a cobertura florestal da paisagem mais desmatada e da mais florestada foi reduzida, enquanto que houve um pequeno aumento na paisagem com 30% de cobertura florestal. O oposto foi observado entre os anos 1980 e 2000. Neste período, a regeneração florestal foi maior do que o desmatamento nas paisagens com 10% e 50% de cobertura florestal e, como consequência, a cobertura florestal aumentou; a cobertura florestal foi drasticamente reduzida na paisagem com 30% de cobertura florestal. As mudanças observadas no uso e cobertura das terras não apresentaram uma trajetória aleatória, não foram constantes ao longo do tempo em uma determinada paisagem e não foram constantes no espaço em um determinado período de tempo. Em geral, os fragmentos florestais tornaram-se mais isolados quando o desmatamento foi maior do que a regeneração florestal e se tornaram mais conectados quando regeneração foi maior do que o desmatamento. Como resultado da dinâmica da paisagens estudadas, fragmentos florestais consistem, atualmente, de um mosaico de florestas com diferentes idades de regeneração, o que provavelmente tem um impacto sobre a biodiversidade. Além disso, as dinâmicas de duas das três paisagens estudadas sugerem o início de uma transição florestal. Este processo pode ser importante para a conservação da biodiversidade na Mata Atlântica já que as florestas regeneradas podem reduzir o isolamento dos

remanescentes florestais e ajudar na manutenção de uma quantidade significativa da biodiversidade original.

Palavras-chave: dinâmica da paisagem, desmatamento, regeneração, estrutura da paisagem, idade do fragmento florestal.

Abstract

The Atlantic Forest is one of the most threatened tropical biomes, with much of the standing forest in small (less than 50 ha), disturbed and isolated patches. The pattern of land-use and land-cover change which has resulted in this critical scenario of the Atlantic Forest has not yet been fully investigated. Here, we describe the land-use and land-cover change dynamics in three Atlantic Forest fragmented landscapes (São Paulo, Brazil) between 1960s-1980s and 1980s-2000s. The three studied landscapes differ in the current proportion of forest cover, having 10%, 30% and 50% respectively. Between the 1960s and 1980s, forest cover of two landscapes was reduced while the forest cover in the third landscape increased slightly. The opposite trend was observed between the 1980s and 2000s; forest regeneration was greater than deforestation at the landscapes with 10% and 50% of forest cover and, as a consequence, forest cover increased. By contrast, the percentage of forest cover at the landscape with 30% of forest cover was drastically reduced between the 1980s and 2000s. Land-use and land-cover change deviated from a random trajectory, were not constant through time in a given landscape and were not constant across space in a given time period. In general, forest patches became more isolated when deforestation was greater than forest regeneration and became more connected when forest regeneration was greater than deforestation. As a result of the dynamic experienced by the three studied landscapes, individual forest patches currently consist of a mosaic of different forest age classes which is likely to impact biodiversity. Furthermore, landscape dynamics suggests the beginning of a forest transition in some Atlantic forest regions, what could be of great importance for biodiversity conservation due to the potential effects of young secondary forests in reducing forest isolation and maintaining a significant amount of the original biodiversity.

Key-words: Landscape dynamics, Deforestation, Regeneration, Landscape structure, Forest fragment age

2.1. Introduction

The Brazilian Atlantic Forest supports one of the highest degrees of species richness and rates of endemism on the planet (Myers et al. 2000, Mittermeier et al. 2005). Nonetheless, a recent broad-scale study (Ribeiro et al. 2009) revealed a serious situation about the spatial structure of Atlantic Forest remnants: more than 80% of the Atlantic Forest patches are less than 50 ha, almost half the remaining forest is less than 100 m from a forest edge and the average distance between forest patches is 1,440 m. In addition, much of the standing Atlantic Forest is secondary rather than mature forest (Ribeiro et al. 2009).

This critical scenario of the Atlantic Forest with small, disturbed and isolated forest patches is a consequence of five centuries of intense human occupation (Dean 1996). The pattern of land-use and land-cover change which has directly resulted in this critical scenario for the Atlantic Forest has not yet been fully investigated (but see Teixeira et al. 2009), contrary to the large number of studies on landscape dynamics for the Brazilian Amazon (e.g. Soares-Filho et al. 2004, Soares-Filho et al. 2006, Ewers & Laurance 2006, Ewers et al. 2008, Michalski et al. 2008).

The ecological consequences of land-use and land-cover change depend not only on the resulting spatial structure of the forest and how this varies both temporally and spatially (Echeverria et al. 2006), but also on the resulting proportion of forest with different ages of regeneration (Barlow et al. 2007a, Barlow et al. 2007b, Etter et al. 2005). Small and disturbed secondary forests patches can sustain a significant amount of biodiversity, but many species need large and more pristine forest patches to survive (Laurance 2005, Barlow et al. 2007b). Consequently, population of many species are now thought to be on a deterministic path to extinction in Atlantic Forest landscapes (Brooks & Balmford 1996, Brooks et al. 1999, Metzger et al. 2009). Both the spatial patterns and the age structure of forest are important determinants of

the maintenance of species in human-modified landscapes (Gardner et al. 2009), and therefore important components of land-cover to consider when assessing landscape conditions.

In this context, this study aimed to describe the land-use and land-cover change of three Atlantic Forest fragmented landscapes (São Paulo, Brazil) between 1960s-1980s and 1980s-2000s in order to: (1) evaluate if land-use and land-cover change deviate from a random trajectory; (2) determine if trajectories of land-use and land-cover change are constant through time and across space; (3) investigate the effects of the landscape dynamics on the spatial structure of the remaining forest in terms of size, shape and degree of isolation of forest patches; and (4) verify the effects of landscape dynamics on the current proportion and distribution of forest stands with different regeneration ages.

2.2. Methods

2.2.1. Study area

This study was conducted in three 10,000-ha Atlantic Forest fragmented landscapes located in the Atlantic Plateau of São Paulo, Brazil. The whole region of the Atlantic Plateau was once covered with Atlantic forest classified as Lower Montane Atlantic Rain Forest (Oliveira-Filho & Fontes 2000), but nowadays much of the region is reduced to secondary forest patches in different stages of regeneration (Ribeiro et al. 2009, Teixeira et al. 2009). The altitude in the Atlantic Plateau of São Paulo varies between 700-1,100 m above sea level with steep hillslopes, mountain with moderate to gentle hillslopes, and alluvial plains (Ponçano et al. 1981); the annual rainfall is between 1,350-2,000 mm and the mean annual temperature varies from 15°C to 22°C (www.cpa.unicamp.br). Originally, 60% of the Brazilian Atlantic Forest was located between 400 and 1,200 m above sea level and on steeper relief, nowadays 50% of the remaining forest is

located in those altitudinal range and 30% on steeper relief (Ribeiro et al. in press, Tabarelli et al. 2010).

In the studied landscapes, remaining forest patches were composed of intermediate to old second growth forest (from 20 to > 60 years old) while the matrix habitat surrounding forest patches was dominated by agriculture and cattle pastures. Although similar in terms of topography, relief, climate, type of forest, and type of human-use, the studied landscapes differ in the proportion of forest cover, varying from 11%, to 31% and 49% respectively (Figure 1; hereafter referred as 10, 30 and 50% forest cover (FC) landscapes). Additionally, all three landscapes are at a similar distance to the “Serra do Mar”, which contains the largest continuous tract of Atlantic forest (1,109,546 ha) remaining in Brazil (Ribeiro et al. 2009), and are relatively close to each other being separated by distances of less than 120 km.

2.2.2. Land-use and land-cover change

To describe the landscape dynamics for each studied landscape between 1960s-1980s and 1980s-2000s, we used aerial photographs and SPOT satellite images from the 1960s, 1980s and 2000s. For the 10% FC landscape, aerial photographs from 1962 (1:25,000) and 1980 (1:35,000) and a SPOT satellite image of 2005 (10 m resolution) were used; for the 30% FC landscape, aerial photographs from 1962 (1:25,000), 1981 (1:35,000) and 2000 (1:10,000) were used; and, finally, for the 50% FC landscape, aerial photographs from 1962 (1:25,000), 1978 (1:35,000) and a SPOT image of 2005 (10 m resolution) were used. Aerial photographs were scanned at 1.5 m resolution and georeferenced using at least 30 control points well distributed in each photograph (RMS error < 5 m), before being combined into a mosaic (one for each year) using ArcGIS software.

The aerial photographs and SPOT satellite images were categorised into five land-use or land-cover classes based on the level of detail available for the lowest resolution imagery (1:35,000). These classes were: (1) urban and rural buildings, (2) crop fields and pastures, (3) forest plantation, (4) young secondary vegetation and (5) forest (see Table 1 for a more detailed description of each category). Hereafter, those classes are referred as urban, fields, forestry, young vegetation and forest respectively. Aerial photographs and satellite images were visually interpreted (using stereoscopy for aerial photographs), and polygons were digitalized directly over the mosaic in the computer screen using ArcGIS software. The interpretation was performed by four trained people in order to reduce errors related with different abilities of interpretation. Intense field validation indicates high accuracy levels for land-use/cover maps of recent dates (2000s) (Silva et al. 2007, Ribeiro et al. 2009).

The final land-use/cover maps were transformed to a similar resolution (15 m) to avoid biases arising from differences in resolution among images from different years or landscapes. Transitions among land-use/cover categories in each studied landscapes between 1960s-1980s and 1980s-2000s were quantified using ArcGIS software. All transitions among the five land-use/cover classes were considered plausible within each period analysed (16 to 27 years) and the resulting transition matrices were used to assess land-use and land-cover change between 1960s-1980s and 1980s-2000s in each of the three landscapes.

We performed chi-square tests to investigate, individually for each landscape $\times$ time period combination (i.e. each transition matrix), if land-use/cover change deviated from a random expectation. In a statistical sense, landscape dynamics are a random process if transitions among different land-use/cover classes occur in proportion to the size of each class in time one and time two. We also performed chi-square tests to investigate if landscape dynamics were constant through time (i.e. was the pattern of land-use and land-cover change within a landscape the same

in the two time periods analysed), and across space (i.e. did the difference in land-use and land-cover change among landscapes at a given time period differ from the expected by chance).

2.2.3. Effects of land-use and land-cover change on the spatial structure of forest

To investigate the effects of landscape dynamics on the spatial structure of the forest, we measured size, shape and degree of isolation for all forest patches in each landscape $\times$ time period using the Fragstats software (McGarigal & Marks 1995). Patch size was measured in hectares and the shape and degree of isolation of each forest patch was measured using the shape index (Patton 1975) and the proximity index (Gustafson & Parker 1992), respectively. Shape index equals patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the corresponding patch area; the index equals one when the patch is maximally compacted and increases without limit as patch shape becomes more irregular. The proximity index equals the sum of each patch size divided by the square of its edge-to-edge distance to the focal patch of all patches whose edges are within a specified search radius of the focal patch (600 m in this study); the index equals zero if a patch has no neighbours and increases as the neighbourhood is increasingly occupied by patches of the same type. Patch size, shape and proximity indexes were log-transformed in order to normalize the data and ANOVA was used to determine if the size, shape and degree of isolation of forest patches differed significantly among years (1960s, 1980s and 2000s) and landscapes.

We also investigated the effects of landscape dynamics on the current proportion of forest cover at different ages of regeneration. It was, however, impossible to establish the exact age of regeneration because we do not have images for every year. Consequently, we categorised forest ages into three ordinal classes presented in Table 2.

2.3. Results

2.3.1. *Land-use and land-cover change*

The dominant land-use/cover classes for all three studied landscapes between the 1960s and 2000s were fields and forest. In the 1960s and 1980s, urban and forestry were uncommon in the 30% FC landscape, but by the 2000s they accounted for almost one-quarter of the land area. At the 10% and 50% FC landscapes, urban accounted for a small and constant proportion of the landscape, whereas forestry increased steadily over time. Young vegetation declined between the 1960s and 2000s in all landscapes. Trajectories of forest change were more complex. Between the 1960s and 1980s, forest cover in the 10% and 50% FC landscapes was reduced while the forest cover in the 30% FC landscape increased slightly. The opposite trend was observed between the 1980s and 2000s; forest cover increased in the 10% and 50% FC landscapes whereas almost one-third of the forest cover at the 30% FC landscape was removed (Table 3).

Both time periods analysed were highly dynamic for the 30% and 50% FC landscapes; 50% and 47% of the landscapes respectively experienced land-use/cover change between the 1960s and 1980s and 47% and 42% respectively between the 1980s and 2000s. By contrast, only 19% of the 10% FC landscape was transformed between the 1960s and 1980s and 17% between the 1980s and 2000s (Figure 2, Table S1).

In all landscapes and at all time periods, land-use/cover dynamics were significantly non-random apart from the 30% FC landscape between the 1960s-1980s ($\chi^2 = 13.6$, $p = 0.63$). In the 10% FC landscape (1960s-1980s: $\chi^2 = 54.0$, $p < 0.001$; 1980s-2000s: $\chi^2 = 39.5$, $p < 0.001$), the non-random dynamic was driven mostly by the higher than expected persistence of urban and forest areas in both time periods analysed, whereas in the 30% FC landscape between the 1980s-2000s ($\chi^2 = 39.5$, $p < 0.001$) and in the 50% FC landscape in both periods analysed (1960s-1980s: $\chi^2 = 37.5$, $p = 0.002$; 1980s-2000s: $\chi^2 = 51.9$, $p < 0.001$) the non-random dynamic was driven by

the higher than expected persistence of forest, forestry and fields, complemented by a lower than expected exchange between fields and forest.

The pattern of landscape dynamics in the two time periods analysed changed in all landscapes, with the patterns observed in the 1960s-1980s differing from those observed in the 1980s-2000s (10% FC landscape: $\chi^2 = 27.1$, $p < 0.05$; 30% FC landscape: $\chi^2 = 179.3$, $p < 0.001$; 50% FC landscape: $\chi^2 = 119.3$, $p < 0.001$). At the 10% and 50% FC landscape, the transition of fields to forest between 1980s-2000s was greater than expected according to the dynamic experienced by those landscapes between 1960s-1980s. At the 30% FC landscape, gain of urban areas between 1980s-2000s were greater than expected according to the dynamic experienced between 1960s-1980s. New urban and rural buildings were established mostly in former areas of forest and fields.

Landscape dynamics were not always constant across space. The dynamics experienced by the 10% and 30% FC landscapes and by the 10% and 50% FC landscapes between 1960s-1980s were significantly different ($\chi^2 = 51.5$, $p < 0.001$; $\chi^2 = 101.9$, $p < 0.001$; respectively), and the same was true for the dynamics between 1980s-2000s ($\chi^2 = 70.98$, $p < 0.001$; $\chi^2 = 90.3$, $p < 0.001$; respectively). However, land-use and land-cover change experienced by the 30% and 50% FC landscapes was not significantly different, either between 1960s-1980s ($\chi^2 = 11.3$, $p > 0.05$) or between 1980s-2000s ($\chi^2 = 26.8$, $p > 0.05$).

