

Milton Cezar Ribeiro

Modelos de simulação aplicados à conservação de paisagens  
fragmentadas da Mata Atlântica brasileira

Simulation models applied to the conservation of fragmented  
landscapes in the Brazilian Atlantic Forest

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Tese apresentada ao Instituto de Biociências  
da Universidade de São Paulo, para a  
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Orientador: Dr. Jean Paul Metzger  
Co-orientadora: Dra. Marie Josée Fortin

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Prof. Dr. Jean Paul Metzger  
Orientador

# Dedicatória 1

Aos meus pais Francisco e Juraci, e irmãos Ari, Lilian e John, por acreditarem que se estava fazendo algo, este algo seria para o bem. Mamãe, agora a senhora é um anjinho, pode ver de uma posição privilegiada o que realmente seu filho andou fazendo. Dai-me Luz!

À Keila Cornetta, co-autora de cada linha deste documento. Aos filhos e anjinhos Pedrinho, Camillo, Mirella e Nicolas: obrigado do papai: conseguimos!

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## Dedicatória 2

Ao Mestre Cosmo, pelas lições que  
a "academia" jamais teria condições  
de me proporcionar.

# Agradecimentos 1

[abre aspas]

Complicado, porém de simples solução! Assim diria o macanudo Tank. Realmente esta parte da tese é a mais injusta, pois é impossível hierarquizar fases, pessoas, contribuições e responsabilidades. Já que o Sr. Alexandre, o ACM da Ecologia da Paisagem se figurou quase que acidentalmente na primeira linha, continuemos com ele então. Desde minha época de ESALQ (90's) tenho me aventurado, interessado e trabalhado com "ciência". Entretanto, foi o Tank que conseguiu me fazer a pensar em ciência como se deve, em especial em ciências biológica e ecológica, mas acima de tudo como Ecólogo de Paisagem. Injusto dizer que esta é minha tese, já que é impossível "untangle" o efeito Martensen de cada capítulo que aqui se apresenta. Foi aprendendo com ele que entendi o verdadeiro espírito de bando que buscamos imprimir diuturnamente no time lepaciano. Impossível negar sua responsabilidade por passamos a lidar com *model selection*, com AIC, e por rascunhar o primeiro curso de modelagem ecológica avançado (que caiu em solo fértil!) do departamento. Se hoje falo (falamos?) sobre "escala" com tanta propriedade, posso (podemos?) culpá-lo nominalmente. Gastar bota e olhar pela janela da L200 é outro ensinamento (quase um segredo!) para se tornar um verdadeiro ecólogo da paisagem (vide ACM). Foi com ele também que descobri a diferença entre o "preço" e o "valor" do gado, quando resolvi me tornar um pecuarista em parceria com papai (chegamos a 15 cabeças!). Poucos conhecem e sabem onde está localizada a Pedra Fundamental da EP (pelo menos no segmento Serra do Paranapiacaba). Ele sabe. Claro que com a boa "energia" de salinas tudo ficou mais fácil, claro e cristalino. Outro dia, enquanto estava em Quebec, assisti dois velhos amigos, veteranos em Ecological Modelling, fundadores desta série de revistas, fazendo algumas sátiras e lembrando velhos tempos. O que mais marcou foi que um dos amigos, já com suas 80 voltas ao mundo, pergunta ao outro: qual o artigo mais importante de nossas vidas? Dr. Sven E. Jørgensen responde, sem vacilar, um título sugestivo que agora me foge à mente. O outro pergunta novamente: quando começamos? Em 1973, e estamos começando a discussão. Logo, meu camarada, meus caros, não se frustre(m). A maioria das boas idéias vão permanecer nesta forma. Algumas delas irão adiante. Tank, o mais importante: anote tudo, mas guarde em um lugar que possa ser resgatado. Hasta la victoria, siempre.

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Orientação dada, lição aprendida. Ao chegar na USP fui naturalmente muito bem recebido (2s para perceberam que eu era do interior), quase que adotado, pelas amigas Dalva, Bernadete e Vanildes. Ali aprendi não apenas como "funcionava" o departamento, mas aprendi também receitas práticas de culinária. Aprendia ali, testava em casa. Keila é quem se beneficiava. As mocinhas me faziam sentir-se em casa. Sem falar na dona Celina, que embora sempre brigasse comigo quando eu usava o chuveiro do 3º andar, sempre me tratou com muito carinho, dispensando seu precioso tempo para trocar algumas palavras, fosse o tema que fosse (ela insiste em dizer que não vai ao forró). A vocês todas sou muito grato.

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[fecha aspas] Deus vos abençoe.

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## Resumo

Uma efetiva ação de conservação depende de um claro entendimento de como as espécies respondem às características ambientais, em particular à cobertura, configuração espacial e qualidade do habitat. No entanto, nem sempre esses dados estruturais da paisagem estão disponíveis em extensão e escala compatíveis com o planejamento ambiental. Ademais, a obtenção de dados empíricos sobre as respostas das espécies à estrutura da paisagem é longa e custosa, o que exige abordagens alternativas para o entendimento destas relações. Esta tese teve dois objetivos principais: i. gerar informações atualizadas sobre as características espaciais dos remanescentes de Mata Atlântica, estimando a quantidade e distribuição de mata existente ao longo de todo o Domínio fitogeográfico, além de avaliar a distribuição da floresta em relação a características do relevo; ii. avaliar, através de modelos de simulação, o efeito da estrutura da paisagem, qualidade de habitat e atributos das espécies, em processos associados à movimentação de aves. A Mata Atlântica é uma das florestas com maior biodiversidade do planeta, mas está também entre as mais ameaçadas, dado o avançado estágio de perda e fragmentação do habitat, o que a coloca entre os principais “hotspots” do planeta. Na primeira parte desta tese, estimamos que a cobertura da Mata Atlântica está entre 12 a 16% (em função de erros de mapeamento), o que representa um valor intermediário em relação às estimativas anteriores (7-8%, ou 22-23%). Os dados de configuração mostram uma situação pouco favorável para conservação das espécies. Mais de 80% dos fragmentos remanescentes são menores que 50 hectares, tamanho extremamente reduzido e incapaz de preservar a maioria das espécies florestais. Ademais, quase a metade da floresta existente está a menos de 100 m de ambientes antropizados, sendo que as áreas mais distantes da borda ficam a aproximadamente 12 km da matriz. Outro fato alarmante é a grande distância média entre os remanescentes de mata (1.440 m), o que torna difícil a movimentação de indivíduos entre fragmentos. A quantidade de unidades de conservação é extremamente reduzida, correspondendo apenas a aproximadamente 1% da Mata Atlântica original, bem abaixo dos 10% sugeridos como mínimo para a manutenção de espécies. As faixas de altitude acima de 1200 m mantêm mais de 20% da cobertura original, enquanto as faixas mais baixas conservam somente 10% da floresta. Algumas diretrizes de conservação e restauração por sub-regiões biogeográficas foram propostas, porém tais regiões apresentaram-se muito extensas para a definição de ações de manejo. Este fato nos levou a sugerir a subdivisão do domínio em 55 novos compartimentos, considerando características de clima e relevo, além dos aspectos biogeográficos. Na segunda parte desta tese, foi desenvolvido o BioDIM (*Biologically scaled dispersal model*), um modelo baseado em indivíduos que simula a movimentação de aves florestais calibradas para espécies encontradas na Mata Atlântica. O BioDIM inclui vários perfis (i.e. sensibilidades) de espécies, permitindo simular desde espécies muito sensíveis (preferência pelo interior dos fragmentos), até espécies moderadamente generalistas (cruzam até 120 m através de ambientes abertos). Além da sensibilidade a ambientes abertos ou de borda, a área de vida (i.e. requerimento de habitat), e o deslocamento máximo diário ou explorativo (i.e. quando o indivíduo está dispersando) também foram considerados. As simulações com o BioDIM foram feitas para 10.000 paisagens simuladas, apresentando grande variação de porcentagem (de 5 a 70%), agregação e qualidade do habitat, o que nos permitiu estudar uma ampla gama de paisagens, o que não seria viável em estudos empíricos. Os resultados sugerem as características das espécies e a estrutura da paisagem foram igualmente importantes para explicar os processos ecológicos analisados, porém a

qualidade de habitat foi pouco influente. A sensibilidade das espécies foi o fator mais importante para explicar a mortalidade de indivíduos e a taxa de dispersão, sendo um fator de efeito secundário para o custo de movimentação e para a taxa de encontros entre indivíduos. A porcentagem de cobertura foi o fator mais influente para custo de movimentação, enquanto para a taxa de encontros o efeito primário foi o tamanho da área de vida. Uma surpresa foi que, ao se avaliar os efeitos para cada perfil de espécie, observou-se que a agregação de habitat foi tão importante quanto a quantidade de habitat para explicar alguns processos, independente da quantidade de habitat, oposto do que tem sido sugerido na literatura. Isto sugere que as variáveis de paisagem são importantes ao longo de todo o processo de conversão do habitat, e devem ser cuidadosamente consideradas na tomada de decisão voltada ao manejo para a conservação de espécies.