2.3.1. Effects of land-use/cover change on the spatial structure of forest cover

Patch size and degree of isolation were significantly different among landscapes ($F_{2, 3715} = 57.8$, $p < 0.001$; $F_{2, 3715} = 1815.4$, $p < 0.001$, respectively), among time periods ($F_{2, 3715} = 146.4$, $p < 0.001$; $F_{2, 3715} = 285.8$, $p < 0.001$, respectively), and among time periods in a given landscape ($F_{4, 3715} = 38.2$, $p < 0.001$; $F_{4, 3715} = 187.3$, $p < 0.001$, respectively). Patch size increased

significantly from the 1960s to the 1980s in the 10% FC landscape and from the 1980s to the 2000s in the 30% and 50% FC landscape. Patch size decreased significantly from the 1960s to the 1980s in the 30% FC landscape. The degree of patch isolation at the 10% and 50% FC landscape increased significantly from the 1960s to 1980s but decreased significantly from the 1980s to 2000s. At the 30% FC landscape, degree of patch isolation was not significantly different between the 1960s and 1980s but increased significantly from the 1980s to 2000s (Figure 3).

Patch shape was not significantly different among landscapes ($F_{2, 3715} = 0.3, p > 0.05$) but was significantly different among time periods ($F_{2, 3715} = 3.4, p < 0.001$) and among time periods in a given landscape ($F_{4, 3715} = 9.9, p < 0.001$). Patch shape at the 10% and 50% FC landscape were not significantly different among years; on the other hand, at the 30% FC landscape, patch shape became significantly more irregular in the 2000s (Figure 3).

The current amount of forest with different age of regeneration at the three studied landscapes is also a consequence of the land-use and land-cover change experienced between 1960s and 2000s. The largest proportion of the forest cover at the 30% FC landscape corresponds to remnant mature forest (54%) while the largest proportion of forest at the 10 and 50% FC landscapes corresponds to secondary forests that have regenerated during the last 25 years (Table 4). Individual forest fragments at all three studied landscapes consists of a mosaic of different forest age classes, including mature forests as well as secondary forests (Figure 4).

2.4. Discussion

Land-use and land-cover were highly dynamic for the two more forested landscapes in both time periods analysed and more intense than in some Amazonian regions of agricultural expansion (Lu et al. 2007, Ferraz et al. 2005), while landscape persistence was much greater than transition

among land-use/cover classes at the landscape dominated by crop fields and pastures. Landscape dynamics were significantly non-random in all landscapes and at all time periods, with only one exception. Non-random land-use/cover change suggests that systematic transitions (i.e. transitions between land-use/cover classes that occur independently of the size of the classes in time one and time two) are occurring in the studied landscapes. The identification of systematic transitions allows land use researches and planners to focus on those dominant signals of landscape change, investigate the possible causes using auxiliary qualitative or other quantitative data, and hence initiate measures to prevent or minimize the undesirable impacts of land-use/cover change (Braimoh 2006, Pontius et al. 2004). Moreover, we have also found that land-use/cover changes are not constant across time and space and as a consequence systematic transitions may also vary in time and space; this is fundamental to take into account when planning strategies to prevent the negative effects of land-use/cover change on biodiversity.

Teixeira et al. (2009) identified the influence of proximate causes on the dynamic of deforestation and forest regeneration in the same Atlantic forest region. Deforestation was higher near roads, in lower and less steep terrain and far from rivers while forest regrowth showed an opposite pattern, occurring far from roads, on steep terrain and near rivers and young secondary vegetation (Teixeira et al. 2009). Moreover, a land speculation process due to the close proximity to the city of São Paulo was the main cause of the huge deforestation observed at the 30% FC landscape between 1980s and 2000s (Teixeira et al. 2009), especially in less declivous areas and at lower altitude (Silva et al. 2007). As a consequence, the present-day (2000s) forest cover pattern at the 30% FC landscape is similar to the one described for the remaining Brazilian Atlantic Forest (Ribeiro et al. in press); forest cover is larger than expected in steeper areas and/or at higher altitudes (Silva et al. 2007).

Effects of landscape dynamics between the 1960s and 2000s on the spatial structure of forest cover (i.e. size, shape and degree of isolation of forest patches) were different at the three studied landscapes. In general, the degree of patch isolation in a given landscape increased significantly when deforestation was greater than forest regeneration and decreased significantly when forest regeneration was greater than deforestation. It is well known that isolation and the connectivity level of patches are key components for maintaining species in fragmented landscapes (Damschen et al. 2006, Boscolo & Metzger 2011); well-connected patches can sustain a higher number of species and also a large number of individuals/ population sizes (Martensen et al. 2008) because (re)colonization (Pires et al. 2002) and rescue effect (Brown and Kodric-Brown 1977) are often occurring in those patches (Pardini et al. 2010). Effects of land-use/cover change on the shape of forest patches was only observed at the 30% FC landscape; forest patches were significantly more irregular in the 2000s than in 1980s. Forest patches with irregular shapes are more susceptible to edge effects than patches with more compact shapes (Ewers & Didham, 2007), and many species have been reported to be negatively affected by edges (Ewers & Didham 2006, Ries et al. 2004). At the 50% FC landscape, edge effects were reported as one of the most important determinants of avifauna community structure (Banks-Leite et al. 2010).

The relationship between the temporal pattern of change in patch size and the dynamic of deforestation and forest regeneration was not so clear. Patch size is considered to be related with population size and consequently with extinction probability in a given patch; thus, patch size is an important structural characteristic influencing species persistence in fragmented landscapes. Although patch size might not have changed through time, the mosaic of forest ages within patches may have and this is also likely to impact biodiversity (Brown & Lugo 1990, Guariguata & Ostertag 2001).

Half of the remaining forest at the 10% and 50% FC landscape is secondary forest that has regenerated during the last 25 years, while at the 30% FC landscape half of the remaining forest regenerated at least 60 years ago. The amount of forest with different regeneration ages at the studied landscapes is a consequence of the forest cover trajectory experienced by each landscape between 1960s and 2000s. Between 1980s-2000s, forest regeneration was greater than deforestation at the 10% and 50% FC landscapes explaining the large amount of secondary forest with more or less 25 years nowadays and also suggesting the beginning of a forest transition in those landscapes, i.e. the change from decreasing to expanding of forest area (Mather & Needle 1998, Rudel et al. 2002).

Forest transitions are associated with socio-economic transformations towards increased industrialization and urbanization (Rudel et al. 2002) but other conditions leading to the abandonment of agricultural land (e.g. war, scarcity of wood, land adjustment and environmental legislation) have been found to play important roles in some cases (Perz & Skole 2003, Lambin & Meyfroidt 2010). Forest transition has taken place over a century or more in several European countries and in North America (Mather et al. 1999, Rudel et al. 2005) but some recent studies have reported signs of significant reforestation at some tropical regions (Rudel et al. 2000, Rudel et al. 2002), including regions in the Brazilian Atlantic Forest (Baptista & Rudel 2006, Becker et al. 2004).

The beginning of a forest transition would be highly positive in the long term for biodiversity conservation of the extremely imperiled Brazilian Atlantic Forest; however it is important to keep in mind that although the growing young secondary forest can sustain a significant amount of biodiversity, many species need older and more pristine forest to survive (Laurance 2005, Barlow et al. 2007b). Forest cover trajectory and the resulting age structure of forest patches are very important to assess current landscape conditions (Brown & Lugo 1990,

Guariguata & Ostertag 2001, Ferraz et al. 2009). Forest cover legacies can influence many processes that are observed in the present-time forest patches which may have different biodiversity values depending on their regeneration stage (Borges & Stouffer 1999). It is important to highlight that individual forest patches at the three studied landscapes consist of a mosaic of different forest age classes. Studies on the effects of landscape structure on different taxonomic groups have dealt until now with landscape characteristics such as forest cover and forest configuration (e.g. Martensen et al. 2008, Pardini et al. 2010) but seldom consider forest cover trajectory and age structure (Etter et al. 2005). However those landscape characteristics are important determinants for the maintenance of species in human-modified landscapes. We hypothesize that forest-dependent species should show a stronger response to current landscape structure if forest cover trajectory and age structure are considered.

Habitat loss and fragmentation have been recognized as a major cause of global biodiversity loss (Tilman et al. 2001), but recent studies have found that it often takes a considerable amount of time for declining populations to disappear following landscape change, resulting in an extinction debt (Tilman et al. 1994). Metzger et al.'s (2009) findings suggest a time-lag in the response of trees, birds and frogs to the landscape modification at the 30% FC landscape reinforcing the importance of landscape history. Time delay in species response gives an opportunity to revert the negative effects of landscape change through habitat maintenance and restoration. However, the expected species colonization and re-colonization following habitat regeneration might also not be immediate, resulting in a species credit (Hanski 2000, Jackson & Sax 2010). As the dynamic of the three studied landscapes were variable between the two time periods analysed, the current number of forest-dependent species in forest patches might be a result of the effects of forest cover contraction and expansion on species extinction and (re) colonization. Our results suggests that conceptual models aiming to predict biodiversity patterns

in Atlantic Forest fragmented landscapes should take into account landscape history in order to make more reliable predictions.

2.5. Conclusions

Land-use and land-cover change in the Atlantic Forest is not random and not constant through time and across space. Moreover, the present-day spatial and age structure of forest patches in Atlantic Forest landscapes are influenced by the landscape dynamics. Furthermore, some Atlantic Forest landscapes seem to be starting to experience a forest transition process, what could be of great importance for biodiversity conservation since young secondary forest can contribute in reducing isolation among fragments, and can also sustain a significant amount of biodiversity.

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Table 1. Description of the five land-use and land-cover classes observed in the aerial photographs and satellite images. In parentheses, the short name used throughout the text to refer to each class.

Land-use and land-cover categories		Description
<i>Land-use</i>		
Urban and rural buildings	(Urban)	Isolated buildings, grouped buildings, settlements
Crop fields and pastures	(Fields)	Crop fields or fallow fields, areas used for cattle ranching, abandoned/disturbed herbaceous vegetation, with or without shrubs
Forest plantation	(Forestry)	Forest plantation with exotic species, eg. <i>Pinus</i> spp. and <i>Eucalyptus</i> spp.
<i>Land-cover</i>		
Young secondary vegetation	(Young vegetation)	Shrub to arboreal vegetation with up to 5-6 m height continuous canopy
Forest	(Forest)	Intermediate to old secondary forest with canopy height usually > 10 m, with or without emergent trees up to 30-35 m

Table 2. Ordinal scale of forest age classes determined according with the temporal sequence of forest changes in three partially forested landscapes on the Atlantic Plateau of Sao Paulo. Non-forest is all land-use and land-cover classes presented in Table 1 apart from forest.

Forest change sequence			Forest age classes
1960s	1980s	2000s	
Non-forest	Non-forest	Forest	SF20: Secondary forests ~ 20-25 years of age
Forest	Non-forest	Forest	
Non-forest	Forest	Forest	SF40: Secondary forests ~ 40-45 years of age
Forest	Forest	Forest	MF60: Mature forests (never cleared during the study period); at least 60 years of regeneration.

Table 3. Percentage of each land-use and land-cover class for three Atlantic Forest fragmented landscapes (São Paulo, Brazil), and how they changed between the 1960s and 2000s.

Land-use/cover	10% FC landscape			30% FC landscape			50% FC landscape		
	1962	1980	2005	1962	1981	2000	1962	1978	2005
Urban	0.32	0.44	1.57	0.64	1.48	15.87	0.12	0.35	0.12
Fields	79.72	88.14	81.83	36.93	38.98	38.13	33.89	47.55	42.47
Forestry	0.20	0.63	1.19	2.12	2.97	7.12	0.90	4.36	5.06
Young vegetation	8.39	3.75	4.10	16.25	10.24	7.59	21.52	19.85	3.01
Forest	11.37	7.04	11.31	44.06	46.33	31.28	43.57	27.88	49.35

Table 4. Percentage of forest cover of each forest age class at three Atlantic Forest fragmented landscapes located in São Paulo, Brazil. Values are the cover as a percentage of the total landscape area and, in parentheses, as a percentage of the total forest cover.

Forest age class	10% FC landscape	30% FC landscape	50% FC landscape
SF20	6.8 (60.7)	5.9 (18.9)	25.9 (52.9)
SF40	1.4 (12.5)	8.5 (27.2)	4.9 (10.0)
MF60	3.0 (26.8)	16.8 (53.9)	18.2 (37.1)
Total	11.2 (100.0)	31.2 (100.0)	49.0 (100.0)

Figure 1. Location of the three studied Atlantic Forest fragmented landscapes in the State of São Paulo (south-eastern – Brazil) and their forest cover dynamics between the 1960s and 2000s (from right to left). The percentage of forest cover is shown at the bottom of each forest cover map.

Figure 2: Land-use/cover persistence and change between the 1960s-1980s and the 1980s-2000s at three Atlantic Forest landscapes, in São Paulo, Brazil. Values are % of landscape that experienced persistence (inside boxes) or transition among land-use/cover classes (on the left or below arrowheads). Values lower than 1% were omitted but can be assessed in the Supplementary Material (Table S1).

Figure 3: Forest cover (%) dynamics and the consequent variation on the spatial structure of the forest (patch size, shape index and proximity index) in three Atlantic Forest fragmented landscapes (São Paulo, Brazil). The main horizontal line shows the median, boxes represent quartiles and whiskers depict either the maximum or 1.5 times the interquartile range of the data (whichever is smaller). Points are outliers. Classes that do not have a letter in common differ significantly (Tukey's honest significant differences test: $P < 0.05$).

Figure 4: Spatial distribution of forest patches of different forest age classes at the landscape with 10% (a), 30% (b) and 50% (c) of forest cover (São Paulo, Brazil). Note that individual forest patches are a mosaic of different forest age classes.

Supplementary Material

Table S1: Land-use/cover persistence and change between (a) the 1960s-1980s, and (b) the 1980s-2000s at three Atlantic Forest landscapes, São Paulo, Brazil. Values are % of the landscape that experienced persistence or transition among land-use/cover classes.