## Abstract

Effective conservation actions depend on a clear understanding of how species respond to environmental factors, particularly to the amount of habitat and the spatial arrangement and quality of this habitat. However, landscape structure information is not always available to the extent and scale needed to promote effective conservation planning. Additionally, acquiring biological information of how species respond to landscape structure is particularly expensive in time and money. This thesis has two main goals: i. to generate updated information about the amount and spatial distribution of the remnants of the Brazilian Atlantic Forest, combining information on the remaining forest and landscape relief; ii. untangle the effects of landscape structure, habitat quality, and species traits on ecological processes related to the movements of Atlantic Forest bird species, using simulation models. The Atlantic Forest is one of the most biodiverse regions on the planet, but is also among the most threatened because of the high degree of habitat loss and fragmentation, which confer the status of biodiversity "hotspot" on the region. In the first part of the thesis, I estimated that the remaining Brazilian Atlantic Forest occupies between 12-16% of its original extent (considering mapping errors), which is an intermediate estimate compared to previous ones (7-8%, or 22-23%). The spatial distribution of this forest indicates poor conditions for species conservation. More than 80% of the remaining forest is distributed in patches smaller than 50 ha, which is extremely reduced in size and incapable of preserving most of the forest species. Additionally, half of the remaining forest is less than 100 m distant from any edge, and the farthest point within any forest is about 12 km from the surrounding matrix. Another critical point is the high degree of isolation between patches (mean 1 440 m), which impedes the movement of individuals between forest fragments. Protected areas are extremely small, approximately 1% of the original extent, which is below the 10% suggested as the minimum amount for species maintenance. Higher-altitude areas (> 1200 m) retain more than 20% of the original cover; whereas in lower altitudes, such as from 400 to 800 m, only about 10% of the original forest still exists. Some conservation and restoration measures for the entire region and within biogeographical sub-regions are suggested, but I consider the sub-regions too extensive for defining appropriate management actions. Thus, I refined the subdivision of the entire region into 55 new sub-regions, considering climate and relief characteristics, as well as biogeographical aspects. In the second part of this thesis I developed a program called BioDIM (*Biologically scaled dispersal model*), an individual-based model calibrated to simulate the movement of Atlantic Forest bird species in fragmented landscapes. Five species profiles (i.e., species sensitivity) are already available in BioDIM, which allows us to simulate movements from highly sensitive species (which avoid forest edges), to moderately generalist ones (capable of crossing 120 m of open matrix). Home-range size (a surrogate for habitat amount requirement) and maximum routine and explorative distances per day can also be set. I generated 10 000 simulated landscapes, varying in habitat amount (5 to 70%), aggregation, and quality, which made it possible to evaluate landscape variability to a degree that would not be possible in real conditions. The results suggest that species traits and landscape structure were both important to explain the ecological processes, but habitat quality contributed relatively little. Species sensitivity was the prime factor in explaining dispersal rate and mortality, and had a secondary effect on movement cost and encounter rate. Habitat amount was the most influential factor to explain movement cost, and home-range size was the prime factor for encounter rate. Astonishingly, we

observed that, within species profiles, habitat aggregation was as important as habitat amount to explain several ecological processes, independently of the percentage of forest amount. This is the opposite of what has been observed in the literature. These results indicate that landscape variables are important for all habitat conversion processes, and that they must be carefully considered in decision-making for species conservation management.

# **CAPÍTULO 1**

## **INTRODUÇÃO**

# CAPÍTULO I

## 1.1 – Introdução

A estrutura da paisagem influencia a distribuição e a conservação da biota, e desta maneira, tem sido usada como indicador (em inglês "surrogate") de biodiversidade em diferentes etapas do planejamento voltado à conservação, especialmente na seleção de áreas prioritárias para restauração e conservação (Williams et al., 2002; Lindenmayer et al., 2008; Metzger et al., 2008). Regras gerais têm sido comumente aplicadas considerando o arcabouço conceitual da Ecologia de Paisagens, como, por exemplo, a conservação dos maiores fragmentos, com elevada conectividade estrutural (Martensen et al., 2008), seja por corredores florestais ou por trampolins ecológicos (Boscolo et al., 2008), ou o aumento da permeabilidade da matriz que circunda os fragmentos de interesse (Antongiovanni e Metzger, 2005; Umetsu et al., 2008; Pardini et al., 2009). Também tem sido evidenciada a necessidade de seleção de alvos para a preservação que contemplem, tanto quando possível, uma grande variedade de tipos de habitat e uma grande heterogeneidade natural (Forman e Collinge, 1997; Haila, 2002; Fischer et al., 2006; Lindenmayer et al., 2006; Metzger, 2006). Apesar de algumas limitações, tais como não considerar a percepção distinta dos elementos da paisagem pelas diferentes espécies, parâmetros da estrutura da paisagem podem ser particularmente úteis para estabelecer algumas regras gerais para a conservação onde inventários em larga escala não estão disponíveis e os padrões de distribuição da biodiversidade em escalas amplas não são conhecidos (Fairbanks et al., 2001; Uehara-Prado et al., 2009), como é o caso da maioria das áreas tropicais.

A Mata Atlântica é uma das maiores florestas tropicais das Américas, cobrindo uma área de 150 milhões de hectares, estando imersa em condições ambientais bastante heterogêneas. Sua amplitude latitudinal é da ordem de 29 graus, estendendo-se por regiões tropicais e sub-tropicais. A amplitude longitudinal também é importante, produzindo diferenças nas composições florestais como resposta à diminuição da precipitação, que é menor no interior. Estas características têm proporcionado condições para a ocorrência de um elevado grau de diversidade e endemismo, resultando em mais de 20 000 espécies de plantas, 261 espécies de mamíferos, 688 espécies de aves, 200 de répteis e 280 de anfíbios, sendo que muitas espécies ainda estão por ser cientificamente descritas (Goerck, 1997; Mittermeier et al., 1999; Silva e Casteleti, 2003), o que pode representar algo entre 1 a 8% das espécies do planeta.

Contudo, os remanescentes de Mata Atlântica são em geral de tamanho pequeno (<50 ha, Ribeiro et al. 2009), isolados uns dos outros, além de serem compostos por florestas secundárias em estádios iniciais e intermediários de regeneração (Viana et al., 1997; Metzger, 2000; Metzger et al., 2009; Ribeiro et al., 2009). Os poucos grandes fragmentos remanescentes estão localizados em terrenos montanhosos, onde a ocupação humana foi menos intensa (Silva et al., 2007; Tabarelli et al., 2010; Ribeiro et al., aceito). O elevado grau de fragmentação da Mata Atlântica tem levado boa parte das espécies desta região a ser considerada ameaçada de extinção; como é o caso de mais de 70% das 199 espécies de aves endêmicas do bioma (Parker et al., 1996; Stotz et al., 1996; Goerck, 1997). Nestas florestas naturalmente heterogêneas e altamente diversas, que comportam muitas espécies ainda desconhecidas (Lewinsohn e Prado, 2005), inventários de biodiversidade são complexos, caros e demandam muito tempo (Gardner et al., 2008; Uehara-Prado et al., 2009). Apesar da grande quantidade de informações biológicas levantadas nas décadas mais recentes (Silva e Casteleti, 2003; Silva et al., 2004), a falta de protocolos

padronizados para amostragens, bem como a pobre distribuição espacial dos locais de amostragem, têm perpetuado significantes lacunas de informação, fazendo particularmente difícil o uso desse conhecimento para o planejamento voltado à conservação da biota (Margules e Pressey, 2000; Groves et al., 2002). Em escalas locais (i.e. poucos km<sup>2</sup>), uma quantidade suficiente de dados biológicos pode ser encontrada ou coletada, entretanto grandes dificuldades surgem quando o foco de planejamento alcança áreas mais extensas. Além disto, mesmo nos locais bem estudados, a quantidade de informação disponível ainda é insuficiente para dar suporte adequado ao planejamento, sendo que nestes casos os chamados "surrogates" estruturais, tais como parâmetros da estrutura de paisagens, são as alternativas mais viáveis, e, em muitos casos a única viável (Metzger et al., 2008; Banks-Leite, 2009; Martensen et al., em revisão). Neste contexto, a quantidade de habitat e a fragmentação, duas variáveis consideradas fatores-chave para a conservação da biodiversidade (Wilcox e Murphy, 1985; Fahrig, 2003; Martensen, 2008), são fundamentais no planejamento e no manejo da paisagem para a conservação biológica.

Apesar do potencial do uso destes parâmetros para o planejamento voltado a conservação biológica, até pouco tempo atrás eram raras as informações sobre a estrutura da paisagem da Mata Atlântica, sendo este tipo de informação apenas disponível para regiões pequenas (<300.000 ha, Jorge e Garcia, 1997; Viana et al., 1997; Ranta et al., 1998). O único dado disponível para toda a Mata Atlântica era a porcentagem de hábitat remanescente, sendo que mesmo neste caso existia ainda uma grande discrepância entre as estimativas devido à utilização de diferentes métodos (p.ex., 7–8% de floresta remanescente de acordo com a SOS Mata Atlântica/INPE, 1993, 2000 e Galindo-Leal e Câmara, 2003; 10,6% de acordo com SOS Mata Atlântica/INPE, 2008; e 22% de acordo com IESB et al., 2007; Cruz e Vicens, in press).

Informações sobre a distribuição do tamanho de fragmentos, áreas submetidas a efeitos de borda, conectividade, grau de isolamento, importância dos pequenos fragmentos no isolamento, e áreas protegidas são essenciais para um bom planejamento para a conservação, tanto em se pensando em sub-divisões macro-regionais da Mata Atlântica, quanto para a Mata Atlântica como um todo.

Sub-divisões do espaço podem ser determinadas em diferentes escalas espaço-temporais (Fortin e Dale, 2005; Wagner e Fortin, 2005). Desta forma, a escolha adequada da escala de análise, ou mesmo da forma de partição do espaço para fins de estudos envolvendo índices de paisagem, é uma fase fundamental das avaliações (Birch et al., 2007). As regiões biogeográficas e as zonas de transição definidas por Silva e Casteleti (2003) têm um forte embasamento empírico, tanto do ponto de vista biológico (aves, borboletas e primatas), como ambiental (dados de clima e relevo). Apesar disso, considerando a extensão e a heterogeneidade da Mata Atlântica, a subdivisão em apenas oito grandes regiões dificulta o processo de definição de ações adequadas de manejo de paisagem voltado à conservação. Ademais, o desmatamento é reconhecido como um processo que não segue padrões aleatórios (Seabloom et al., 2002), pois fatores como a fertilidade do solo, os interesses econômicos, a proximidade com centros urbanos e estradas afetam os processos de perda e fragmentação do habitats (Laurance et al., 2001; Gardner et al., 2009). Na Mata Atlântica, os processos de desmatamento e regeneração são notadamente influenciados pela topografia, uso da terra e áreas urbanas (Silva et al., 2007; Teixeira et al., 2009; Freitas et al., 2010; Ribeiro et al., aceito). Desta forma, além da elevada complexidade e variabilidade natural da Mata Atlântica, se sobrepõem a esta um padrão particular de perda e fragmentação da florestal, em grande parte regida pelo relevo e ocupação

pré-existente, que devem também, ser consideradas para um bom planejamento de ações para a conservação do bioma.

O planejamento pode acontecer em diversas escalas, variando desde a de micro-habitat, até as mais amplas, continentais ou globais, passando por escalas intermediárias, como paisagem ou regional (Fortin e Dale, 2005; Wagner e Fortin, 2005). Todas são importantes, entretanto a escala de paisagem é uma das mais relevantes, pois é nesta escala que a maior parte das ações humanas ocorre (Lindenmayer et al., 2008). Desta forma, o entendimento dos processos ecológicos e dos seus condicionantes na escala da paisagem é essencial para um bom planejamento.

Por outro lado, a obtenção de dados biológicos para paisagens com diferentes proporções de cobertura e agregação de habitat é muito custosa, quando factível, uma vez que as espécies respondem de forma particular a tais variáveis (Williams et al., 2002; Lindenmayer et al., 2008). A qualidade de habitat é outro fator importante, o que traz ainda maior complexidade aos estudos. Desta forma, o entendimento das influências das variáveis de cobertura, configuração e qualidade de habitat sobre as respostas das espécies e os processos ecológicos não é uma tarefa trivial, principalmente devido às múltiplas interações entre estas variáveis no espaço e no tempo. Frente a este cenário, o uso de simulações *in silico* (em computadores) tem sido uma alternativa para se lidar com problemas desta magnitude de complexidade. Modelos baseados em indivíduos (do inglês *Individual Based Model, IBM*) são um tipo particular de simulação que permite incorporar variabilidade no nível do indivíduo, enquanto se estuda padrões que emergem em níveis hierárquicos superiores (With e Crist, 1995; Neel et al., 2004; Riitters et al., 2009). Isto permite estudar tanto influências no sentido topo-base (*top-down*; paisagem influenciando espécies e indivíduos), como também base-topo (*botton-up*, variabilidade medida no nível do

indivíduo influenciando processos na escala da paisagem), permitindo, desta forma, identificar propriedades emergentes entre escalas (DeAngelis e Mooij, 2005; Bridle et al., 2010). Todavia, a grande maioria dos *IBM* são calibrados para resolver questões associadas a ecossistemas da América do Norte e Europa, com poucos estudos desta natureza dedicados ao entendimento de problemas tropicais (Drinnan, 2005). O uso de *IBM* para regiões tropicais requer um balanço entre simplificação e performance, tendo-se em vista torná-los mais realistas, sem perder sua capacidade de generalização e aplicação (Ewers e Didham, 2006; Moore et al., 2008; Clobert et al., 2009; Boyle e Smith, 2010; Webb et al., 2010). Assim, o conhecimento mais detalhado sobre como diferentes processos ecológicos e espécies com diferentes características ecológicas são influenciados por múltiplos fatores inter-relacionados (*confounding factors*; *sensu* Ewers e Didham, 2006) é fundamental para o melhor entendimento da dinâmica e do funcionamento de paisagens fragmentadas e degradadas dos trópicos.

## **1.2 - Objetivos**

A tese foi estruturada em seis capítulos, sendo um introdutório, quatro capítulos de tópicos abordados ao longo do doutorado, apresentados em forma de manuscritos ou artigos publicados, além de um capítulo de conclusão geral. Os capítulos com os principais resultados da pesquisa (cap. II a V) estão sub-divididos em dois temas principais: (a) Mata Atlântica - distribuição espacial passada e presente, influência do relevo e proposta de sub-divisão do espaço biogeográfico; (b) Modelos espacialmente explícitos para avaliar a influência da estrutura da paisagem, da qualidade do habitat e dos atributos das espécies em processos ecológicos obtidos para espécies simuladas. A seguir são apresentados os objetivos dos capítulos II a V.

**1.2.1. - Capítulo II: *The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation***

A finalidade deste capítulo foi a de apresentar uma análise descritiva detalhada da Mata Atlântica Brasileira, considerando sua cobertura original e atual, estimando-se o quanto sobrou de floresta, avaliando-se como os remanescentes estão distribuídos, além de apresentar implicações do presente estudo para sua conservação. Utilizou-se o mapeamento da SOS Mata Atlântica/INPE de 2005, sendo avaliados principalmente os ambientes florestais. A análise foi realizada em duas escalas: 1. Mata Atlântica Brasileira como um todo; 2. Dentro de cada sub-região biogeográfica e zonas de transição proposta por Silva e Casteleti (2003). A cobertura remanescente foi estimada para todo o Domínio e para cada sub-região, sendo considerados remanescentes <100 ha que anteriormente eram excluídos nas análises feitas pela SOS Mata Atlântica/INPE (2000). Os remanescentes foram organizados por classes de tamanho, sendo estimado o número de remanescentes e a quantidade de floresta acumulada em cada classe. O mapa de remanescentes foi sobreposto a um mapa de distâncias a partir das bordas, sendo avaliado a quantidade de mata sujeita a efeitos de borda para faixas de distâncias variáveis. Foram também calculadas métricas de conectividade estrutural e funcional para diferentes escalas (i.e. distâncias entre fragmentos). Avaliou-se também o grau de isolamento dos remanescentes e a importância dos fragmentos pequenos na manutenção da conectividade entre os maiores. Foi feito ainda o levantamento das áreas protegidas dentro das Unidades de Conservação de proteção integral, bem como a distância dos demais remanescentes a estas UCs. Aspectos relacionados ao grau de degradação, e as estratégias para conservação foram discutidas para a Mata Atlântica como um todo, bem como para cada sub-região analisada. O artigo foi publicado na fascículo especial da revista “Biological Conservation” sobre a Mata Atlântica (Ribeiro et al., 2009).

### **1.2.2. - Capítulo III: *The Brazilian Atlantic Forest: a shrinking biodiversity hotspot***

Um dos mais importantes resultados obtidos com os estudos conduzidos durante o desenvolvimento do Capítulo II é que a Mata Atlântica não está distribuída de forma uniforme entre as regiões biogeográficas, e nem os padrões dos remanescentes são homogêneos. Além disto, em virtude da grande extensão e elevado grau de complexidade da Mata Atlântica, consideramos importante sub-dividir as oito regiões biogeográficas e zonas de transição em sub-regiões menores, mais homogêneas e mais adequadas para o planejamento e para a seleção de áreas para conservação ou restauração. Também consideramos que dado a extensão da Mata Atlântica, o relevo é um fator importante a ser considerado. Desta forma, desenvolvemos este terceiro capítulo para atender os seguintes objetivos: (a) propor uma sub-divisão da Mata Atlântica considerando as regiões biogeográficas (Silva e Casteleti, 2003), combinando-se dados bioclimáticos (Wordclim 1.4; Hijmans et al. 2005) e de relevo (SRTM/NASA; <http://www2.jpl.nasa.gov/srtm>), considerando 2.650 sub-bacias de 5ª ordem (Pfastetter, 1987); (b) sobrepor a distribuição original e atual dos remanescentes florestais com parâmetros geomorfométricos derivados da altimetria (posição de relevo, elevação e orientação da vertente). Por se tratar de um capítulo convidado para compor um livro sobre *Hotspots* a ser publicado pela editora *Springer*, incluímos também uma síntese dos principais resultados obtidos no capítulo II no presente capítulo. O manuscrito foi aceito com revisões menores e encontra-se em fase de revisão por parte dos editores.