(a)

		1980s					
		Landscape	Urban	Fields	Forestry	Young vegetation	Forest
1960s	Urban	10%	0.18	0.14	0.00	0.01	0.00
		30%	0.09	0.30	0.01	0.09	0.14
		50%	0.05	0.05	0.00	0.01	0.00
	Fields	10%	0.23	75.63	0.42	1.82	1.61
		30%	0.89	20.85	0.90	4.97	9.32
		50%	0.20	26.32	0.69	7.72	1.95
	Forestry	10%	0.00	0.03	0.11	0.03	0.03
		30%	0.01	0.62	0.31	0.21	0.98
		50%	0.01	0.15	0.53	0.14	0.07
	Young vegetation	10%	0.02	6.23	0.03	0.97	1.14
		30%	0.16	5.27	0.30	1.52	9.00
		50%	0.05	10.11	1.27	5.31	4.78
	Forest	10%	0.01	6.12	0.08	0.92	4.25
		30%	0.33	11.93	1.46	3.45	26.89
		50%	0.04	10.91	1.87	9.67	21.07

(b)

		2000s					
		Landscape	Urban	Fields	Forestry	Young vegetation	Forest
1980s	Urban	10%	0.26	0.16	0.00	0.01	0.01
		30%	1.05	0.28	0.05	0.03	0.07
		50%	0.02	0.28	0.01	0.02	0.03
	Fields	10%	1.24	77.81	0.89	3.03	5.17
		30%	7.76	23.91	2.61	1.58	3.06
		50%	0.07	31.44	1.12	1.86	13.01
	Forestry	10%	0.03	0.45	0.13	0.01	0.01
		30%	0.34	0.80	1.48	0.08	0.23
		50%	0.00	1.36	2.45	0.09	0.45
	Young vegetation	10%	0.03	1.58	0.04	0.43	1.66
		30%	1.75	4.17	0.68	1.08	2.54
		50%	0.02	5.69	0.99	0.68	12.49
	Forest	10%	0.01	1.83	0.13	0.62	4.46
		30%	4.96	8.97	2.30	4.82	25.39
		50%	0.00	3.70	0.48	0.37	23.37

CAPÍTULO 3

**EVALUATING THE LEGACY OF LANDSCAPE HISTORY:
EXTINCTION DEBT AND SPECIES CREDIT IN BIRD AND SMALL MAMMAL
ASSEMBLAGES IN THE BRAZILIAN ATLANTIC FOREST**

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Resumo

Embora exista um considerável número de trabalhos sobre débito de extinção como consequência de processos de desmatamento, pouca atenção tem sido dada ao potencial das paisagens de apresentarem um crédito de espécies quando há uma expansão da cobertura florestal. No entanto, tanto o débito de extinção quanto o crédito de espécies são importantes para elaborar estratégias de conservação e de restauração de habitat. Neste estudo, nós avaliamos os efeitos da cobertura florestal local, atual e passada, sobre a riqueza de espécies florestais de dois grupos de vertebrados que apresentam diferentes tempos de geração - aves e pequenos mamíferos - em três paisagens fragmentadas de Mata Atlântica. Investigamos como a probabilidade de débito de extinção e crédito de espécies varia (1) entre paisagens com diferentes proporções de cobertura florestal (10, 30 e 50%) e trajetórias distintas e não-lineares de mudança da cobertura florestal, e (2) entre taxóons com diferentes durações de ciclo de vida. Nossos resultados indicam que a existência de débito de extinção e crédito de espécies assim como o potencial para seus pagamentos futuros, depende não só da trajetória de cobertura florestal (isto é, se a cobertura florestal da paisagem aumentou ou diminuiu), mas também da quantidade de cobertura florestal remanescente na escala da paisagem. Como muitas paisagens estão sofrendo uma inversão, da redução para o ganho de cobertura florestal, entender a associação entre os processos de extinção e de imigração com essa dinâmica florestal não-linear é essencial, pois estas são as forças dominantes que controlam as mudanças na diversidade de espécies no espaço e no tempo.

Palavras-chave: conectividade, dinâmica da paisagem, estrutura da paisagem, fragmentação de habitats, perda de habitat, regeneração, limiar de extinção.

Abstract

Although a considerable body of work on extinction debts following deforestation has been accumulated, little attention has been paid to the potential for species credit in landscapes that have experienced a change from decreasing to expanding forest cover. Nevertheless, both species credit and extinction debt are important to devise biodiversity conservation and habitat restoration strategies. We evaluated the effects of historical and present-day local forest cover on forest-dependent species richness of two vertebrate groups differing in longevity – birds and small mammals – in three Atlantic Forest landscapes. Our work investigated how the probability of extinction debts and species credits varies (1) among landscapes with different proportions of forest cover (10, 30 and 50%) and distinct non-linear trajectories of forest cover change, and (2) between taxa with different life-cycle durations. Our results indicate that the existence of extinction debts and species credits as well as the potential for their future payment depends not only on forest cover trajectory (i.e. increase or decrease in forest cover) but also on the amount of remaining forest cover at the landscape scale. As many landscapes are experiencing a change from decreasing to expanding forest cover, understanding the association of extinction and immigration processes, as well as their interactions, with the non-linear dynamics of landscape change is essential, since these are the dominant forces underlying changes in species diversity on space and time.

Keywords: habitat fragmentation, habitat loss, habitat regeneration, landscape structure, landscape dynamics, landscape connectivity, extinction threshold.

3.1. Introduction

Habitat loss and fragmentation has been recognized as a major cause of global biodiversity loss (Tilman et al. 2001). However, the rate of extinctions has been also accelerated by other disturbances, such as invasion by alien species, overexploitation, climate change, habitat deterioration and extinction cascades, which may interact additively or synergistically with habitat loss and fragmentation (Bradshaw et al. 2009, Ewers & Didham 2006, Gardner et al. 2009, Thomas et al. 2004). Extinction processes can be almost immediate in some cases (Stouffer et al. 2009), but often it takes a considerable amount of time for declining populations to disappear following an environmental disturbance (Brooks et al. 1999a,b, Hanski & Ovaskainen 2002, Helm et al. 2006, Lindborg & Eriksson 2004, Vellend et al. 2006), resulting in what is termed an extinction debt. An extinction debt is the number of extant species that are predicted to go extinct because the threshold condition for their persistence is no longer satisfied (Tilman et al. 1994) and the time taken for a community to reach a new, and reduced, equilibrium number of species after an environmental disturbance is known as relaxation time (Diamond 1972).

Extinction debts and relaxation times can be calculated directly from data on regular monitoring of species after habitat loss and fragmentation (e.g. Ferraz et al. 2003, Stouffer 2009). However as such time series data are rarely available, extinction debts have been predominantly evaluated using four different alternative approaches (see Kuussaari et al. 2009). The approach most frequently used investigate the effects of past and present-day habitat characteristics on current species richness; if the current number of species is better described by past than by present-day habitat characteristics, an extinction debt can be assumed (Cousins et al. 2007, Gustavsson et al. 2007, Lindborg & Eriksson 2004). Although the magnitude of extinction debts cannot be estimated, this approach can successfully detect them and give an idea of the relaxation time (e.g. Krauss et al. 2010, Lindborg & Eriksson 2004).

Studies investigating extinction debts until now have assumed that the dynamic of landscape change is a linear process of habitat loss and fragmentation (e.g. Brooks et al. 1999b). However, the history of fragmented landscapes can be much more complex than that; present-day landscape structure may frequently be the result of alternating periods of habitat contraction and expansion (e.g. Lira et al. unpublished data). This alternation from decreasing to expanding forest area, i.e. forest transition, has taken place over a century or more in several European countries and in North America (Mather et al. 1999, Rudel et al. 2005) and has been recently suggested for tropical regions (Rudel et al. 2000, Rudel et al. 2002, Wright & Muller-Landau 2006), including the Brazilian Atlantic Forest (Baptista & Rudel 2006, Becker et al. 2004, Lira et al. unpublished data). Taking into account these complex, non-linear changes in habitat cover is of foremost importance to understand the legacy of landscape history on current patterns of biodiversity.

Forest regeneration is expected to increase immigration rates across the landscape allowing the rescue of declining populations in forest patches (Brown & Kodric-Brown 1977, Hanski 2000, Pardini et al. 2010, Puettker et al. submitted) and re-colonization of forest patches by species that have already gone locally extinct (Hanski 2000, Nagelkerke et al. 2002, Cristofoli et al. 2010). But, just as in the case of extinction debt following deforestation, the positive effects of forest regeneration should take some time to become evident resulting in a species credit (*sensu* Hanski 2000). As a consequence, if the current number of species in a landscape is better described by past than present-day forest cover and if past forest cover is lower than today, a species credit can be assumed.

It is worth noting though that re-colonization of forest patches by species that have already gone locally extinct may only take place if conspecific populations have survived in nearby patches (Hanski 2000, Pardini et al. 2010). Thus species credit should only be paid in the future if the total amount of habitat in the landscape is not (or has not gone during its history)

below a critical threshold of species regional extinction (Hanski 2000, Pardini et al. 2010). Similarly, extinction debts are less likely to exist in severely fragmented landscapes, since immediate regional extinctions are expected after high levels of habitat loss. By contrast in highly forested landscapes, where many species should be able to persist regionally, both extinction debt and species credit are unlikely. Thus both debt and credit are most likely to exist and be paid in the future in landscapes that have undergone intermediate amounts of habitat loss and fragmentation and where many species might be persisting close to their species-specific extinction threshold at the regional scale (Hanski & Ovaskainen 2002, Pardini et al. 2010).

Additionally, delayed responses should depend on the life history traits of species, especially longevity (Brook et al. 2003, Krauss et al. 2010, Lindborg 2007, Metzger et al. 2009). Short-lived species have already passed through many generations since landscape change and are likely to respond fast (but see Burel 1992, Petit & Burel 1998), while species that have longer generation times and have therefore spent fewer generations after landscape change might respond slowly (Brook et al. 2003, Lindborg 2007, Metzger et al. 2009). The effect of longevity should be observed among habitat specialist species, since habitat generalists are able to occupy altered anthropogenic habitat and should not respond (either rapid or slowly) to habitat loss (Pardini et al. 2010).

Here, we evaluated the effects of historical and present-day local forest cover surrounding surveyed sites on the richness of two vertebrate groups with differing longevity – forest-dependent birds and small mammals – in three landscapes from the highly imperilled Atlantic Forest of Brazil (Ribeiro et al. 2009). The study landscapes present a wide variation in the current total amount of forest cover which is a result of alternating periods of forest contraction and expansion in the past four decades (Lira et al. unpublished data). Thus if the current variation in the number of forest-dependent species among patches is better described by historical than

present-day local forest cover, both extinction debt or species credit may be assumed. If forest has shrunk (i.e. present-day forest cover in the whole landscape is lower than in the past) we assumed an extinction debt, if the landscape forest cover has expanded we assumed a species credit. Our work investigated how the probability of detecting extinction debts and species credits varies (1) among landscapes with different amounts of total forest cover and distinct non-linear trajectories of landscape change, and (2) between taxa with different life-cycle durations.

3.2. Methods

3.2.1. Study area

The study was conducted in three ~10,000-ha fragmented Atlantic Forest landscapes located on the Atlantic Plateau of São Paulo, Brazil (Figure 1). The whole region of the Atlantic Plateau was once covered with Atlantic forest classified as Lower Montane Atlantic Rain Forest (Oliveira-Filho & Fontes 2000), but nowadays much of the region is reduced to secondary forest patches in different stages of regeneration (Ribeiro et al. 2009, Teixeira et al. 2009). The altitude in the Atlantic Plateau of São Paulo varies between 700-1,100 m above sea level with steep hillslopes, mountain with moderate to gentle hillslopes, and alluvial plains (Ponçano et al. 1981); the annual rainfall is between 1,350-2,000 mm and the mean annual temperature varies from 15°C to 22°C (www.cpa.unicamp.br).

In the study landscapes, remaining forest patches are composed of intermediate to old second growth forest (from 20 to > 60 years old) while the matrix habitat surrounding forest patches is dominated by agriculture and cattle pastures. All three landscapes are at a similar distance to the “Serra do Mar”, which contains the largest continuous tract of Atlantic forest (1,109,546 ha) remaining in Brazil (Ribeiro et al. 2009), and are separated to each other by distances of less than 120 km. Although similar in terms of topography, relief, climate, type of

forest, and type of human-use, the study landscapes differ in the proportion of total forest cover, varying from 11%, to 31% and 49% (Figure 1). Hereafter, the studied landscapes are referred as 10, 30 and 50% forest cover (FC) landscapes.

Present-day total amount of forest cover in each study landscape is a result of the balance between deforestation and forest regeneration over the past five hundred years of human occupation. We were able to directly quantify forest dynamics in the study landscapes over the past four decades (1960s to 2000s) using forest cover maps based on aerial photographs and SPOT 5 satellite images from three different dates, early 1960s (1962), 1980s (1978-1981) and 2000s (2000-2005) (Lira et al. unpublished data). Between the 1960s and 1980s, total amount of forest cover at the 10 and 50% FC landscapes was reduced while in the 30% FC landscape it increased slightly. The opposite trend was observed between the 1980s and 2000s; forest regeneration was greater than deforestation at the 10 and 50% FC landscapes and, as a consequence, the total amount of forest cover increased. By contrast, the percentage of forest cover at the 30% FC landscape was drastically reduced between the 1980s and 2000s (Figure 1). In summary, total amount of forest cover at the 30% FC landscape was fairly constant between the 1960s and 1980s but a considerable deforestation was observed more recently. On the other hand, both the 10% and 50% FC landscapes have experienced a similar forest cover trajectory – a historical deforestation followed by recent forest regeneration. However, an important difference between these two landscapes is their current total amount of forest cover: the 10% FC landscape is below the extinction threshold for many species while the 50% FC landscape is well above (Andrén 1994, Pardini et al. 2010, Hanski 2011).

3.2.2. *Bird and small mammal sampling*

Birds and small mammals were surveyed in a set of forest patches at each landscape. Birds were sampled in a total of 53 forest patches: 17 in the 10% and in the 30% FC landscape, and 19 in the 50% FC landscape (Martensen et al. 2008, Banks-Leite et al. 2011). Each patch was sampled using 10 mist nets (12 m length, 2.5 m high, 31 mm mesh) in a straight line and located at least 50 m from the forest edge. Capture sessions were conducted from 2001 to 2002 in the 30% FC landscape, from 2004 to 2005 in the 10% FC landscape and from 2005 to 2007 in the 50% FC landscape. All captured birds were identified to species in the field and marked with a numbered aluminium band provided by Center of Research for Conservation of Wild Birds (CEMAVE-IBAMA) and released in the vicinity. There was a small variation in sampling effort among landscapes; the mean effort per forest patch was 699 net-hours (SD = 21.7) in the 10% FC landscape, 537 net-hours (SD = 6.2) in the 30% FC landscape and an equal sampling effort of 680 net-hours per forest patch in the 50% FC landscape.

Rodents and marsupials were sampled in 15, 20 and 15 patches in the 10, 30 and 50% FC landscapes respectively (Pardini et al. 2005, Pardini et al. 2010). Four capture sessions of eight days each were conducted in each forest patch, two per summer during two consecutive summers, totalling 352 trap-nights in each forest patch. Trap lines within patches comprised a 100-m sequence of 11 pitfall traps (60 L), separated by 10 m and connected by a plastic fence. Capture sessions were conducted during the summers of 2001-2002 and 2002-2003 at the landscape with 30% of forest cover and, in the other two landscapes, during summers of 2005-2006 and 2006-2007. Animals were marked with numbered tags at first capture.

3.2.3. *Data analysis*

Only forest-dependent species were considered in the analysis as habitat generalist species are not expected to be sensitive to forest cover modification and, consequently, focusing on the species richness of an entire assemblage may mask important differences among species in their likelihood of showing an extinction debt (Kuussaari et al. 2009) or species credit. We considered as forest-dependent birds those species listed by Stotz et al. (1996) as occurring only in forest habitats; species occurring in naturally disturbed or human-created habitats or in non-forest habitats, even when they occur in primary forest as well, were excluded from the analysis (Brooks et al. 1999b). Small mammal species whose geographical distribution is restricted to the two Brazilian forested biomes (Atlantic forest and Amazon forest) and do not occupy the core areas of the adjacent savanna-like biomes (Cerrado and Caatinga) were considered forest-dependent species; those species that also occupy the adjacent savanna-like biomes were considered habitat generalists and were excluded from the analysis (Pardini et al. 2010). This classification based on geographical range is consistent with the available information on habitat requirement; opposed to habitat generalist small mammals, forest-dependent species are not able to occupy open anthropogenic habitats (Umetsu & Pardini 2007).

Bird species richness in each forest patch was calculated as the observed number of forest-dependent species while small mammal species richness was calculated as the average number of forest-dependent species observed in the two samplings to avoid overestimating the number of species present simultaneously in each patch (Pardini et al. 2010) as a turnover of species was observed between years (Felinks et al. 2011).

For each landscape and date we measured the amount of forest cover in a circle of 800 m radii around each sampling point using forest cover maps and the Fragstats software (McGarigal & Marks 1995). Hereafter, the amount of forest cover surrounding surveyed sites is referred as

local forest cover. We selected an 800 m scale based on previous information about the spatial scale bird and small mammal species respond to local forest cover (Umetsu et al. 2008, Boscolo & Metzger 2009).

3.2.4. *Statistical analysis*

To investigate the effects of historical (1960s and 1980s) and present-day (2000s) local forest cover on the number of forest-dependent species, we used the variation partitioning procedure (Legendre and Legendre 1998). As the local forest cover was highly correlated across years, we used variation partitioning to measure how much of the variation in species richness could be attributed exclusively to past or present-day local forest cover (unique contributions) and how much of this variation is indifferently attributed to past and present-day local forest cover (shared contributions). As inspection of model residuals showed that Poisson errors and log link function provided the best fit for regressions models of species richness, we used Generalised Linear Models for the analyses which did not alter the variation partitioning procedure. We report the deviance explained (pseudo- R^2) as a measure of the explanatory power of the models and the chi-squared test as a measure of statistical significance (Crawley 2007). All analyses were repeated separately for each taxa $\times$ landscape combination and statistical analyses were performed using the software R 2.12.1 (R Development Core Team 2010).

3.3. **Results**

We recorded a total of 117 bird species and 30 small mammal species at the three study landscapes but only 51 and 18 were classified as forest-dependent species, respectively (Table S1 and S2), and considered in the analysis. The number of forest-dependent birds per forest patch varied from five to 16 at the 10% FC landscape, from eight to 16 at the 30% FC landscape and from eight to 23 at the 50% FC landscape. Bird richness in forest patches at the 10% FC

landscape is significantly lower than at the 50% FC landscape, while the number of species in forest patches at the 30% FC landscape is similar to the number observed in forest patches at the 10% and 50% FC landscapes (Figure 2). Forest-dependent small mammal richness per forest patch at the 10% FC landscape varied from 0.5 to two and was significantly lower than at the 30% and 50% FC landscape where richness per forest patch varied from three to seven and from three to 7.5, respectively (Figure 2).

The temporal change in the amount of forest cover surrounding surveyed sites in a given landscape was similar to the temporal variation in the total amount of forest cover at the landscape. Between the 1960s and 1980s, the amount of local forest cover at the 10 and 50% FC landscapes was reduced while it increased slightly in the 30% FC landscape. The opposite trend was observed between the 1980s and 2000s; local forest cover in the 10 and 50% FC landscapes increased while it was reduced in the 30% FC landscape (Figure 3).

The current distribution of species richness within each study landscape was not always predicted by variation in local forest cover as attested by the regression models. Neither present-day (2000s) nor historical (1960s and 1980s) local forest cover seems to be important in explaining species richness of small mammals at the 10% (Table 1). On the other hand, current distribution of richness of birds within the three study landscapes and of small mammals within the 30% and 50% FC landscape were associated with the variation in either past or present-day local forest cover (Table 1).

The importance of the unique contributions of historical and present-day local forest cover and their shared contribution varied widely among taxa $\times$ landscape combinations for which the variation in species richness was explained by forest cover. The number of birds at the 10% FC landscape was better explained by the unique effect of the local forest cover in the 1980s, suggesting that the number of birds at the 10% FC landscape is still reflecting the lower

local forest cover of 20 years ago and not the one observed nowadays (Table 1, Figure 4a). No evidence of time-delayed responses to local forest cover change was detected for birds and small mammals at the 30% FC landscape as species richness was better explained by the unique effect of present-day local forest cover (Table 1, Figure 4b,d). Finally, unique effects of past and present-day local forest cover explained just 2% to 6% of the variance in the number of birds and small mammals at the 50% FC landscape; it was impossible to disentangle the effects of past and present-day local forest cover on species richness as most of their influence was in the shared contribution (correlation) among them (Table 1, Figure 4c,d).

3.4. Discussion

Although a considerable body of work on extinction debts following habitat loss and fragmentation has been accumulated (see references in Kuussaari et al. 2009), until now little attention has been paid to the potential for species credit following a change from decreasing to expanding forest cover (but see Cristofoli et al. 2010, Piqueray et al. 2011). However, both extinction debt and species credit are important to devise biodiversity conservation and habitat restoration strategies. The identification of extinction debts indicate that some species are committed to extinction and that just maintaining current landscape cover is insufficient to guarantee the long-term survival of habitat specialist species. Consequently, habitat restoration has become an important goal to rescue these species and understanding how immigration dynamics can cancel part of the extinction debt is critical. Our results indicate that the existence of extinction debts and species credits as well as the potential for their future payment depends not only on forest cover trajectory (i.e. increase or decrease in forest cover) but also on the amount of remaining forest cover at the landscape scale. Below we discuss our findings starting with the interpretation of results from both taxa in each study landscape, and ending with an

overview of the importance of the total amount and the trajectory of forest cover in determining the probability and future payment of extinction debts and species credits.

Accumulated evidence suggests that the probability of extinction debts should decline through time following landscape change (Vellend et al. 2006) and should exhibit a non-linear relationship to the strength of the landscape change, being higher at landscapes with intermediate levels of habitat loss where many species persist close to their species-specific regional extinction threshold (Hanski & Ovaskainen 2002). Hence, intermediate forest cover just above the regional extinction threshold of many species is expected to present the highest potential to respond to local conservation interventions as forest regeneration (Pardini et al. 2010). Therefore among our study landscapes, time-delayed responses – specifically extinction debts – are theoretically more likely to exist at the 30% FC landscape which is the only one that has experienced a recent forest cover contraction (~ 2,160 ha of forest were lost between the 1980s and the 2000s) and currently presents an intermediate amount of total forest cover (30%). However, we found no evidence of extinction debt for either birds or small mammals in this landscape, since forest-dependent species richness was best explained by the unique contribution of present-day rather than past local forest cover.

The non-detection of an extinction debt at the 30% FC landscape indicates that both small vertebrate groups present the potential to react quickly to forest cover change (in less than ~ 20 years). Short-lived small mammals have passed through many generations since forest cover contraction and, as a consequence, extinction debt has probably been already paid (but see Burel 1992, Petit & Burel 1998). Species with longer generation times might persist longer in a modified landscape as they have spent fewer generations near a critical extinction threshold (Brook et al. 2003, Krauss et al. 2010, Lindborg 2007). Although birds have longer generation times than small mammals, our results suggest that the difference in their life cycles seems to be

insufficient to affect differently their probability of showing an extinction debt. Birds might have a larger ability to disperse than small mammals at landscapes with intermediate overall forest connectivity and this might be an explanation for the non-detection of bird extinction debt at the 30% FC landscape as was expected.

It is important to highlight that extinction debt has been previously suspected for birds in the Atlantic Forest (Brooks et al. 1999b, Uezu 2006, Metzger et al. 2009). Furthermore, a previous study carried out in the same three study landscapes have found that local forest connectivity – which was not considered in the present study – was the most plausible predictor of bird richness and abundance at the 30% FC landscape (Martensen 2008). Indeed, Metzger et al. (2009) have found that present-day forest connectivity as well as changes in local forest connectivity between the 1980s and 2000s were important to explain forest interior bird abundances which slightly suggests a time-delayed response of birds to landscape modification, i.e. extinction debt, at the 30% FC landscape (Metzger et al. 2009). Moreover, the presence of an extinction debt were particularly clear for trees at the 30% FC landscape suggesting that long-lived species often takes a longer time to disappear following an environmental disturbance than short-lived species (Metzger et al. 2009).

Differently to the 30% FC landscape, deforestation at the 10% and 50% FC landscapes occurred longer ago (from the 1960s to the 1980s), suggesting that the potential bird and small mammal extinction debts should have already been paid. Moreover, small mammals seem to react quickly to habitat loss (Metzger et al. 2009, this study). More recently (1980s and the 2000s), however, those landscapes experienced a forest cover expansion, but the potential (and possibly delayed) positive effects of forest regeneration were only evident for birds at the 10% FC landscape.

The total amount of forest cover at the 10% FC landscape is below the regional extinction threshold for many species (Andrn 1994, Pardini et al. 2010, Hanski 2011) for at least 40 years and, as a consequence, the number of species in this landscape is lower than in the other two study landscapes, especially for small mammals (Pardini et al. 2010) which are short-lived and dispersal-limited species. We found no evidence of small mammal species credit at this highly deforested landscape as well as any relationship with present-day local forest cover as most forest-dependent small mammals have already gone regionally extinct (Pardini et al. 2010). On the other hand, current richness of forest-dependent birds in forest patches at the 10% FC landscape is still reflecting the lower local forest cover of 20 years ago; that is, the number of species in forest patches is lower than expected by its current surrounding forest cover. This result indicates a potential species credit of forest-dependent birds at the 10% FC landscape. However, it is important to highlight that in such a species-poor landscape, forest regeneration – at least as small as the one observed (only ~ 300 ha of forest regenerated) – might not be efficient to halt population decline and to support local species recovery (Hanski 2000, Schrott et al. 2005); i.e. species credit may not be paid.

The great forest contraction experienced by the 50% FC landscape between the 1960s and the 1980s (a decrease of ~ 2,500 ha in forest cover) may have resulted in an extinction debt in the past. However, the great forest expansion experienced between the 1980s and 2000s (an increase of ~ 2,900 ha in forest cover) was probably able to revert local species extinctions by re-colonization and to prevent local extinctions by rescue-effect. Thus we can speculate that the present-day distribution of forest-dependent species of birds and small mammals among forest patches at the 50% FC landscape might be a result of the interaction between the effects of the recent forest cover expansion on immigration rates and the effects of the historical forest cover contraction on extinction rates (Jackson & Sax 2010). Such a capacity of quick recovery without

any future human intervention is indeed expected to occur in highly forested landscapes, well above the regional extinction threshold of many species (Pardini et al. 2010).

In summary, we found that (1) the dynamics of forest cover change is not necessarily linear and, as a consequence, either extinction debt or species credit are possible; (2) a small forest regeneration – as the one observed at the 10% FC landscape – might not be efficient to revert extinctions following deforestation at landscapes where the total amount of forest cover has dropped below the regional extinction threshold a long time ago i.e. species credit might not be paid; (3) forest-dependent species of two vertebrate groups with different longevity – birds and small mammals – respond fairly in a similar way to landscape change; however we suggest that more comparative studies are needed to investigate how the occurrence of delayed responses varies between groups of species varying in traits.

As many landscapes are experiencing a change from decreasing to expanding forest cover (e.g. Baptista & Rudel 2006, Becker et al. 2004), understanding the potential for extinction debt and species credit is extremely valuable to guide conservation and restoration strategies. Knowledge on fauna recovery during forest succession (Prach & Walker 2011), and on the suitability of young forests to forest-dwelling species (Gardner et al. 2007), is also essential, because the deforestation-reforestation transition also imply in a reduction of the average age of the forest at a landscape. Both vegetation structure and composition are drastically different across chronosequences (Clark 1996, Brown & Lugo 1990, Guariguata & Ostertag 2001, DeWalt et al. 2003) and this might have important consequences for wildlife populations since many animals rely on forest resources that vary in abundance across forests of different ages.

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Table 1: Explained deviance for simple and multiple regression models of historical (1960s and 1980s) and present-day (2000s) forest cover on forest-dependent bird and small mammal richness at the three study landscapes (10%, 30% and 50% forest cover landscapes). In parentheses, the amount of variation in the response variable attributed exclusively to each explanatory variable (unique contribution) and the amount indifferently attributed to two or three explanatory variables (shared contribution). Results significant at $P \leq 0.05$ are marked in bold, $*0.05 < P \leq 0.08$. The effect of explanatory variables on the response variable was always positive irrespectively of their size or significance. Shared contribution may show negative values when the interaction of explanatory variables explain the response variable better than the sum of individual effects.

Response variable	Landscape	Simple regressions (Unique Contributions)			Multiple regressions (Shared contributions)			
		1960s	1980s	2000s	1960s+1980s	1960s+2000s	1980s+2000s	1960s+1980s+2000s
Birds	10%	0.28 (0.00)	0.54 (0.17)	0.27 (0.04)	0.54 (0.13)	0.41 (0.00)	0.58 (0.09)	0.58 (0.14)
	30%	0.13 (0.00)	0.17 (0.05)	0.38 (0.22)	0.21 (0.00)	0.38 (0.04)	0.42 (0.03)	0.42 (0.09)
	50%	0.10 (0.04)	0.32 (0.05)	0.33 (0.06)	0.34 (-0.03)	0.34 (-0.02)	0.36 (0.17)	0.40 (0.11)
Small mammals	10%	0.01 (0.01)	0.11 (0.07)	0.06 (0.01)	0.12 (-0.01)	0.06 (0.00)	0.12 (0.04)	0.13 (0.01)
	30%	0.09 (0.00)	0.16 (0.00)	0.34* (0.15)	0.20 (0.00)	0.34 (0.04)	0.35 (0.11)	0.35 (0.05)
	50%	0.33* (0.02)	0.41 (0.06)	0.36 (0.04)	0.46 (0.05)	0.43 (0.02)	0.47* (0.07)	0.49 (0.24)

Figure 1: Location of the three studied Atlantic Forest fragmented landscapes in the State of São Paulo (south-eastern – Brazil) and its forest cover dynamics between the 1960s and 2000s (from right to left). The percentage of forest cover is shown at the bottom of each forest cover map.