### **1.2.3. - Capítulo IV: *Assessing simulated bird species responses to habitat amount, aggregation, and quality: a spatially explicit model***

A literatura aponta que não somente a cobertura e a configuração das florestas são importantes para estudos de paisagens fragmentadas, sendo também essencial considerar atributos das espécies, bem como incorporar a qualidade de habitat durante as análises. Todavia, a realização de estudos empíricos envolvendo diferentes padrões de cobertura, agregação e qualidade de habitat, além de se considerar espécies com diferentes atributos é extremamente custosa. Por esta razão, modelos de simulação em computador têm sido desenvolvidos para se lidar com questões complexas deste tipo. Este capítulo é dedicado a apresentar um simulador de movimentação de indivíduo calibrado para aves florestais da Mata Atlântica. O modelo utiliza os princípios de *Individual Based Model* (IBM), e é denominado BioDIM (*Biologically scaled Dispersal Model*). O BioDIM permite investigar efeitos independentes e interações da estrutura da paisagem, qualidade de habitat e diversos atributos de espécies simuladas (sensibilidade à fragmentação, requerimento de habitat, movimentação diária e movimentação durante a dispersão). O simulador utiliza um modelo plenamente contínuo, calibrado com funções de sensibilidade à posição (interior, borda ou matriz), permitindo simular espécies com diferentes capacidades de uso de ambientes florestais (preferência pelo interior dos remanescentes, utilizando ou não corredores, e com capacidades distintas de cruzar matrizes abertas). O tempo de simulação (em dias) é definido pelo usuário. Na versão 1.0 do BioDIM, as seguintes variáveis-resposta são mensuradas para cada paisagem ou simulação: mortalidade, porcentagem de dispersão, custo de movimentação e variabilidade de movimentação. Como o objetivo deste capítulo é o de apresentar o BioDIM, simulamos somente o perfil de espécie dedicado à espécies tolerantes a borda e que utilizam corredores < 60 m de largura. O BioDIM permite a realização de diversos experimentos para um melhor entendimento dos fatores que influenciam a movimentação de

indivíduos em paisagens fragmentadas. Desta forma, permite um melhor entendimento das relações entre padrões e processos ecológicos observáveis em paisagens fragmentadas, permitindo-se um melhor desenvolvimento teórico e prático relacionado ao planejamento e manejo de paisagens reais em ambientes tropicais. Este quarto capítulo foi apresentado durante a 9ª conferência da *International Society for Ecological Modelling (ISEM09)*, Quebec-CA, sendo convidado para compor a edição especial da revista *Ecological Modelling* sob o tema "Static and dynamic modelling for habitat responses within fragmented landscapes". O manuscrito foi submetido e encontra-se em fase de revisão.

#### **1.2.4. - Capítulo V: *Untangling the effects of landscape structure, habitat quality, and species traits on ecological processes***

A cobertura, agregação, qualidade de habitat e atributos das espécies são fatores que afetam a persistência de populações em paisagens fragmentadas. Entretanto poucos estudos avaliaram todos esses efeitos de forma combinada. Este capítulo foi dedicado a simular a movimentação de indivíduos de diferentes espécies utilizando-se, para isso, um modelo espacialmente explícito orientado a indivíduo (BioDIM), apresentado no capítulo anterior. Utilizou-se análises de sensibilidade (*Standardized Regression Coefficient*) para estimar a contribuição relativa da estrutura da paisagem, da qualidade de habitat e dos atributos das espécies, sendo avaliados seus efeitos em cinco processos ecológicos: mortalidade, porcentagem de dispersão, custo de movimentação, taxa de encontro de indivíduos (encontro macho-fêmea), e variabilidade de movimentação. Num primeiro momento avaliou-se o efeito dos três grupos de fatores (estrutura da paisagem, qualidade de habitat e atributos das espécies) sobre a síntese dos cinco processos avaliados. Num segundo momento, avaliou-se o efeito relativo de nove variáveis explanatórias

representativas dos grupos de fatores (estrutura da paisagem; qualidade de habitat; atributo das espécies) para explicar individualmente cada um dos cinco processos ecológicos. Posteriormente foi realizada uma análise para cada um dos perfis de espécies (n=5), considerando oito variáveis explanatórias. Por fim, avaliou-se também se a magnitude dos efeitos e se estes foram constantes ou se apresentaram gradiente, em se considerando a sensibilidade das espécies. O presente manuscrito está formatado para ser submetido à revista *Ecology Letters*.

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# CAPÍTULO II

## **The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation**

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# **The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation**

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## Abstract

The neotropical Atlantic Forest supports one of the highest degrees of species richness and rates of endemism on the planet, but has also undergone a huge forest loss.

5 However, there exists no broad-scale information about the spatial distribution of its remnants that could guide conservation actions, especially when systematic biodiversity data are not available. In this context, our objectives were to quantify how much of the forest still remains, and analyze its spatial distribution. We considered the entire Atlantic Forest, and eight sub-regions, defined according to species distribution. The results revealed a serious situation: more than 80% of the fragments are <50 ha, almost 10 half the remaining forest is <100 m from its edges, the average distance between fragments is large (1 440 m), and nature reserves protect only 9% of the remaining forest and 1% of the original forest. On the other hand, our estimates of existing Atlantic Forest cover were higher than previous ones (7-8%), ranging from 11.4 to 16%. 15 The differences among estimates are mainly related to our inclusion of intermediate secondary forests and small fragments (<100 ha), which correspond to approximately 32-40% of what remains. We suggest some guidelines for conservation: i) large mature forest fragments should be a conservation priority; ii) smaller fragments can be managed in order to maintain functionally linked mosaics; iii) the matrix surrounding 20 fragments should be managed so as to minimize edge effects and improve connectivity; iv) restoration actions should be taken, particularly in certain key areas. The clear differences in the amount remaining and its spatial distribution within each sub-region must be considered when planning for biodiversity conservation.

*Key-words:* Atlantic Forest, conservation, landscape ecology, fragment size,

25 connectivity, matrix influence, edge effects, core area.

## 1. Introduction

Landscape structure parameters have been recognized as useful biodiversity surrogates, and are used in different steps of conservation planning (Williams et al., 2002; Lindenmayer et al., 2008). Some rules of thumb are employed within a landscape perspective, such as the conservation of large fragments with high structural connectivity, whether provided by corridors, stepping stones, or high permeability of the surrounding matrix (Umetsu and Pardini, 2007; Umetsu et al., 2008; Uezu et al., 2008; Fonseca et al., 2009; Pardini et al., 2009; Vieira et al., 2009); as well as targeting the preservation of as much as possible of all natural landscape heterogeneity (Forman and Collinge, 1997; Haila, 2002; Fisher et al., 2006; Lindenmayer et al., 2006; Metzger, 2006). Although they have some limitations, such as not considering how different species perceive features of the landscape (e.g., functional connectivity), landscape structure parameters can be particularly useful to establish general guidelines for conservation planning where broad-scale species inventories and biodiversity distribution patterns are still unavailable (Fairbanks et al., 2001; see Uehara-Prado et al., 2009 for an example of ecological indicators), which is the case for most tropical areas.

The Atlantic Forest was one of the largest rainforests of the Americas, originally covering around 150 million ha (Figure 1), in highly heterogeneous environmental conditions. Its latitudinal range is around 29°, extending into tropical and subtropical regions. The wide longitudinal range is also important in producing differences in forest composition, because of the decreased rainfall away from the coasts. Coastal areas receive large amounts of rain year-round, reaching more than 4 000 mm, while inland forests receive around 1 000 mm/year (Câmara, 2005). These geographical characteristics, combined with the large altitudinal range, have favored high diversity

and endemism, including more than 20 000 species of plants, 261 species of mammals, 688 species of birds, 200 species of reptiles, 280 species of amphibians, and many more species that still require scientific description (Goerck, 1997; Mittermeier et al., 1999; Silva and Casteleti, 2005). The Atlantic Forest flora and fauna may include 1 to 8% of  
55 the world's total species (Silva and Casteleti, 2005).

Most of the remaining Atlantic Forest exists in small fragments (<100 ha; Ranta et al., 1998) that are isolated from each other and are composed by second-growth forests in early to medium stages of succession (Viana et al., 1997; Metzger, 2000; Metzger et al., 2009). The few large fragments survived in locations where the steep  
60 terrain made human occupation particularly difficult (Silva et al., 2007). This present-day fragmentation has led to a large proportion of the forest's vast biodiversity being threatened to extinction; for example more than 70% of the 199 endemic bird species are threatened or endangered (Parker et al., 1996; Stotz et al., 1996; Goerck, 1997).

In these heterogeneous and highly diverse forests, which still hold many still-  
65 unknown species (Lewinsohn and Prado, 2005), biodiversity inventories are complex, expensive and time-consuming (Gardner et al., 2008; but see Uehara-Prado et al., 2009). Despite the large amount of biological data generated in the Atlantic Forest region in recent decades (Silva et al., 2004; Silva and Casteleti, 2005), the lack of standardized inventory protocols and sampling efforts with poor spatial distribution have resulted in  
70 significant geographical data gaps, making it particularly difficult to use this information for conservation planning by the usual methods (see Margules and Pressey, 2000; Groves et al., 2002). At local scales, enough biological data is available for some areas to support conservation plans, but great difficulties arise in planning conservation actions for large regions. Moreover, most of the data are insufficient to properly support  
75 conservation planning, and thus, abiotic surrogates such as landscape structure

parameters are in most cases the only alternative (Metzger et al., 2008). In this context, the amount of habitat and fragmentation, which are key factors for biodiversity conservation (Wilcox and Murphy, 1985; Fahrig, 2003), are important variables to be considered in landscape planning and management for biodiversity conservation.