Figure 2: Species richness of forest-dependent birds (a) and small mammals (b) in forest patches at three Atlantic Forest fragmented landscapes with different percentages of forest cover. The main horizontal line shows the median, boxes represent quartiles and whiskers depict either the maximum or 1.5 times the interquartile range of the data (whichever is smaller). Points are outliers. Landscapes that do not have a letter in common differ significantly in species richness (Tukey's honest significant differences test: $P < 0.05$).

Figure 3: Forest cover (%) dynamics in three Atlantic Forest fragmented landscapes, São Paulo-Brazil (a) and the consequent variation of forest cover (%) in a circle of 800 m radii around sampling points where birds (b) and small mammals (c) were sampled. The main horizontal line shows the median, boxes represent quartiles and whiskers depict either the maximum or 1.5 times the interquartile range of the data (whichever is smaller). Points are outliers. Classes that do not have a letter in common differ significantly in forest cover (Tukey's honest significant differences test: $P < 0.05$).

Figure 4: Venn diagram representing the unique and shared contributions of historical (1960s and 1980s) and present-day (2000s) local forest cover in explaining the variation in forest-dependent species richness of birds at the 10% (a), 30% (b), and 50% (c) FC landscapes and of small mammals at the 30% (d) and 50% (e) FC landscape. Each circle represents forest cover in the 1960s, 1980s and 2000s, with circle size being proportional to the explained

deviance obtained for each variable in a simple regression of that variable on the response variable (for values see Table 1). Overlapping sections represent the shared contribution between two or three variables. Most of the influence of forest cover was in the unique contribution of forest cover in the 1980s (a), in the unique contribution of forest cover in the 2000s (b, d), and in the shared contribution as unique contributions of either historical or present-day forest cover explained just small proportion of the variation in species richness (c, e).

(a)

(b)

(c)

(a)

(b)

(c)

(d)

(e)

Supplementary Material

Table S1: Number of forest patches at three Atlantic Forest fragmented landscapes (São Paulo, Brazil) with different amounts of forest cover (FC) where each forest-dependent bird species was captured.

Species	10% FC (n=17)	30% FC (n=17)	50% FC (n=19)
Apodiformes			
<i>Phaethornis eurynome</i>	4	14	17
Columbiformes			
<i>Geotrygon montana</i>	5		3
Falconiformes			
<i>Micrastur ruficollis</i>	1		4
Passeriformes			
<i>Pyroderus scutatus</i>			1
<i>Dendrocincla turdina</i>			2
<i>Dendrocolaptes platyrostris</i>	2	12	1
<i>Lepidocolaptes fuscus</i>	1	17	19
<i>Lepidocolaptes squamatus</i>			1
<i>Xiphocolaptes albicollis</i>		1	3
<i>Arremon semitorquatus</i>	5		
<i>Haplospiza unicolor</i>	3	2	11
<i>Chamaeza meruloides</i>			1
<i>Dryophila malura</i>		1	1
<i>Dryophila ochropyga</i>		1	
<i>Dysithamnus mentalis</i>	16	17	16
<i>Formicarius colma</i>			1
<i>Grallaria varia</i>			4
<i>Mackenziaena leachii</i>			1
<i>Myrmeciza squamosa</i>		5	8
<i>Myrmotherula gularis</i>			7
<i>Pyriglena leucoptera</i>	1	15	17
<i>Thamnophilus caerulescens</i>	13	12	5
<i>Anabacerthia amaurotis</i>			2
<i>Anabazenops fuscus</i>			2
<i>Automolus leucophthalmus</i>	17	7	5
<i>Cichlocolaptes leucophris</i>			1
<i>Cranioleuca pallida</i>		1	
<i>Heliobletus contaminatus</i>			1
<i>Lochmias nematura</i>	5	2	3
<i>Sclerurus scansor</i>	3	1	14

cont.

Species	10% FC (n=17)	30% FC (n=17)	50% FC (n=19)
<i>Synallaxis cinerascens</i>	1		
<i>Syndactyla rufosuperciliata</i>	13	13	12
<i>Xenops minutus</i>		7	6
<i>Scytalopus speluncae</i>			1
<i>Euphonia pectoralis</i>			2
<i>Habia rubica</i>	5		4
<i>Tangara desmaresti</i>		1	1
<i>Thraupis cyanoptera</i>			1
<i>Turdus albicollis</i>	16	14	18
<i>Attila rufus</i>	2	2	8
<i>Corythopsis delalandi</i>	5		
<i>Hemitriccus diops</i>	1	2	2
<i>Hemitriccus orbitatus</i>	1	4	
<i>Mionectes rufiventris</i>	13	15	12
<i>Myiobius barbatus</i>			1
<i>Onychorhynchus coronatus</i>			1
<i>Phylloscartes ventralis</i>	2		1
<i>Platyrinchus mystaceus</i>	16	17	18
<i>Ramphotrigon megacephala</i>			1
Piciformes			
<i>Malacoptila striata</i>		8	
<i>Colaptes melanochloros</i>	1		2

Table S2: Number of forest patches at three Atlantic Forest fragmented landscapes (São Paulo, Brazil) with different amounts of forest cover (FC) where each forest-dependent small mammal species was captured.

Species	10%FC (n=15)	30%FC (n=20)	50%FC (n=15)
Didelphimorphia			
<i>Monodelphis sp.n.</i>			3
<i>Philander frenatus</i>			2
<i>Marmosa paraguayana</i>	3		1
<i>Marmosops incanus</i>		19	15
<i>Monodelphis scallops / M. americana</i>		17	11
<i>Monodelphis sorex</i>		2	3
<i>Gracilinanus microtarsus</i>	10	16	11
Rodentia			
<i>Oxymycterus dasytrichus</i>		5	
<i>Rhagomys rufescens</i>		1	
<i>Abrawayaomys ruschii</i>			1
<i>Akodon serrensis</i>			2
<i>Brucepattersonius soricinus</i>		13	14
<i>Delomys sublineatus</i>		18	13
<i>Euryoryzomys russatus</i>		5	4
<i>Phyllomys nigrispinus / P. sulinus</i>		6	3
<i>Thaptomys nigrita</i>		3	9
<i>Juliomys pictipes / J. ossitenuis</i>	8	4	5
<i>Sooretamys angouya</i>	5	19	11

CAPÍTULO 4

IMPORTANCE OF CONSIDERING FOREST AGE FOR MODELLING BIRD SPECIES DISTRIBUTION IN HIGHLY DYNAMIC ATLANTIC FOREST LANDSCAPES

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Abstract

Highly dynamic landscapes are comprised by forest patches of varying age of regeneration surrounded by a matrix with different types of human modified habitats. While matrix quality has been increasingly taken into account in studies investigating the influence of landscape structure on species distribution, the effects of forest age has been mostly ignored. Here, we compared models of native vegetation cover on species richness and abundance considering or not forest age. We used a large dataset of birds in 53 forest patches from three Atlantic Forest landscapes with different proportions of total forest cover (~10, 30 and 50%). We categorised birds according to their habitat preferences as dependent on mature forests or forest generalists. We employed a model selection framework to identify the best models describing species richness and abundance of each bird category $\times$ landscape combination. Richness and abundance of mature forest species were affected by local amount of older forests but only at landscapes with low and high total forest cover, suggesting that the response to changes in the availability of older forests is landscape-dependent. Contrary, forest generalist birds were associated with younger vegetation, particularly at the most forested landscape. Our results indicate that the heterogeneity within native vegetation plays an important role in defining species richness and abundance in fragmented landscapes and responses to this heterogeneity are defined by habitat requirements and depend on landscape connectivity, being clearer where landscape connectivity is high and species persistence is mainly determined by the quality of the surrounding habitat.

Resumo

Paisagens altamente dinâmicas são compostas por fragmentos florestais de diferentes idades de regeneração circundados por uma matriz de diferentes tipos de habitats modificados pelo homem. Enquanto a qualidade da matriz tem sido cada vez mais levada em conta quando se investiga a influência da estrutura da paisagem sobre a distribuição de espécies, o efeito da idade de regeneração das florestas tem sido quase sempre ignorado. Aqui, nós comparamos modelos do efeito da cobertura vegetal nativa sobre riqueza de espécies e abundância, considerando ou não a idade da floresta. Nós usamos dados de aves em 53 fragmentos florestais localizados em três paisagens de Mata Atlântica com diferentes proporções de cobertura florestal total (~10, 30 e 50%). As aves foram categorizadas como dependentes de floresta madura ou generalistas de floresta de acordo com suas preferências de habitat. Utilizamos um protocolo de seleção de modelos para identificar os modelos que melhor descrevem a riqueza e a abundância de cada um dos dois grupos de aves em cada paisagem estudada. A riqueza e abundância de espécies dependentes de florestas maduras foram afetadas pela quantidade de florestas mais velhas, mas apenas nas paisagens com baixa e alta cobertura florestal total, sugerindo que a resposta a mudanças na disponibilidade de floresta mais velhas é dependente da cobertura florestal total na paisagem. Por outro lado, aves generalistas de floresta foram afetadas pela vegetação nativa mais jovem, particularmente na paisagem com maior cobertura florestal. Nossos resultados indicam que a heterogeneidade da vegetação nativa desempenha um papel importante na definição da riqueza de espécies e abundância em paisagens fragmentadas e que as respostas a essa heterogeneidade são definidas pelos requerimentos de habitat e dependem de conectividade da paisagem, sendo mais claras onde a conectividade da paisagem é alta ou onde a persistência de espécies é determinada principalmente pela qualidade do habitat.

4.1. Introduction

Despite the increasingly large literature on the effects of forest loss and fragmentation, most studies ignore landscape heterogeneity by simplifying it into a binary combination of forest and non-forest (Fisher & Lindenmayer 2007). Beyond the heterogeneous nature of anthropogenic habitats (Gustafson & Gardner 1996, Cook et al. 2002, Perfecto & Vandermeer 2002, Ewers & Didham 2006), forests are also not homogeneous since landscape dynamics is frequently complex and results in forest patches of varying age and stage of regeneration (Etter et al. 2005, Lira et al. unpublished data). While matrix quality has been increasingly taken into account in forest fragmentation studies (e.g. Gascon et al. 1999, Antongiovanni & Metzger 2005, Umetsu & Pardini 2007, Umetsu et al. 2008), the effects of forest age has been mostly ignored.

The degree of suitability of altered habitats varies among species and depends not only on the structural similarity between original and altered habitat (Taylor et al. 1993, Ricketts 2001, Barlow et al. 2007, Garden et al. 2007, Umetsu & Pardini 2007, Umetsu et al. 2008), but also on landscape characteristics, such as the amount of original habitat (Faria et al. 2007, Umetsu 2010). Forest age, i.e. how long ago a native vegetation patch had been established, should also influence habitat suitability. Forest age is directly related to successional stage as vegetation structure and plant species composition of secondary forests became more similar to old-growth forest with increasing forest age (DeWalt et al. 2003, Liebsch et al. 2008). The drastic modification of vegetation structure and plant species composition across chronosequences (Clark 1996, Brown & Lugo 1990, Guariguata & Ostertag 2001, DeWalt et al. 2003) may have important consequences for wildlife populations since many animals rely on forest resources as sites for foraging, nesting, and protection that vary in abundance within forests of different ages, i.e. different successional stages (DeWalt et al. 2003, Dunn 2004). It is worth noting, though, that the structural aspects of secondary forests converge to old-

growth characteristics more quickly than plant species composition (DeWalt et al. 2003, Liebsch et al. 2008).

Forest age should thus be an important factor determining species distribution in human-modified landscapes. However, the ability of individuals to reach and use its preferred type of forest, as well as the effects of varying quality of forests on population demography, should depend on landscape connectivity. Because landscape connectivity is defined by total habitat cover in a landscape (Andrén 1994, With & Crist 1995, Fahrig 2003), the effects of varying forest age among patches should differ among landscapes with different total forest cover.

To test the importance of forest age to species distribution in human-modified landscapes, we compared models of the effects of native vegetation cover on species richness and abundance which considered either total native vegetation cover or the cover of different forest age categories. To this aim we used a large dataset on the distribution of birds in 53 forest patches from three Atlantic Forest landscapes with different proportions of total forest cover (~10, 30 and 50%), and categorised birds into two groups according to their habitat preferences: (1) species dependent on primary forests; and (2) species that also occur in secondary forests or non-forested habitats. We hypothesized that the best models of native vegetation cover on species richness and abundance for the former group are those considering the cover of older (i.e. mature) forests while the best model describing species richness and abundance of the latter group is the one considering total native vegetation cover. We also hypothesize that these contrasting responses of groups of species with distinct habitat preferences to forest age depend on landscape connectivity, and thus on the amount of total forest cover at the landscape-scale.

4.2. Methods

4.2.1. Study area

The study was conducted in three ~10,000-ha fragmented Atlantic Forest landscapes located on the Atlantic Plateau of São Paulo, Brazil (Figure 1). The whole region of the Atlantic Plateau was once covered with Atlantic forest classified as Lower Montane Atlantic Rain Forest (Oliveira-Filho & Fontes 2000), but nowadays much of the region is reduced to secondary forest patches in different stages of regeneration (Ribeiro et al. 2009, Teixeira et al. 2009). The altitude in the Atlantic Plateau of São Paulo varies between 700-1,100 m above sea level with steep hill slopes, mountain with moderate to gentle hill slopes, and alluvial plains (Ponçano et al. 1981). The annual rainfall is between 1,350-2,000 mm and the mean annual temperature varies from 15°C to 22°C (www.cpa.unicamp.br).

In the study landscapes, remaining forest patches are composed of intermediate to old second growth forest (from 20 to > 60 years old). The matrix surrounding forest patches is dominated by agriculture and cattle pastures (Lira et al. unpublished data), but also includes a native vegetation at initial stages of regeneration, which correspond to shrub to arboreal vegetation with up to 5–6 m height continuous canopy. All three landscapes are at a similar distance to the “Serra do Mar”, which contains the largest continuous tract of Atlantic forest (1,109,546 ha) remaining in Brazil (Ribeiro et al. 2009), and are separated to each other by distances of less than 120 km. Although similar in terms of topography, relief, climate, and type of human-use, the study landscapes differ in the total proportion of forest cover, varying from 11%, to 31% and 49%. Hereafter, the study landscapes are referred as 10, 30 and 50% forest cover (FC) landscapes.

4.2.2. *Bird survey*

Birds were surveyed in a set of sampling sites at each landscape, all of them located in forests patches: 17 in the 10% and in the 30% FC landscapes, and 19 in the 50% FC landscape (Martensen 2008, Banks-Leite et al. 2011). Each site was sampled using 10 mist nets (12 m length, 2.5 m high, 31 mm mesh) in a straight line and located at least 50 m from the forest edge. Capture sessions were conducted from 2001 to 2002 in the 30% FC landscape, from 2004 to 2005 in the 10% FC landscape and from 2005 to 2007 in the 50% FC landscape. All captured birds were identified to species in the field and marked with a numbered aluminium band provided by Centre of Research for Conservation of Wild Birds (CEMAVE-IBAMA) and released in the vicinity. There was a small variation in sampling effort among landscapes; the mean effort per sampling site was 699 net-hours ($SD = 21.7$) in the 10% FC landscape, 537 net-hours ($SD = 6.2$) in the 30% FC landscape and an equal sampling effort of 680 net-hours per sampling site in the 50% FC landscape.

4.2.3. *Data Analysis*

We categorised bird species into two groups according to their habitat preference using information provided by Stotz et al. (1996). Species occurring only in primary forest were considered more dependent on mature (i.e. older) forests than species also occurring in naturally disturbed or human-created forests or in non-forested habitats. Hereafter, we refer to the former group as mature forest species and to the latter as forest generalists. Bird species occurring preferably or only in non-forested habitats were excluded from the analyses. For each surveyed forest patch, we calculated the number of recorded species (species richness) and individuals (abundance) for each group.

We classified natural vegetation into four ordinal categories: (1) young secondary vegetation (YSV, shrub to arboreal vegetation up to ~ 5 m height), (2) secondary forests with

~ 20-25 years-old (SF20), (3) secondary forests with ~ 40-45 years-old (SF40), and (4) mature forests never cleared during the last 60 years (MF60). Forest (age) categories (from category 2 to 4) were defined by overlapping forest cover maps (forest and non-forest) from three different dates, early 1960s (1962), 1980s (1978-1981) and 2000s (2000-2005) and young secondary vegetation patches were identified when mapping the most recent image (2000s) (Lira et al. unpublished data).

We then defined ten different groups of native vegetation: all four native vegetation categories together, all three forest categories together (SF20 + SF40 + MF60), a subset of three younger vegetation categories (YSV + SF20 + SF40), three subsets of two native vegetation categories (YSV+ SF20, SF20 + SF40 and SF40 + MF60), and each of the four native vegetation categories alone. These are all possible combinations of the four native vegetation categories excluding those that group together categories that are not sequential in terms of age of regeneration. Using ArcGIS software, we measured the local native vegetation cover for each categories or groups of categories in a search radius of 800 m from each 53 sampling points, considering the whole area of patches included in the search radius. We selected an 800-m scale based on previous information about the spatial scale bird species respond to local forest cover (Boscolo & Metzger 2009).

4.2.4. Statistical analysis

We evaluated the effects of local native vegetation cover on species richness and abundance for each group $\times$ landscape combination with 11 alternative models, and employed a model selection framework to identify the most plausible candidates (Burnham & Anderson 2002). Candidate models encompassed a null hypothesis (i.e. no effect of local native vegetation cover), and 10 simple regression models containing each of the ten groups of native vegetation categories (Table 1). As inspection of model residuals showed that Poisson errors

and log link function provided the best fit for regressions models of species richness and abundance, we used Generalized Linear Models for the analyses.

The Akaike Information Criterion corrected for small samples (AICc) was calculated for each model. The plausibility for alternative models was estimated by the AICc differences in relation to the smallest AICc in a set of models (ΔAICc). We assumed that $\Delta\text{AICc} < 2$ indicates equally plausible models. We have also calculated the Akaike weights (W_i), which expresses the relative likelihood of each model to be selected as the most plausible in the set of models. Statistical analyses were performed in the R environment, version 2.12.1 (R Development Core Team 2010).

4.3. Results

We recorded a total of 117 bird species at the three study landscapes; 51 were classified as mature forest species and 58 as forest generalists (Table S1). Two species occurring preferably in non-forested habitats, five species occurring only in non-forested habitats and one migratory species were excluded from the analyses.

There was a gradual increase in the number of mature forest species per sampling site with increasing total amount of forest cover in the landscape with mean species richness at the 50% FC landscape being significantly higher than at the 10% FC landscape. On the other hand, the abundance of mature forest species per sampling sites was not significantly different among landscapes (Figure 2a).

The opposite trend was observed for forest generalist species. The mean number of species at the 10% FC landscape was significantly higher than at the 30% FC landscape while mean species richness at the 30% and 50% FC landscape were fairly similar. Similarly, the mean abundance of forest generalists at the 10% FC landscape was significantly higher than at the 30% and 50% FC landscapes (Figure 2b).

The largest proportion of the native vegetation cover at the 10% and 50% FC landscapes corresponds to secondary forests that have regenerated during the last 20 years (~ 44% and 50% of the total native vegetation cover, respectively) while mature forests (≥ 60 years of regeneration) represents the largest proportion of the native vegetation cover at the 30% FC landscape (43%) (Figure 1). It is also important to highlight that ~ 35% of the total native vegetation cover at the 50% FC landscape is composed of mature forests which is mainly concentrated at the south-eastern portion of the landscape and also that young secondary vegetation represents an important proportion of the native vegetation cover at the landscapes with 10% and 30% of forest cover (Figure 1). As a consequence, native vegetation cover in an 800-m search radius from sampling points at the 10 and 50% FC landscapes is mainly composed of vegetation classes that consider secondary forests with ~ 20 years-old while at the 30% FC landscape the vegetation surrounding surveyed sites is mainly composed of mature forests (Figure 3).

Richness of mature forest species at the 30% FC landscape as well as the richness of forest generalists at the 10% and 30% FC landscapes were not related to the variation in local cover of any of the categories or groups of categories of native vegetation, as the null model was within the selected models (Table 2, Table S2). When an effect of local vegetation cover on species richness and abundance was observed, models considering separate categories or groups of categories of native vegetation of different age were more plausible than the one not considering.

Mature forest species were, as expected, more affected by the availability of older forests. Selected models indicated that both species richness and abundance at the 10% and 50% FC landscapes were positively affected by the amount of neighbouring forests with or more than 40 years-old (Table 2). In contrast, at the 30% FC landscape species richness of mature forest birds was not affected by local native vegetation cover (see above) while the

abundance of this group of species was positively affected by the amount of forests with or less than 40 years old (Table 2).

On the other hand, forest generalist birds were, in general, affected by the local cover of native vegetation categories or groups of categories that consider young secondary vegetation and younger forests. While species richness of forest generalists were not affected by native vegetation cover at the 10% and 30% FC landscapes (see above), it was positively affected by the local amount of young secondary vegetation at the 50% FC landscape. Similarly, the abundance of generalist species was also positively related to the local cover of young secondary vegetation at the 50% FC landscape. However, abundance of forest generalists was positively affected by the local cover of 40 years-old forests at the 10% FC landscape and by all three forest categories together at the 30% FC landscape.

In summary, richness and abundance of mature forest species were affected by local availability of older forests but only at landscapes with low and high total forest cover, and forest generalists were associated with young secondary vegetation only at the 50% FC landscape.

4.4. Discussion

Our results suggest that the heterogeneity within native vegetation associated with varying age and regeneration stages is crucial to understand the effects of landscape structure on bird communities. For every group $\times$ landscape combination that we have detected an effect of local native vegetation availability, models considering separate categories or groups of categories of native vegetation of different age were more plausible in explaining bird species distribution than the model considering total native vegetation cover irrespective of age. Moreover, our data also indicate that the distribution of distinct groups of birds respond to this heterogeneity in opposite ways, indicating that habitat requirements lead to differences among

species in their likelihood of using vegetation patches in different successional stages. As expected, species that are known to be dependent on mature forests are affected by the availability of older forests, while species that are more flexible in using forests of different degrees of disturbances are more associated with younger forests and young secondary vegetation. In fact, a review on faunal recovery during tropical forest regeneration has shown that forest successional stage determines the richness and composition of animal assemblages (Dunn 2004). Moreover, structure and composition of several animal assemblages differ markedly among primary and secondary forests in the Neotropics (Barlow et al. 2007, Pardini et al. 2009).

However, responses to changes in local cover of native vegetation were dependent on the total forest cover at the landscape scale. The distribution of mature forest birds was best explained by the amount of neighbouring older forests only at the landscapes with low and high levels of forest cover, suggesting that the response of mature forest birds to changes in the local amount of older forest is landscape-dependent. Species persistence in forest patches (and consequently species richness and abundance) at fragmented landscapes is mediated by immigration, survival and recruitment rates as those demographic parameters are directly related with population size and, thus, with extinction risk (Gaggiotti & Hanski 2004). Where the total proportion of forest cover is high, immigration rates are high throughout the landscape (because of the proximity among forest patches) (Andrén 1994, Pardini et al. 2010, Puettker et al. submitted) allowing individual species to reach and use its preferred type of forest where survival and recruitment rates are higher. When connectivity among patches is reduced at landscapes with intermediate levels of forest cover, species persistence in forest patches should depend on local forest connectivity (Andrén 1994, Martensen 2008). In this situation, the degree of local connectivity should be more important than the heterogeneity of forests to define species survival and recruitment. At landscapes with low levels of total forest

cover, connectivity among forest patches is eroded and immigration rates are extremely low across the landscape (Pardini et al. 2010, Puettker et al. submitted). Therefore, species persistence should be again dependent on the quality of neighbouring native vegetation cover and survival and recruitment rates should be higher at sites surrounded by the preferred habitats. Indeed, a previous study has shown that local connectivity was the best predictor of bird species richness and abundance at the landscape with 30% of forest cover but not in the landscapes with low and high levels of forest cover (Martensen 2008, Martensen et al. 2008).

Contrary to our expectations, the distribution of forest generalists was also best explained by local native vegetation cover when taking age and regeneration stage into account. However, the association of forest generalists with younger forests or young secondary vegetation was clearer at the 50% FC landscape, where mature forest species were associated with older forests. Although forest generalist species are able to use forests of varying age of regeneration and degree of disturbance, population survival, recruitment rates and thus abundance may be higher in younger forests (e.g. Umetsu et al. 2008). Our results suggest that the segregation between mature forest specialists and forest generalists across forests of different ages seems to be stronger where landscape connectivity is high and both groups can reach preferred habitats.

As reported elsewhere, many forested landscapes are becoming dominated by progressively younger secondary forests (e.g. Lugo & Helmer 2004, Ribeiro et al. 2009, Teixeira et al. 2009) with increasingly less capacity of hosting species which are dependent on mature forests (Laurance 2005, Barlow et al. 2007, Gardner et al. 2007). In the short-term, the growing young secondary forest can contribute with biodiversity conservation by sustaining a significant number of forest generalist species but also rescuing (by increasing the overall landscape connectivity) mature forest species populations which are unlikely to persist in mature forest patches at highly deforested landscapes where connectivity are

extremely low. Moreover, those growing young forests will possibly be future habitat areas for those mature forest species since most young forests have the potential to attain in the long term a structure and species composition similar to mature forests (Wright & Muller-Landau 2006). This latter prospect of young secondary forests to the conservation of mature forest species should be maximized where the ratio of young forest to mature forest is relatively low and mature forest have persisted close to the areas where secondary young forests are growing (Guariguata & Ostertag 2001, Etter et al. 2005, Chazdon et al. 2009).

In summary, our results indicate that (1) the heterogeneity within native vegetation plays an important role in defining species richness and abundance in fragmented landscapes, (2) responses to this heterogeneity are defined by habitat requirements and depend on landscape connectivity, being more clear where landscape connectivity is high and species persistence is mainly determined by the quality of the surrounding habitat, (3) young secondary vegetation and younger forests can contribute to biodiversity conservation in the short term mainly by harbouring forest generalist species.

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Table 1: Simple regression models explaining bird richness and abundance per sampling sites as a function of native vegetation cover in three Atlantic Forest landscapes with different amounts of remaining forest, São Paulo, south-eastern Brazil.

Model	Explanatory variable
NULL	None
YSV	Young secondary vegetation cover
SF20	~ 20-years-old forest cover
SF40	~ 40-years-old forest cover
MF60	Mature forest (≥ 60 -years-old) cover
YSV-SF20	Cover of young secondary vegetation and ~ 20-years-old forest
SF	Cover of forests with 20-40 years old
SF40-MF60	Cover of forests with more than 40-years-old
YSV-SF	Cover of young secondary vegetation and forests with or less than 40-years-old
SF-MF	Forest cover (irrespective of forest age)
YSV-SF-MF	Native vegetation cover

Table 2: Selected regression models explaining bird richness and abundance in sampling sites as a function of local native vegetation cover in three Atlantic Forest landscapes with different proportions of forest cover, São Paulo, south-eastern Brazil. The effect of explanatory variables on the response variable was always positive. See Table 1 for model description. n: number of sampling sites in each study landscape; K: number of estimated parameters; AICc: Akaike Information Criterion corrected for small samples; ΔAICc : difference between the AICc of a given model and of the best model; W_i : Akaike weights (based on AICc).

(a) Mature forest species

Landscape	Richness					Abundance				
	Model	K	AICc	Δ AICc	Wi	Model	K	AICc	Δ AICc	Wi
10% FC (n=17)	SF40-MF60	2	81.09	0.00	0.39	SF40-MF60	2	117.48	0.00	0.99
	SF40	2	81.59	0.50	0.30					
30% FC (n=17)	SF-MF	2	84.69	0.00	0.13	SF	2	137.70	0.00	0.70
	SF40-MF60	2	84.81	0.12	0.13	YSV-SF	2	139.53	1.83	0.28
	YSV-SF	2	84.83	0.14	0.12					
	YSV-SF-MF	2	84.88	0.19	0.12					
	SF	2	84.94	0.25	0.12					
	NULL	1	85.15	0.46	0.11					
	SF20	2	85.86	1.17	0.07					
	SF40	2	85.90	1.21	0.07					
	MF60	2	86.33	1.64	0.06					
50% FC (n=19)	SF40	2	101.50	0.00	0.52	SF40-MF60	2	210.48	0.00	0.47
	SF40-MF60	2	102.44	0.94	0.32	SF40	2	210.70	0.22	0.42

(b) Forest generalist species

Landscape	Richness					Abundance				
	Model	K	AICc	Δ AICc	Wi	Model	K	AICc	Δ AICc	Wi
10%FC (n=17)	NULL	1	86.31	0.00	0.19	SF40	2	154.06	0.00	0.98
	SF40	2	86.89	0.58	0.14					
	SF40-MF60	2	87.41	1.10	0.11					
	YSV-SF20	2	88.13	1.82	0.08					
	SF20	2	88.15	1.84	0.08					
	SF-MF	2	88.19	1.88	0.08					
	MF60	2	88.28	1.97	0.07					
30%FC (n=17)	SF	2	85.09	0.00	0.21	SF	2	136.96	0.00	0.88
	SF40	2	85.57	0.48	0.17					
	NULL	1	85.89	0.80	0.14					
	YSV-SF	2	86.19	1.10	0.12					
50%FC (n=19)	YSV	2	101.03	0.00	0.71	YSV	2	158.92	0.00	0.96

Figure 1: Proportion and spatial distribution of native vegetation categories and location of the 53 surveyed sampling sites at three Atlantic Forest fragmented landscapes (São Paulo – south-eastern Brazil) with 10% (a), 30% (b) and 50% (c) of total forest cover. Native vegetation was classified into four categories: young secondary vegetation (YSV), ~20-years-old secondary forests (SF20), ~40-years-old secondary forests (SF40) and ≥ 60 -years-old mature forests (MF60). Note that individual patches are a mosaic of different native vegetation categories.