80           Despite the potential of using landscape structure parameters in conservation planning, information on landscape structure in the Atlantic Forest is only available for small regions (< 300 000 ha, Jorge and Garcia, 1997; Viana et al., 1997; Ranta et al., 1998). The only data available for the entire Atlantic forest region is the percentage of the remaining forest, but even in this case there are huge discrepancies among the  
85 different methods employed (e.g., 7-8% of the forest remains according to SOS Mata Atlântica/INPE, 1993, 2002 and Galindo-Leal and Câmara, 2003; 10.6% according to SOS Mata Atlântica/INPE, 2008; and 27% according to IESB et al., 2007; Cruz and Vicens, in press).

          We analyzed for the first time the spatial distribution of all the remaining  
90 Atlantic Forest, in order to provide precise information about how much forest is left and how this forest is spatially arranged. We calculated parameters such as fragment size, amount of edge area, isolation, structural connectivity, and distance to conservation reserves of all existing fragments of the Atlantic Forest region (ca. 245 000 fragments). These spatial analyses were performed on a multi-scale approach  
95 (Urban, 2005), in order to facilitate the biological interpretation of the landscape indices (within a perspective of *ecologically scaled landscape indices*; following Vos et al., 2001). This approach ensures a variety of biological behaviors, considering for example a wide range of sensitivity to gap-crossing abilities and to edge influences. Additionally, to refine our understanding about the Atlantic Forest spatial structure, considering its  
100 different regional contexts, we performed the same analyses dividing the region by

biogeographical sub-regions (BSRs). The implications of the observed spatial patterns are discussed with regard to future conservation and restoration priorities for the entire Atlantic Forest in Brazil.

## 105 **2. Methods**

### *2.1. Study region and biogeographical sub-regions (BSRs)*

The Brazilian Atlantic Forest originally extended from 3°S to 31°S, and from 35°W to 60° W, covering 148 194 638 ha (Figure 1), mainly extending along the Brazilian coast (92%), but also reaching into Paraguay (Cartes and Yanosky, 2005; Huang et al., 2007) and Argentina (Giraudó, 2005). The forest encompasses 17 Brazilian states, and is narrow in the north and wider in the south. It has complex boundaries with other types of formations such as the pampas in the south and the drier inland formations, such as the Bolivian Chaco and the Pantanal (west-southwest), the Cerrado (South American savanna, west) and the Caatinga (northwest).

115 We analyzed 139 584 893 ha (~94%) of the original Atlantic Forest region, based on the extent defined in Brazilian legislation (Federal Decree No. 750/93 and Atlantic Forest law No. 11 428, of December 22, 2006), and slightly expanded according to the delimitation of BSRs by Silva and Casteleti (2005). The geographical, historical and relief complexities observed in the Atlantic Forest region generate a scenario in which species are not homogeneously distributed, but rather are grouped in different BSRs (Silva et al., 2004; Silva and Casteleti, 2005). In order to properly approach this complexity, we chose to conduct our analyses at two different geographical scales: i) the entire Atlantic Forest; and ii) by the BSRs proposed by Silva and Casteleti (2005). These authors defined five centers of endemism (Bahia, Brejos Nordestinos, Pernambuco, Diamantina and Serra do Mar) and three transitional regions

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(São Francisco, Araucaria and Interior Forests), based on bird, butterfly and primate distributions (Figure 1). For general descriptions we used all eight BSRs. For structural landscape analyses, the Brejos Nordestinos sub-region (1 251 783 ha) was excluded because of its naturally scattered distribution and relatively small area (<1% of the area studied). A detailed spatial analysis is thus provided for seven different BSRs (Table 1). Within these regions, the Interior is the largest (49%), followed by the Araucaria (17%), and then by the Bahia, Serra do Mar and São Francisco regions with about 8-9% each.

## 2.2. Forest cover

Forest cover analyses were based on an Atlantic Forest vegetation map (reference year 2005; [www.sosma.org.br](http://www.sosma.org.br) and [www.inpe.br](http://www.inpe.br)) produced by the SOS Mata Atlântica/INPE (2008). The map was projected to the Albers projection and the South America 1969 datum to assure accurate area calculation for large regions such as this one. These institutions have been mapping the Atlantic Forest cover since 1986, at 5-year intervals (SOS Mata Atlântica/INPE, 2002 and 2008). The map used for the analysis was constructed by visual interpretation of TM/Landsat-5 (TM) and CCD/CBERS-2 (CCD) images from 2005 (with a few images from 2004 when cloud cover did not allow image acquisition in 2005), viewed as color compositions on a digital orbital image mosaic with bands TM3 (red region in the blue filter), TM4 (near infrared, NIR, in the red filter) and TM5 (short wavelength infrared, SWIR, in the green filter) for Landsat-5, CCD-2 (green in blue filter), CCD-3 (red in green filter) and CCD-4 (NIR in red filter) for CBERS-2. This map shows three main vegetation classes, grouping several physiognomically and floristically distinct forests: mangroves, “restinga” (lowland forests on sandy soils near the coast) and forests (including coastal forests, *Araucaria* mixed forests, and semi-deciduous forests; Oliveira-Filho and Fontes, 2000). The three

classes were included in the forest cover analysis, but mangroves and restingas were not considered in the configuration analyses because of their small spatial extent (~4% of the remaining area) and biological differences. The mapping scale was 1:50 000 in vector format, which was then converted to raster, with a 50 m spatial resolution (60 000 x 48 000 cells), in order to improve metrics computation.

The “forest” class included secondary forests in intermediate to advanced successional stages. The distinction between old growth and secondary forest is particularly difficult for the entire Atlantic Forest region because information about forest age is very scarce and available only at local scales. The old history of disturbances in the region ended in a lack of good age estimation, especially for old forests which regenerated before the 1970’, when satellite images started to be available. We are aware that forest definition could originate differences in forest cover and configuration results, and thus we opted to consider as forest areas which have an arboreal structure as seen by TM and CCD orbital images. This definition corresponds to forests > 15 years of regeneration, with dense arboreal vegetation and canopy height >10 m (Teixeira et al., 2009).

### 2.3. *Map quality*

At the end of the visual classification procedure, the preliminary thematic map was reviewed by vegetation experts from each Brazilian state located in the Atlantic Forest region. Fieldwork was also conducted in order to resolve questions of interpretation.

To assess the accuracy of the final map, we superposed the SOS Mata Atlântica map on ten reference cover maps (Table 1S), which were produced with high spatial accuracy (scales ranging from 1:10 000 to 1:50 000) and extensive field checking. Of these maps, eight were available for the state of São Paulo (covering areas from 10 400

to 24 800 000 ha), one for the state of Minas Gerais (143 900 ha), and another for the state of Paraná (748 500 ha). The ten selected regions have very different reliefs and climates, but were limited to the forest pattern observed in southeast Brazil. As a consequence, our accuracy analysis may be biased towards the patterns that occur in this area. We estimated the Kappa (Landis and Kock, 1977) and the G (percentage of pixels correctly classified) statistics to check map accuracy (Table 1S). The Kappa values ranged from 0.167 to 0.818 (mean= 0.486). The SOS Mata Atlântica map showed low accuracy for only the region of one reference map. For the other nine reference maps the analyzed map was classified as acceptable (n= 3), intermediate (n= 4), high (n= 1) and very high (n= 1) accuracy (according to the categories defined by Landis and Kock, 1977). To arrive at an overall statistic, we calculated a Kappa value weighted for the area of the reference maps, and obtained K= 0.4 (i.e., acceptable according Landis and Kock, 1977 classification).

We also estimated the errors of commission and omission, to capture the bias of our map. The commission error ranged from 0.2% to 8% (mean= 3%), with an area weighted mean of 2.9%. The omission error ranged from 3% to 89% (mean= 49%), with an area weighted mean of 37%. These results indicate that the map used for the analysis tends to underestimate the actual remaining vegetation. This underestimation may occur because (1) early successional stages are poorly mapped and (2) it is difficult to correctly map the small fragments (<30 ha). We also noticed that for some regions, the map does not accurately show remnants on slopes, which resulted in some confusion between “forest” and *Eucalyptus ssp.* plantations or early successional vegetation stages. Riparian forests were also poorly mapped, either because of their narrow shape or their overall small area. Despite these errors, the overall accuracy (G) ranged between 76 and 97%, which is an acceptable rate for maps at this large regional scale.

#### 2.4. Forest configuration indices

Forest cover and configuration metrics were computed for the entire study region and for each of the different BSRs using GRASS 6.3 (Neteler and Mitasova, 2008; 205 <http://www.grass-gis.org>), with some procedures done on ArcGis 9.2 (Esri, 2007) and Erdas 9.1 (Leica, 2006). The R language version 2.7.1 (R Development Core Team, 2008) was used for all data processing. We selected five configuration metrics that could be easily employed in conservation planning: fragment size, edge area, connectivity, isolation and distance to nature reserves (Table 2). For edge area (and core 210 area), connectivity and isolation, we performed a multi-scale approach (Urban, 2005) in order to consider different species' perception of landscape structure.

Fragment size distributions allowed us to account the forest amount and number of fragments for different classes of size (Table 2). Edge area was computed as the amount and percentage of forest area submitted to edge effects for different edge 215 widths. All forest pixels with distances higher than an edge width level (Table 2) were classified as core area.