Figure 2: Species richness and abundance of (a) mature forest and (b) forest generalist birds at the study landscapes with different percentages of forest cover (10, 30 and 50%), São Paulo, south-eastern Brazil. The main horizontal line shows the median, boxes represent quartiles and whiskers depict either the maximum or 1.5 times the interquartile range of data obtained in sampling sites (whichever is smaller). Points are outliers. Landscapes that do not have a letter in common differ significantly in species richness or abundance (Tukey's honest significant differences test: $P < 0.05$).

Figure 3: Variation in the cover (in hectares) of different groups of native vegetation categories in an 800-m search radius from sampling sites in three Atlantic Forest fragmented landscapes, São Paulo, south-eastern Brazil. Native vegetation groups are described in the Data analysis section and in Table 1. The main horizontal line shows the median, boxes represent quartiles and whiskers depict either the maximum or 1.5 times the interquartile range of the data (whichever is smaller). Points are outliers.

(a) Mature forest birds

(b) Forest generalist birds

Supplementary Material

Table S1: Bird species captured in three Atlantic Forest fragmented landscapes (São Paulo, Brazil) with different amounts of forest cover (FC). Birds were categorised – using information provided by Stotz et al. (1996) – as mature forest species if they occur only in primary forest and as forest generalist species if they also occur in naturally disturbed or human-created forests or in non-forest habitats.

Species	Mature forest	Forest generalist
Apodiformes		
TROCHILIDAE		
<i>Amazilia lactea</i>		X
<i>Amazilia versicolor</i>		X
<i>Clytolaema rubricauda</i>		X
<i>Leucochloris albicollis</i>		X
<i>Melanotrochilus fuscus</i>		X
<i>Phaethornis eurynome</i>	X	
<i>Phaethornis pretrei</i>		X
<i>Phaethornis squalidus</i>		X
<i>Thalurania glaucopis</i>		X
Columbiformes		
COLUMBIDAE		
<i>Geotrygon montana</i>	X	
<i>Leptotila rufaxilla</i>		X
<i>Leptotila verreauxi</i>		X
Cuculiformes		
CUCULIDAE		
<i>Piaya Cayana</i>		X
Falconiformes		
ACCIPITRIDAE		
<i>Rupornis magnirostris</i>		X
FALCONIDAE		
<i>Micrastur ruficollis</i>	X	
Passeriformes		
CARDINALINAE		
<i>Saltator similis</i>		X
COTINGIDAE		
<i>Pyroderus scutatus</i>	X	
DENDROCOLAPTIDAE		
<i>Dendrocincla turdina</i>	X	
<i>Dendrocolaptes platyrostris</i>	X	
<i>Lepidocolaptes fuscus</i>	X	

cont.

Species	Mature forest	Forest generalist
<i>Lepidocolaptes squamatus</i>	X	
<i>Sittasomus griseicapillus</i>		X
<i>Xiphocolaptes albicollis</i>	X	
EMBERIZINAE		
<i>Arremon semitorquatus</i>	X	
<i>Haplospiza unicolor</i>	X	
<i>Tiaris fuliginosus</i>		X
FORMICARIIDAE		
<i>Batara cinerea</i>		X
<i>Chamaeza meruloides</i>	X	
<i>Conopophaga lineata</i>		X
<i>Dryophila malura</i>	X	
<i>Dryophila ochropyga</i>	X	
<i>Dysithamnus mentalis</i>	X	
<i>Formicarius colma</i>	X	
<i>Grallaria varia</i>	X	
<i>Mackenziaena leachii</i>	X	
<i>Mackenziaena severa</i>		X
<i>Myrmeciza squamosa</i>	X	
<i>Myrmotherula gularis</i>	X	
<i>Pyriglena leucoptera</i>	X	
<i>Thamnophilus caerulescens</i>	X	
FURNARIIDAE		
<i>Anabacerthia amaurotis</i>	X	
<i>Anabazenops fuscus</i>	X	
<i>Automolus leucophthalmus</i>	X	
<i>Cichlocolaptes leucophris</i>	X	
<i>Cranioleuca pallida</i>	X	
<i>Heliobletus contaminatus</i>	X	
<i>Lochmias nematura</i>	X	
<i>Sclerurus scansor</i>	X	
<i>Synallaxis cinerascens</i>	X	
<i>Synallaxis ruficapilla</i>		X
<i>Syndactyla rufosuperciliata</i>	X	
<i>Xenops minutus</i>	X	
PARULINAE		
<i>Basileuterus culicivorus</i>		X
<i>Basileuterus leucoblepharus</i>		X
<i>Coereba flaveola</i>		X
<i>Conirostrum speciosum</i>		X
<i>Chiroxiphia caudata</i>		X
<i>Manacus manacus</i>		X

cont.

Species	Mature forest	Forest generalist
<i>Neopelma chrysolophum</i>		X
<i>Schiffornis virescens</i>		X
RHINOCRYPTIDAE		
<i>Scytalopus speluncae</i>	X	
THRAUPINAE		
<i>Euphonia pectoralis</i>	X	
<i>Habia rubica</i>	X	
<i>Pipraeidea melanonota</i>		X
<i>Pyrrhocomma ruficeps</i>		X
<i>Tachyphonus coronatus</i>		X
<i>Tangara cayana</i>		X
<i>Tangara desmaresti</i>	X	
<i>Thlypopsis sordida</i>		X
<i>Thraupis cyanoptera</i>	X	
<i>Thraupis sayaca</i>		X
<i>Trichothraupis melanops</i>		X
TURDINAE		
<i>Platycichla flavipes</i>		X
<i>Turdus albicollis</i>	X	
<i>Turdus amaurochalinus</i>		X
<i>Turdus leucomelas</i>		X
<i>Turdus rufiventris</i>		X
TYRANNIDAE		
<i>Attila rufus</i>	X	
<i>Camptostoma obsoletum</i>		X
<i>Cnemotriccus fuscatus</i>		X
<i>Corythopsis delalandi</i>	X	
<i>Hemitriccus diops</i>	X	
<i>Hemitriccus orbitatus</i>	X	
<i>Knipolegus cyanirostris</i>		X
<i>Lathrotriccus euleri</i>		X
<i>Leptopogon amaurocephalus</i>		X
<i>Mionectes rufiventris</i>	X	
<i>Myiarchus swainsoni</i>		X
<i>Myiobius atricaudus</i>		X
<i>Myiobius barbatus</i>	X	
<i>Myiodynastes maculatus</i>		X
<i>Onychorhynchus coronatus</i>	X	
<i>Pachyramphus polychopterus</i>		X
<i>Phylloscartes ventralis</i>	X	
<i>Platyrinchus mystaceus</i>	X	
<i>Ramphotrigon megacephala</i>	X	

cont.

Species	Mature forest	Forest generalist
<i>Todirostrum plumbeiceps</i>		X
<i>Tolmomyias sulphurescens</i>		X
VIREONIDAE		
<i>Cyclarhis gujanensis</i>		X
<i>Hylophilus poicilotis</i>		X
<i>Vireo olivaceus</i>		X
Piciformes		
BUCCONIDAE		
<i>Malacoptila striata</i>	X	
PICIDAE		
<i>Celeus flavescens</i>		X
<i>Colaptes melanochloros</i>	X	
<i>Dryocopus lineatus</i>		X
<i>Picumnus cirratus</i>		X
<i>Picumnus temminckii</i>		X
<i>Veniliornis spilogaster</i>		X
Trogoniformes		
TROGONIDAE		
<i>Trogon rufus</i>		X

Table S2: Eleven candidates models of local vegetation cover on richness and abundance of mature forest (a, b) and forest generalist birds (c, d) at the three study landscapes with different percentages of forest cover (FC). Plausible models are marked in bold. n: number of forest patch sampled in each study landscape; K: number of estimated parameters; AICc: Akaike Information Criterion corrected for small samples; $\Delta AICc$: difference between the AICc of a given model and that of the best model; W_i : Akaike weights (based on AICc); (-): the effect of explanatory variables on the response variable was negative.

(a) Richness of mature forest species

10% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF40-MF60	2	81.09	0.00	0.39
SF40	2	81.59	0.50	0.30
MF60	2	84.46	3.37	0.07
YSV	2	84.56	3.47	0.07
NULL	1	85.75	4.66	0.04
YSV-SF20	2	85.83	4.74	0.04
YSV-SF	2	86.64	5.55	0.02
SF-MF	2	87.14	6.05	0.02
SF20	2	87.24	6.15	0.02
YSV-SF-MF	2	87.25	6.16	0.02
SF	2	87.32	6.23	0.02

30% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF-MF	2	84.69	0.00	0.13
SF40-MF60	2	84.81	0.12	0.13
YSV-SF	2	84.83	0.14	0.12
YSV-SF-MF	2	84.88	0.19	0.12
SF	2	84.94	0.25	0.12
NULL	1	85.15	0.46	0.11
SF20	2	85.86	1.17	0.07
SF40	2	85.90	1.21	0.07
MF60	2	86.33	1.64	0.06
YSV	2	87.12	2.43	0.04 (-)
YSV-SF20	2	87.74	3.05	0.03

50%FC landscape (n=19)				
Model	K	AICc	ΔAICc	Wi
SF40	2	101.50	0.00	0.52
SF40-MF60	2	102.44	0.94	0.32
SF	2	105.39	3.89	0.07
YSV-SF	2	107.65	6.15	0.02
RF60	2	107.91	6.41	0.02
SF-MF	2	109.29	7.79	0.01
NULL	1	109.35	7.85	0.01
YSV-SF-MF	2	110.34	8.84	0.01
SF20	2	110.55	9.05	0.01
YSV	2	111.01	9.51	0.00 (-)
YSV-SF20	2	111.39	9.89	0.00

(b) Abundance of mature forest species

10% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF40-MF60	2	117.48	0.00	0.99
MF60	2	127.20	9.72	0.01
YSV	2	172.62	55.14	0.00
SF40	2	174.00	56.52	0.00
SF-MF	2	176.18	58.70	0.00
YSV-SF20	2	177.96	60.48	0.00
YSV-SF-MF	2	178.16	60.68	0.00
YSV-SF	2	179.30	61.82	0.00
NULL	1	180.78	63.30	0.00
SF	2	182.25	64.77	0.00
SF20	2	182.88	65.40	0.00

30% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF	2	137.70	0.00	0.70
YSV-SF	2	139.53	1.83	0.28
SF40	2	145.03	7.33	0.02
SF-MF	2	161.44	23.74	0.00
SF40-MF60	2	161.62	23.92	0.00
SF20	2	166.46	28.76	0.00
NULL	1	168.03	30.33	0.00
YSV	2	169.72	32.02	0.00 (-)
MF60	2	169.83	32.13	0.00
YSV-SF-MF	2	170.26	32.56	0.00
YSV-SF20	2	170.56	32.86	0.00

50%FC landscape (n=19)				
Model	K	AICc	ΔAICc	Wi
SF40-MF60	2	210.48	0.00	0.47
SF40	2	210.70	0.22	0.42
MF60	2	214.06	3.58	0.08
SF	2	217.12	6.64	0.02
YSV-SF	2	221.87	11.39	0.00
NULL	1	222.39	11.91	0.00
SF20	2	223.23	12.75	0.00
YSV	2	224.44	13.96	0.00
YSV-SF-MF	2	224.61	14.13	0.00
SF-MF	2	224.73	14.25	0.00
YSV-SF20	2	224.87	14.39	0.00

(c) Richness of forest generalist species

10% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
NULL	1	86.31	0.00	0.19
SF40	2	86.89	0.58	0.14
SF40-MF60	2	87.41	1.10	0.11
YSV-SF20	2	88.13	1.82	0.08
SF20	2	88.15	1.84	0.08
SF-MF	2	88.19	1.88	0.08
MF60	2	88.28	1.97	0.07
YSV-SF	2	88.44	2.13	0.07
SF	2	88.48	2.17	0.07
YSV-SF-MF	2	88.70	2.39	0.06
YSV	2	88.76	2.45	0.06

30% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF	2	85.09	0.00	0.21
SF40	2	85.57	0.48	0.17
NULL	1	85.89	0.80	0.14
YSV-SF	2	86.19	1.10	0.12
SF40-MF60	2	87.20	2.11	0.07
SF-MF	2	87.24	2.15	0.07
SF20	2	88.24	3.15	0.04
MF60	2	88.29	3.20	0.04
YSV	2	88.37	3.28	0.04
YSV-SF-MF	2	88.39	3.30	0.04
YSV-SF20	2	88.48	3.39	0.04

50% FC landscape (n=19)				
Model	K	AICc	ΔAICc	Wi
YSV	2	101.03	0.00	0.71
NULL	1	105.73	4.70	0.07
MF60	2	106.12	5.09	0.06
SF-MF	2	107.86	6.83	0.02
SF20	2	108.10	7.07	0.02
SF40-MF60	2	108.15	7.12	0.02
SF40	2	108.20	7.17	0.02
YSV-SF20	2	108.20	7.17	0.02
SF	2	108.22	7.19	0.02
YSV-SF-MF	2	108.22	7.19	0.02
YSV-SF	2	108.24	7.21	0.02

(d) Abundance of forest generalist species

10% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF40	2	154.06	0.00	0.98
SF40-MF60	2	161.97	7.91	0.02
YSV-SF20	2	165.81	11.75	0.00
YSV	2	167.78	13.72	0.00
YSV-SF	2	168.41	14.35	0.00
MF60	2	170.29	16.23	0.00
SF-MF	2	170.38	16.32	0.00
SF	2	170.67	16.61	0.00
SF20	2	170.82	16.76	0.00
NULL	1	171.78	17.72	0.00
YSV-SF-MF	2	173.97	19.91	0.00

30% FC landscape (n=17)				
Model	K	AICc	ΔAICc	Wi
SF	2	136.96	0.00	0.88
SF40	2	140.97	4.02	0.12
YSV-SF	2	147.10	10.15	0.01
YSV	2	156.39	19.43	0.00
YSV-SF20	2	157.90	20.95	0.00
SF-MF	2	158.02	21.07	0.00
SF40-MF60	2	158.03	21.08	0.00
NULL	1	160.62	23.66	0.00
SF20	2	161.60	24.64	0.00
MF60	2	163.19	26.24	0.00
YSV-SF-MF	2	163.21	26.25	0.00

50% FC landscape (n=19)				
Model	K	AICc	ΔAICc	Wi
YSV	2	158.92	0.00	0.96
SF40-MF60	2	166.91	7.99	0.02
MF60	2	168.58	9.66	0.01
YSV-SF20	2	170.42	11.50	0.00
SF20	2	170.48	11.56	0.00
NULL	1	171.82	12.90	0.00
SF-MF	2	171.94	13.20	0.00
SF40	2	172.13	13.21	0.00
YSV-SF-MF	2	173.57	14.65	0.00
SF	2	173.88	14.96	0.00
YSV-SF	2	173.91	14.99	0.00

CAPÍTULO 5

CONSIDERAÇÕES FINAIS

5.1. Considerações finais

Os resultados gerados por esta tese contribuíram para o melhor entendimento dos efeitos da dinâmica de paisagens de Mata Atlântica sobre aves e de pequenos mamíferos. O capítulo 2 descreveu a dinâmica de três paisagens de Mata Atlântica, localizadas no Planalto Atlântico de São Paulo, e mostrou suas consequências não só na estrutura das paisagens (tamanho, formato e isolamento dos fragmentos florestais) como também na estrutura etária de suas florestas. No capítulo 3 foram investigadas as consequências, em longo prazo (débito de extinção e crédito de espécies), da alteração das paisagens sobre aves e pequenos mamíferos. Finalmente, os resultados do capítulo 4 mostraram a importância de considerar a idade das florestas (i.e. estágio sucessional) ao investigar os efeitos da estrutura da paisagem sobre a comunidade de aves.

A cobertura florestal atual em cada paisagem estudada (Ribeirão Grande: ~ 10%, Caucaia: ~ 30% e Tapiraí: ~ 50%) é resultado do balanço entre desmatamento e regeneração florestal nos últimos 500 anos de ocupação humana (Fonseca 1985, Dean 1996). No Capítulo 2, foi avaliada a dinâmica dessas três paisagens nas últimas quatro décadas (1960 a 2000) através do mapeamento de cada paisagem em três datas distintas (1960, 1980 e 2000). Entre os anos 1960 e 1980, a cobertura florestal em Ribeirão Grande e Tapiraí foi reduzida, enquanto que em Caucaia houve um aumento sutil. A tendência oposta foi observada entre os anos 1980 e 2000; a regeneração florestal foi maior do que o desmatamento em Ribeirão Grande e Tapiraí e, como consequência, a cobertura florestal aumentou. Por outro lado, a cobertura florestal em Caucaia foi drasticamente reduzida entre 1980 e 2000. Em resumo, a cobertura florestal em Caucaia foi relativamente constante entre os anos 1960 e 1980, mas um desmatamento considerável foi observado mais recentemente. Por outro lado, Ribeirão Grande e Tapiraí apresentaram uma dinâmica florestal similar – a cobertura florestal foi reduzida entre 1960 e 1980, mas foi observado um ganho líquido de floresta entre 1980 e 2000 (Figura 1, Capítulo 2).

Sendo assim, os resultados do capítulo 2 mostraram que a estrutura das paisagens fragmentadas do Planalto Atlântico Paulista, assim como outras paisagens de Mata Atlântica (Becker et al. 2004, Baptista & Rudel 2006) e outras paisagens florestais ao redor do mundo (Rudel et al. 2005), não é necessariamente o resultado de uma dinâmica linear de perda de cobertura florestal. Desta forma, fica evidente que precisamos entender não só os impactos da perda e fragmentação da cobertura florestal – já amplamente reportados na literatura (ver referências em Ewers & Didham 2006) – como também os efeitos do aumento de cobertura florestal em paisagens alteradas. O processo de perda e fragmentação florestal – uma das maiores ameaças à biodiversidade global (Tilman et al. 2001) – causa, em alguns casos, a perda imediata de muitas espécies, mas em outras situações pode existir um período de tempo bastante prolongado entre a alteração da paisagem e a extinção de espécies, gerando um débito de extinção (Tilman et al. 1994). No entanto, o conhecimento sobre os efeitos do aumento da cobertura florestal em paisagens fragmentadas ainda é muito restrito (mas veja Cristofoli et al. 2010 e Piqueray et al. 2011). Com o aumento da conectividade e, portanto, da taxa de imigração em toda a paisagem, extinções locais em fragmentos florestais podem ser revertidas (através de re-colonização) e as extinções previstas para o futuro (débito de extinção) podem ser evitadas (através do resgate de populações em declínio). Entretanto, vale destacar que esses efeitos positivos, podem demorar um pouco para se manifestar, gerando um crédito de espécies (Hanski 2000).

Portanto, no Capítulo 3, foram investigados os efeitos das dinâmicas não-lineares das paisagens estudadas sobre a comunidade de aves e pequenos mamíferos que cada uma delas abriga. O objetivo principal desse capítulo era verificar a existência de débitos de extinção ou créditos de espécies. Os resultados não revelaram a existência de débito de extinção para nenhum dos dois grupos taxonômicos estudados na paisagem de Caucaia – onde ocorreu drástica e

recente perda de cobertura florestal. Os pequenos mamíferos apresentam ciclo de vida curto e, portanto, era esperado que seu débito de extinção fosse pago rapidamente (neste estudo, em menos de 20 anos) (mas veja Burel 1992, Petit & Burel 1998). No entanto, espécies com maior tempo de geração podem persistir por mais tempo em uma paisagem onde houve redução de cobertura florestal, já que poucas gerações tiveram que sobreviver perto de um limiar crítico de extinção (Brook et al. 2003, Krauss et al. 2010, Lindborg 2007). Embora as aves tenham ciclo de vida mais longo do que os pequenos mamíferos, essa diferença não foi suficiente para que os dois grupos apresentassem diferentes probabilidades de débito de extinção. No entanto, é importante destacar que estudos anteriores sugeriram a existência de um débito de extinção de aves na Mata Atlântica (Brooks et al. 1999, Uezu 2006), inclusive para paisagem de Caucaia (Metzger et al. 2009).

Ao contrário de Caucaia, a perda de cobertura florestal aconteceu há muito tempo atrás nas paisagens de Ribeirão Grande e Tapiraí (entre 1960 e 1980) sugerindo que possíveis débitos de extinção já devem ter sido pagos (Vellend et al. 2006). Além disso, mais recentemente, ambas as paisagens ganharam cobertura florestal. No entanto, apesar de apresentarem histórico semelhante, há uma diferença importante entre essas duas paisagens: a cobertura florestal atual. A porcentagem de cobertura florestal de Ribeirão Grande (~ 10%) é inferior ao limiar de extinção para muitas espécies (há pelo menos 40 anos), enquanto que a cobertura florestal de Tapiraí (~ 50%) está bem acima (Andrén 1994, Pardini et al. 2010, Hanski 2011). Como consequência, o número de espécies florestais em Ribeirão Grande é menor do que nas outras duas paisagens estudadas (Figura 2, Capítulo 3), especialmente para pequenos mamíferos (Pardini et al. 2010). Apesar da pequena expansão da cobertura florestal em Ribeirão Grande, não foi encontrada nenhuma evidência de crédito de espécies de pequenos mamíferos, assim como também não foi observada qualquer relação com a cobertura florestal atual, pois a maioria dos pequenos

mamíferos florestais já foi extinta dos fragmentos florestais dessa paisagem (Pardini et al. 2010). Por outro lado, a riqueza atual de aves florestais nos fragmentos florestais dessa paisagem ainda está refletindo a menor cobertura florestal do passado sugerindo um potencial crédito de espécies. No entanto, em uma paisagem onde tantas espécies florestais já foram perdidas, é possível que somente um pequeno aumento da cobertura florestal não seja suficiente para promover a recolonização de fragmentos florestais por espécies que haviam sido localmente extintas e evitar o desaparecimento de populações em declínio (Hanski 2000, Schrott et al. 2005); ou seja, o crédito espécies pode não ser pago. Por fim, a distribuição de espécies florestais de aves e pequenos mamíferos nos fragmentos florestais de Tapiraí parece ser resultado da interação dos efeitos da redução da cobertura florestal nas taxas de extinção com os efeitos da expansão da cobertura florestal nas taxas de imigração.

Além de mostrar que as paisagens estudadas não apresentavam uma dinâmica florestal linear, a análise do histórico das paisagens, descrita no Capítulo 2, também mostrou que, atualmente, os fragmentos florestais dessas paisagens são mosaicos de florestas com diferentes idades de regeneração. A distribuição de fragmentos com florestas em diferentes estádios de regeneração é resultado do histórico altamente dinâmico dessas paisagens e também do aumento recente da cobertura florestal (em Ribeirão Grande e Tapiraí), pois ambos contribuem com aparecimento de novas manchas florestais. Fragmentos florestais com diferentes idades de regeneração apresentam valores distintos para a conservação da biodiversidade (Barlow et al. 2007, Gardner et al. 2007); de fato os resultados do Capítulo 4 mostraram que a heterogeneidade da vegetação nativa (i.e. idade de regeneração) tem um papel importante na definição de riqueza e abundância de aves em paisagens fragmentadas e que as respostas a essa heterogeneidade são definidas pelos requerimentos de habitat das espécies e dependem da cobertura florestal total da paisagem.

Em geral, espécies que são mais dependentes de florestas maduras são afetadas pela cobertura de florestas mais antigas, enquanto as espécies que são mais flexíveis no uso de florestas em diferentes estádios de regeneração estão mais associadas com as florestas mais jovens e até mesmo com vegetação secundária inicial. No entanto, essas respostas à heterogeneidade da vegetação nativa foram mais claras quando a cobertura florestal da paisagem era alta ou baixa. Em paisagens com alta proporção de cobertura florestal, as taxas de imigração são elevadas em toda a paisagem (por causa da alta conectividade) (Andrén 1994, Pardini et al. 2010) permitindo que os indivíduos de determinada espécie consigam alcançar e usar seus tipos preferidos de floresta onde as taxas de sobrevivência e recrutamento são mais altas. Já em paisagens com níveis intermediários de cobertura florestal, a conectividade é reduzida e a persistência das espécies nos fragmentos florestais deve depender mais da conectividade florestal local (Andrén 1994, Martensen 2008) do que da heterogeneidade das florestas. Em paisagens onde a cobertura florestal total é baixa, as taxas de imigração são extremamente baixas em toda a paisagem (Pardini et al. 2010) e, portanto, a persistência das espécies é novamente dependente da qualidade da vegetação nativa.

Assim, os resultados desta tese sugerem que: (1) a dinâmica de paisagens fragmentadas de Mata Atlântica não é necessariamente um processo linear de perda de cobertura florestal; duas paisagens do Planalto Atlântico de São Paulo parecem estar passando por um processo de transição florestal (i.e. redução seguida de expansão da cobertura florestal); (2) em paisagens onde houve uma inversão dos padrões de dinâmica florestal é preciso entender o potencial tanto para extinção quanto para imigração de espécies, pois estas são as forças que governam mudanças na biodiversidade em escalas de tempo de décadas a milênios e escalas espaciais de local a regionais; e (3) para o pleno entendimento das relações entre paisagens altamente

dinâmicas e as comunidades biológicas que elas sustentam é preciso considerar a heterogeneidade da floresta (i.e. estádios sucessionais).

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RESUMO

Apesar da vasta literatura sobre os efeitos da perda e fragmentação florestal sobre a biodiversidade, poucos estudos incorporaram o aspecto temporal, ou seja, a história da paisagem, em suas análises. No entanto, o histórico de alterações da paisagem é um dos fatores que, ao ser ignorado, pode levar a interpretação errada dos reais efeitos da perda e fragmentação florestal sobre a diversidade de espécies. Assim, o objetivo desta tese foi avaliar os efeitos do histórico de mudança da paisagem sobre aves e pequenos mamíferos na Mata Atlântica. Para atingir este objetivo eu investiguei (1) a dinâmica de três paisagens fragmentadas de Mata Atlântica entre 1960-1980 e 1980-2000, (2) os efeitos da cobertura florestal passada e atual sobre a riqueza de espécies e abundância, considerando ou não a heterogeneidade da vegetação nativa. Para investigar essas questões, foram usados dados de aves e pequenos mamíferos em 53 fragmentos florestais localizados em três paisagens com diferentes proporções de cobertura florestal (10, 30 e 50%) na Mata Atlântica do Planalto Atlântico de São Paulo. Os resultados mostraram que (1) a trajetória da cobertura florestal entre os anos 1960 e 2000 nas três paisagens estudadas foi não-linear e, atualmente, fragmentos florestais consistem de um mosaico de florestas com diferentes idades de regeneração, (2) a existência do débito de extinção e do crédito de espécies, assim como o potencial para o seu pagamento futuro, depende não só da trajetória de cobertura florestal, mas também da cobertura florestal remanescente na escala da paisagem, e (3) a heterogeneidade da vegetação nativa desempenha um papel importante na definição da riqueza de espécies e abundância e que as respostas a essa heterogeneidade são definidas pelos requerimentos de habitat e dependem de cobertura florestal da paisagem.

ABSTRACT

Despite the extended literature on the effects of forest loss and fragmentation on biodiversity, few studies incorporated the temporal aspect, i.e. the history of change of habitat amount and configuration over time at a given landscape, in the analysis. However, ignoring landscape change history might lead to inaccurate interpretation of the impact of forest loss and fragmentation on species diversity. Thus, the aim of this thesis was to evaluate the effects of landscape change history on birds and small mammals in the Atlantic Forest. To achieve this aim I investigated (1) the land-use and land-cover change dynamics in Atlantic Forest fragmented landscapes between 1960s-1980s and 1980s-2000s, (2) the effects of historical and present-day forest cover on species richness and, (3) the potential of explaining species richness and abundance patterns by inclusion or exclusion of present native vegetation heterogeneity in model frameworks. To address these objectives I used data on birds and small mammals in 53 forest fragments from three landscapes with different proportions of forest cover (10, 30 and 50%) in the Atlantic Forest of Brazil. The results showed that (1) forest cover trajectory between the 1960s and 2000s at the three study landscapes was non-linear and that individual forest patches currently consist of a mosaic of different forest age classes, (2) the existence of extinction debt and species credit as well as the potential for their future payment depends not only on forest cover trajectory but also on the present amount of remaining forest cover at the landscape scale, and (3) the heterogeneity within native vegetation plays an important role in defining species richness and abundance in fragmented landscapes and responses to this heterogeneity are defined by habitat requirements and depend on forest cover at landscape scale.