Connectivity metrics were computed based on the graph theory (Urban and Keitt, 2001; O'Brien et al., 2006; Minor and Urban, 2007; Fall et al., 2007), which is a method of measuring the functionally connected clump of fragments based on some 220 simple linkage rules (Urban and Keitt, 2001). As linkage rules for our analysis we considered the distance among fragments reflecting different gap-crossing capacities (Martensen et al., 2008; Boscolo et al., 2008; Awade and Metzger, 2008; Table 2). The connectivity index was then calculated as the sum of the areas of clumped fragments, which can be interpreted as the functional available area (Martensen et al., 2008; 225 Metzger et al., 2009). After generating connectivity maps, we computed the expected

cluster size as the mean clump size for each functional distance. The highest cluster size was also identified for the entire study region, as well as for each sub-region and for each functional distance.

To estimate mean isolation, we proposed an index adapted from the “Empty  
230 Space Function”, which is a spatial point pattern analysis (Baddeley and Turner, 2005; Fortin and Dale, 2005), that represents the mean isolation of a given random pixel from any forested one. We randomized 1 000 000 points over the entire Atlantic Forest region, and a distance map was generated for all fragments. We then successively removed the smaller fragments in several steps (Table 2) and computed the distance to  
235 the nearest forest in each step. These values represent the isolation of forest areas, but are particularly useful in providing insights about the importance of the smaller fragments (or the capacity of the species to use these small fragments as stepping stones; Uezu et al., 2008) in this isolation estimate.

To assess the amount of Atlantic Forest protected by the Brazilian Protected  
240 Area network, we superposed on the remnants map, a map of *Nature Reserves* (strictly protected areas classified as “*proteção integral*”; MMA, 2007), which comprises 249 reserves (2 260 350 ha). The distance from nature reserves was also calculated for each forest pixel (see Table 2 for classes of distance from reserves).

## 245 **3. Results**

### *3.1. Forest cover*

Of the total mapped area (139 584 893 ha), 15 719 337 ha of forest (11.26%) and 658 135 ha (0.47%) of restinga and mangrove vegetation (Table 3) still remain. Thus, 88.27% of the original Atlantic Forest has been lost, and only 11.73% of the original  
250 vegetation (16 377 472 ha) remains (Figure 2 and Figures 1S[a-g]). Considering the

estimated commission and omission errors for the map analyzed (Table 1S; see *Map quality* section for details), we consider that the actual remaining vegetation might range from 11.4% to 16.0% in the entire Atlantic Forest region.

The best-preserved BSR is the Serra do Mar, which holds 36.5% of its original  
255 vegetation, followed by the Bahia (17.7%) and Brejos Nordestinos (16%) regions. In  
contrast, the São Francisco region has only 4.7% of forest cover, and the Interior Forest,  
7.1% (Table 3). However, in absolute terms, more than half of the remaining forest is  
located in the Serra do Mar and Interior Forest regions, whereas less than 15% is  
located in the Diamantina, São Francisco, Brejos Nordestinos and Pernambuco regions  
260 (Table 3).

### *3.2. Number of fragments and size distribution*

The Atlantic Forest is currently distributed in 245 173 forest fragments. The largest  
fragment is located in the Serra do Mar, mainly along the coastal mountains of the state  
265 of São Paulo, and extends from the state's southern border northwards into the southern  
part of the state of Rio de Janeiro. This single fragment contains 1 109 546 ha of  
continuous forests, which represents 7% of what remains (Figures 2 and 1S-f). The  
second- and third-largest fragments are also located in the Serra do Mar, and contain  
508 571 ha (coastal zone of Paraná state) and 382 422 ha (coastal zone of Santa  
270 Catarina state). Altogether, the three largest fragments account for more than 2 million  
hectares, i.e., more than 13% of the remaining forest. In contrast, 83.4% of the Atlantic  
forest fragments (204 469 fragments) are smaller than 50 ha, and together they account  
for 20.2% of the total forest remnants (ca. 3 178 030 ha; Figure 3) according to our  
estimates. Fragments smaller than 250 ha represented more than 97% of the total

275 number, and accounted for almost 42% of the total forest area. In contrast, only 0.03%  
(77 fragments) are larger than 10 000 ha, and together these include almost 4 million ha.

Small fragments (<50 ha) are, by far, the largest part of the number of remnants  
in all BSRs. The distribution of fragments according to their size followed an inverted  
“J” shape (Figure 2S). However, the Serra do Mar region, in addition to having many  
280 small fragments (~ 79% of the fragments is <50 ha), has much of the forest existing as  
large fragments (>50 000 ha), which represent more than 50% of the forest cover in the  
region. This region is the only one with a fragment larger than 1 million ha in size,  
which is located along the coastal mountains of São Paulo. The other regions do not  
contain any fragment larger than 250 000 ha, and only the Araucaria Forest (n= 4) and  
285 the Interior Forest (n= 1) have forest fragments larger than 50 000 ha (Fig. 2S): the  
inland forests of Santa Catarina, including the São Joaquim National Park, and the  
Iguaçu National Park, respectively. In the Bahia region, the largest fragment covers  
approximately 29 000 ha, while in the São Francisco and the Pernambuco regions, none  
exceeds 10 000 ha (see Figure 2S: a-g for detail); and in the Diamantina, none is larger  
290 than 25 000 ha.

### 3.3. Core and edge area

Of the total forest area remaining, 73% is located less than 250 m from any non-forest  
area, and 46% is less than 100 m distant from edge (Figure 4). Only 7.7% is located  
295 farther than 1 000 m from any edge, and 12 km is the maximum distance from any non-  
forested area in the Atlantic Forest region.

A similar pattern was observed for the BSRs, where most of the forest area is  
less than 250 m from non-forest areas (Figure 3S). In the Interior and Pernambuco  
regions, approximately 60% of the forest is less than 100 m from any edge, while São

300 Francisco, Araucaria, Bahia and Diamantina have between 40 and 50% of their forests  
within 100 m from any edge. Only the Serra do Mar region showed a different pattern,  
where only 25% of the remaining forest is located less than 100 m from any edge. This  
is reflected in the highest percentage of core-area forest in this BSR, with 256 040 ha at  
least 2.5 km from the edges, and 56 993 ha at least 5 km from the edges. In addition to  
305 the large fragments of the Serra do Mar region, the Iguaçu National Park is the only one  
that also has areas of forest that are 12 km distant from any edge.

#### *3.4. Connectivity*

For species that are not able to cross open areas, the average functionally connected area  
310 is 64 ha (Figure 5), while for those that are able to cross 300 meters it is 131 ha. The  
largest functionally connected cluster of fragments for species that are able to cross 100  
m, is comprised of the Serra do Mar and the nearby functionally connected fragments,  
which encompass more than 2 803 000 ha (18% of the remaining forest, Figure 6) and  
stretches from the state of Rio de Janeiro all the way south to the state of Rio Grande do  
315 Sul. In the Bahia region, species that are able to make short crossings between  
fragments, such as 100 m, can reach a forest area of more than 50 000 ha (17% of the  
remaining forest in the region); whereas in Diamantina the gap that needs to be crossed  
to reach a functionally connected area of this size is 200 m (Figure 4S-c). Longer  
distances separate fragments in the other regions, such as 400 m to reach 50 000 ha in  
320 the São Francisco (Figure 4S-g) BSR, and more than 500 m in the Pernambuco to reach  
the same area (Figure 4S-e).

325 *3.5. Mean isolation*

The mean isolation for the entire Atlantic Forest region was 1 441 m, with values ranging from a few meters to dozens of kilometers. The small fragments were particularly important in reducing isolation (Figure 7). When we exclude the fragments <50 ha, the mean isolation increases to 3 532 m. If fragments smaller than 200 ha were  
330 lost, the mean isolation would reach more than 8 000 m.

Small fragments were important in reducing isolation in all regions. However, a gradient of importance could be seen, with the Interior and São Francisco BSRs being particularly affected by the exclusion of these small fragments, whereas in the Serra do Mar a relatively low isolation is maintained, since the remaining forest exists as larger  
335 pieces (Figure 7). The isolation in the São Francisco BSR is the most affected by the exclusion of small fragments, since isolation increases from 3.6 to 14.5 km when excluding fragments smaller than 200 ha. The second most-affected BSR is the Interior, where the mean isolation increases from 1 344 m (without fragment removal) to 9 112 m if we remove fragments <200 ha. For other regions, exclusion of fragments of this  
340 size results in an isolation that ranges from 4 182 m (in the Serra do Mar) to 7 048 m (in the Araucaria BSR).

*3.6. Nature reserve cover and proximity*

The total protected area within the Atlantic Forest region is approximately 2.26 million  
345 ha, or 1.62% of the region (Table 4, Figure 8). Nature reserves represent 14.4% of the remaining forest cover, but they protect only 9.3% (Table 4) of this remaining forest, since other types of vegetation or land cover also occur within these reserves. All regions have a small percentage (Figure 5S[a-g]) of their areas covered by nature reserves. However, the Serra do Mar has 25.2% of its remaining forest under protection,

350 followed by the Interior (6.8%) and the Bahia (4.2%). All other regions have less than  
4% of their small amount of remaining forest under protection (Table 4; Figure 5S[a-  
g]). Given these facts, the Serra do Mar accounts for 63% of the total remaining forest  
under protection, followed by the Interior BSR (22%). Moreover, only 1.05% of the  
original forest cover is protected, and in most regions (except Serra do Mar and Bahia)  
355 this percentage is <0.5%.

Some reserves are contiguous, and thus we could identify seven large protected  
regions with areas of about 100 000 ha. Five are in the Serra do Mar region: 1. Serra do  
Mar State Park and Bocaina National Park; 2. Jacupiranga State Park and Superagui  
National Park; 3. Paranapiacaba [Petar State Park, Intervales State Park, Xituê  
360 Ecological Station and Carlos Botelho State Park]; 4. Serra do Tabuleiro State Park and  
5. Jureia [Banhados de Iguape Ecological Station, Jureia-Itatins Ecological Station,  
Itinguçu State Park and Prelado State Park]. The other two regions are in the Interior  
(Iguaçu National Park) and the Diamantina (Chapada da Diamantina State Park)  
regions. Together they have a total area of 1 212 800 ha, which encompasses 53.6% of  
365 the protected areas. Seventeen reserves range in size from 20 000 ha to 60 000 ha (in  
total 585 120 ha; 26% of the protected areas); five of them are in the Serra do Mar, six  
in the Interior, three in the Bahia, two in the Araucaria, and one in the São Francisco  
BSRs.

Only 22.6 % of the remaining forest is located within 10 km of nature reserves,  
370 whereas 61 % is farther than 25 km (Figure 9). Most BSRs have a small amount of  
forests close (<10 km) to nature reserves, whereas a large amount is more distant (>50  
km, Table 4; Figure 5S[a-g]). A different pattern is encountered in the Serra do Mar,  
where 59% (2 163 163 ha) of the remaining forest is less than 10 km, and 41% (1 515  
371 ha) is farther away.

#### 4. Discussion

Our results showed that: i) there is more forest left than previously estimated; ii) most fragments are very small, less than 50 ha (ca. 83% of the total number of fragments); iii) much of the remaining forest is close to forest edges (ca. 45% < 100 m of the edges),  
 380 indicating that matrix influences may have strong effects on many forest ecological processes (Umetsu and Pardini, 2007; Umetsu et al., 2008; Uezu et al., 2008; Fonseca et al., 2009; Pardini et al., 2009; Vieira et al., 2009); iv) short gap-crossings (<100 m) through the matrix can be highly effective to increase the functionally connected area for forest species (Boscolo et al., 2008; Martensen et al., 2008); v) small fragments  
 385 (<200 ha) play a crucial role in reducing fragment isolation among larger fragments, suggesting that they are highly important as stepping stones; vi) nature reserves protect a small amount of the remaining forest in all the BSRs (except in the Serra do Mar), and most of the remaining forest is distant (> 25 km) from the existing nature reserves (61%; 9 564 900 ha).

390

##### *4.1 How much forest is left?*

Our study exposed the extreme degradation of the Atlantic Forest, where only 11.7% of the original vegetation remains (15 719 337 ha). This proportion might range from 11.4 to 16.0% if we consider errors of commission and omission. This estimated area is  
 395 larger than the usual total given for the Atlantic Forest (7-8%; SOS Mata Atlântica/INPE, 1993, and 2002; Galindo-Leal and Câmara, 2003), but below the recent estimate of 27% by IESB et al., 2007 and Cruz and Vicens (in press). Differences among these estimates could be caused by several factors, including mapping errors. However, our field survey demonstrated that the map quality is acceptable for regional

400 analyses. Apparently, one of the main factors causing these discrepancies in estimating the Atlantic Forest cover is related to the criteria used to include secondary forests and small fragments.

IESB et al. (2007) and Cruz and Vicens (in press) included very early stages of succession, even without a forest structure present (vegetation < 2 m high; Cruz, 405 personal communication). The initial evaluations by the SOS Mata Atlântica Foundation (1986-2000) did not consider re-growth; i.e., once mapped as deforested in a recent past (~ 50 years), an area was never again considered as forest (SOS Mata Atlântica/INPE, 2008). They also did not consider forest fragments smaller than 100 ha. On their new report, when considering fragments >3 ha and forests at an intermediate 410 stage of regeneration, they obtained an estimation of the remaining forest cover similar to ours (10.6%; SOS Mata Atlântica/INPE, 2008). Thus, the difference between previous estimates by SOS Mata Atlântica/INPE (1993, 2002) and the present estimate is basically composed of intermediate secondary forests and/or small fragments, which correspond to approximately 32 to 40% of the total mapped vegetation (considering 8% 415 and 7% of the forest cover previously mapped by SOS Mata Atlântica, respectively). The small difference between our estimates and that reported by SOS Mata Atlântica/INPE (2008) may be related to differences on the analyzed extent (slightly larger in our case to include the delimitations of BSRs by Silva and Casteleti, 2005) and because we did not excluded any fragment from the analyses.

420 The Atlantic forest presents a highly dynamic forest cover dynamic (Teixeira et al., 2009) and an old history of disturbance, where even the mature remnants were selective logged in a distant past, sometimes in pre-European time (Dean, 1996; Câmara, 2005). This critical scenario of the Atlantic Forest with large areas of secondary forests and small disturbed fragments is the usual pattern in most tropical

425 regions, where 50% of them are secondary or disturbed (Wright, 2005). The  
implications for species conservation are huge. Even if secondary forests can sustain a  
significant amount of biodiversity (Viana and Tabanez, 1996; Develey and Martensen,  
2006), many species need more pristine forest and large fragments to survive (Aleixo,  
1999; Harris and Pimm, 2004; Develey and Martensen, 2006; Laurance, 2007; Gardner  
430 et al., 2007; Barlow et al., 2007a, b), and the replacement of mature forests by  
secondary ones may lead to the extinction of many species (Metzger et al., 2009).

In this landscape-structure scenario, several general guidelines can be suggested  
to improve or stimulate forest-species conservation in the Atlantic Forest region,  
particularly: i) large mature forest fragments should be assigned a high conservation  
435 priority; ii) smaller fragments could be used to form functionally linked mosaics; iii) the  
matrix surrounding the fragments should be adequately managed to minimize edge  
effects; iv) restoration actions should be put into practice, particularly in some key  
structural conditions.

#### 440 *4.2 Protecting large mature forest fragments*

Particular attention should be paid to the protection of the larger remnants, especially  
for their capacity to maintain larger populations and for their better prospects of  
sustaining species over the long term (Brooks et al., 1999; Lindbord and Eriksson,  
2004). Only large fragments with mature forests are capable of preserving sensitive  
445 species, especially those with large area requirements (Ferraz et al., 2007) or with strict  
habitat requirements, whose survival is particularly problematic in the present  
fragmented state (Aleixo, 1999). Old-growth forests (Laurance, 2007; Gardner et al.,  
2007) are especially important because, even in excellent regeneration conditions, this  
process requires several decades to restore a species composition comparable to a

450 mature stage (Dunn, 2004; Barlow et al., 2007a, b; Liebsch et al., 2008; Rodrigues et al., 2009). Moreover, the early stages of succession on abandoned lands are not protected by Brazilian environmental laws (Metzger et al., 2009), and their suppression is common and part of the rapid dynamic of the landscapes.

In the present extremely fragmented and dynamic scenario of the Atlantic  
455 Forest, the importance of the last large forest remnants increases exponentially, and their management should be cautiously designed and their transformation into nature reserves should be carefully considered. New conservation areas are most urgently needed in Pernambuco, Diamantina and São Francisco, where nature reserves protect less than 3% of the remaining forest, even if the largest fragments are not so large (e.g.,  
460 <10 000 ha). Protection of at least 10% of the original habitat is recommended as a global strategy for conservation (Secretariat of the Convention on Biological Diversity, 2002), but even the Serra do Mar region does not at present fulfill this condition (8.1% of its original cover is protected in nature reserves). This kind of conservation target is subjective, and the degree of protection should vary according to the sensitivity of the  
465 system (which may differ among regions), but it is clear that the proportion of forest cover under legal protection is very low in all the BSRs, and must be enhanced.

Moreover, the largest fragments promote conservation of core areas, which are particularly uncommon since more than 70% of the remaining forest is located less than 250 m from open land, and is thus subject to edge effects. Furthermore, large mature  
470 forest fragments are vital for supporting seeds and allowing recolonization of the small surrounding fragments, and can act as source areas for restoration programs (Rodrigues et al., 2009). The distance (> 25 km) of most of the remaining Atlantic forest fragments from the existing nature reserves reduces their influence as stable sources of individuals and species for the surrounding smaller fragments. Forest regeneration in areas around

475 nature reserves should be stimulated because of their natural regrowth potential,  
increasing forest cover in these regions, and reducing the present unbalanced  
distribution of forest cover in relation to the proximity to nature reserves.

Protecting the last largest blocks of forests of all BSRs should definitely be a  
conservation priority. However, only in the Araucaria, Bahia, and especially the Serra  
480 do Mar regions can large fragments still be found. The Interior Forest also has a few  
large fragments, which together with the large tracts of forests still existing in Argentina  
(Giraud, 2005) and Paraguay (Cartes and Yanosky, 2005; Huang et al., 2007)  
constitute a better conservation prospect for this BSR. All the other BSRs lack large  
fragments, which may severely compromise species conservation (Silva and Casteleti,  
485 2005). In these regions, alternative conservation practices should be implemented for  
the existing remnants.

#### *4.3 Creating functionally linked mosaics*

The conservation of small fragments should not be neglected, because they constitute a  
490 large fraction of the remnants (83.4% with < 50 ha), and are essential in enhancing  
connectivity between the larger ones. The mean distance between fragments for the  
Atlantic Forest is around 1 400 m, considering the small fragments. This is a  
considerable separation for most forest species (Laurance and Gómez, 2005), which  
avoid edge areas (Hansbauer et al., 2008; Lopes et al., 2009) and in some cases do not  
495 even cross roads or small gaps in the canopy (Develey and Stouffer, 2001; Laurance,  
2004; Laurance and Gómez, 2005). As the distances between fragments increase,  
connectivity decreases, and individual crosses became less frequent (Hanski, 1994;  
Haddad, 1999). However, clusters of neighboring fragments (<200 m) that form large  
tracts of forest (>50 000 ha) are common (n= 12; 4 992 700 ha; 32% of the total

500 remaining forest), and should be considered in conservation policies as important potential mosaics for conservation. They can play an important role in animal movement through landscapes, either functioning as stepping stones (Castellón and Sieving, 2005; Sekercioglu et al., 2006; Uezu et al., 2008; Boscolo et al., 2008), or forming networks of functionally connected areas, which could allow species to persist  
505 in disturbed landscapes (Martensen et al., 2008). They can also act as stable sources of seeds and individuals for nearby, smaller fragments.

Especially in cases where no large fragment is left, one option is to consider functionally linked mosaics of smaller fragments (Uezu et al., 2005; Martensen et al., 2008). This is especially the case in the Pernambuco, Diamantina and São Francisco  
510 BSRs. These BSRs are naturally fragmented (Figure 1), and the advanced forest destruction intensified this pattern, increasing the number of small fragments, reducing the forest cover to < 15% and thus threatening the biodiversity that depends on this forest.

Matrix permeability is a key connectivity component (Fonseca et al., 2009).  
515 Different regions of the Atlantic Forest have suffered for centuries under poor soil management and extensive destruction and simplification of the forests, which has intensified in recent decades (Figure 6S), with agricultural mechanization and the use of pesticides and herbicides (Brannstrom, 2001; Durigan et al., 2007). Recent expansions of *Eucalyptus* (Bacha and Barros, 2004; Baptista and Rudel, 2006; Figure 6S) and  
520 sugar-cane plantations (Rudorff and Sagawara, 2007, Nassar et al., 2008; Figure 6S) have caused huge social, economical and environmental impacts, and their influences in reducing patch connectivity have been suggested and need to be better understood (Fonseca et al., 2009).

Matrix management is especially important in a scenario where short  
525 movements through the matrix can promote fragment connections. Increasing matrix  
permeability can allow species to persist in fragmented situations and can be an  
interesting option for conservation of some species (Ricketts, 2001; Baum et al., 2004;  
Antongiovanni and Metzger, 2005; Umetsu et al., 2008; Uezu et al., 2008; Pardini et al.,  
2009; Vieira et al., 2009). Matrix management could be employed in the Araucaria  
530 Forest, where functionally connected areas increase stability through improved gap-  
crossing abilities; and in the Bahia region, where a large network of fragments are  
functionally linked by distances of 100 m of open areas. In all these cases, inter-forest  
management can improve connectivity. The implementation of forested pastures, where  
trees are scattered in different densities, or disposed in lines along fences, has been  
535 suggested as one easy option to improve connectivity in traditional pasture areas, while  
also promoting additional economical gains to the landowner, as well as work in wind  
blocking (Harvey et al., 2004). The establishment of small agroforest patches, with the  
presence of trees dispersed in agricultural fields is also suggested as important to  
improve landscape connectivity (Uezu et al., 2008). Moreover, sugar cane has been  
540 expanding over former pastures, where scattered trees were common (Nassar et al.,  
2008). The suppression of these trees should be avoided, because they can have a  
disproportional effect in biodiversity conservation (Harvey et al., 2004). Finally,  
different management options in the plantations of exotic trees are also pointed out as  
vital to enhance connectivity, as well as in harboring some extremely demanding  
545 species, what could be severely limited with traditional forest management practices  
(Fonseca et al., 2009).

#### *4.4 Reducing edge effects*

550 Because the remaining Atlantic Forest is severely fragmented in small patches edge effects increase in importance. Tropical species, particularly the strictly forest ones, are well known to be highly sensitive to edge alterations, especially because of their high niche specialization (Kapos, 1989; Murcia, 1995; Hansbauer et al., 2008; Lopes et al., 2009). Kapos (1989), Laurance et al., (2007) and Laurance (2008) showed that some  
555 edge effects in the Amazon Forest can extend as far as 300 to 400 m into the forest. In the Atlantic Forest, almost half of the remaining forest is located less than 100 m from open areas, and more than 70% of the remaining forest is located less than 250 m from open land, *i.e.* is subject to strong edge-effect influences.

Because most of the present forest is directly influenced by nearby land use,  
560 matrix influences should also be particularly investigated and their management carefully conducted (Umetsu and Pardini, 2007; Umetsu et al., 2008; Uezu et al., 2008; Fonseca et al., 2009; Pardini et al., 2009; Vieira et al., 2009). Forested or agroforestry matrixes are suggested as efficient in reducing microclimate changes caused by edge conditions (Didham and Lawton, 1999), and thus, to reduce edge effect influences  
565 (Cullen Junior et. al., 2004). In some cases, strip of trees are planted forming a buffer around the remaining patches in order to reduce edge effects (Cullen Junior and Fenimore 2002, Cullen Junior et. al., 2004).

#### *4.5 Stimulating restoration actions in key structural conditions*

570 The present small amount of remaining forest generates a scenario where rapid restoration actions should be undertaken to allow species conservation in the near future (Rodrigues et al., 2009). In this case, careful site selection is necessary in order to maximize restoration achievements. Priority should be given to the bottlenecks of the

large clusters of fragments. In the Serra do Mar region, for example, small disruptions  
575 (<200 m) break apart a potential larger fragment of more than 3 million hectares, and  
restoration of these connections should be a conservation priority. In this region, roads  
are also a key element in breaking apart large fragments, and mitigation policies should  
be analyzed and employed to restore connectivity. Complementarily, efforts should be  
allocated to create new reserves between the large fragments of the Serra do Mar,  
580 enhancing reserve sizes and width, especially in areas where forest areas are relatively  
narrow and disruption of these fragments could occur in the future.

Another key characteristic of the Serra do Mar region is the presence of large  
fragments that extend into the Interior and Araucaria regions. Maintenance or linkage  
restoration of these inter-region fragments is also vital to maintain the biological  
585 evolutionary processes, which could be particularly important in the present scenario of  
climate changes. These linkages may be especially important in the case of the  
Araucaria BSR, since these inter-region fragments are also the largest ones found in this  
BSR, and the region has been undergoing profound impacts from the recent changes in  
land use, with the expansion of *Eucalyptus* plantations (Bacha and Barros, 2004;  
590 Baptista and Rudel, 2006).

The northern Atlantic Forest is presently in worst state of conservation compared  
to the southern part, except for the large mosaic in the south of the Bahia region. This  
mosaic should be a key target for biological conservation, and the restoration of forest  
connections should be a main concern in this region. The absence of forest in the area  
595 between Bahia and the Serra do Mar makes it particularly difficult for individual  
animals to pass between the southern and northern Atlantic Forests, which could  
severely impact evolutionary processes and could be particularly deleterious in a  
climate-change scenario.

Finally, restoration priority should also be given to link the smaller fragments  
600 surrounding larger ones, especially in the cases where these large fragments are nature  
reserves. Enhancing the connectivity between fragments, especially linking to a large  
one that can act as a source of individuals, can improve conservation possibilities in  
highly fragmented regions (Uezu et al., 2005, Martensen et al., 2008).

## 605 **5. Conclusion**

This report quantifies for the first time the extremely degraded state of the Atlantic  
Forest distribution, showing that most fragments cover less than <50 ha, almost half the  
remaining forest is <100 m from forest edges, and the present conservation network is  
insufficient to support the long-term survival of this rich and endangered tropical forest.  
610 Urgent conservation and restoration actions should be implemented to mitigate this  
situation, based on careful planning and with clear targets.

The management of the region as a whole must begin with the transformation of  
the large mature forest tracts into conservation reserves and the reestablishment of key  
connectivity linkages, especially between the larger remnants. The matrix, mainly  
615 between and surrounding these large fragments, is also important to manage, since a  
large fraction of the forest is influenced by the close proximity to edges. In sections  
where not a single large fragment remains, which is common in most sub-regions,  
management should focus on the reestablishment of functionally connected clusters of  
fragments, enhancing landscape connectivity. In the present critical conservation  
620 scenario of the Atlantic Forest, every remnant is important for species conservation. The  
clear differences in the amount of forest remaining and how they are organized in each  
sub-region must be considered when planning biodiversity conservation.

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Table 1. Extent of the Atlantic Forest in the biogeographical sub-regions (BSRs, as proposed by Silva and Casteleti, 2005), and area mapped by SOS Mata Atlântica/INPE (2008).

<b>BSR</b>	<b>Abbreviation</b>	<b>Atlantic Forest Domain Area (ha)</b>	<b>Mapped by SOS Mata Atlântica/INPE (2008)</b>		
			<b>Area (ha)</b>	<b>% mapped</b>	<b>% of total mapped *</b>
Araucaria	arauc	25 379 316	25 379 316	100%	17%
Bahia	bahia	12 241 168	12 241 168	100%	8%
Brejos Nordestinos	brejo	1 251 783	85 249	7%	1%
Diamantina	diama	8 289 516	8 200 259	99%	6%
Interior	inter	72 784 790	68 417 731	94%	49%
Pernambuco	perna	3 893 730	3 132 167	80%	3%
Serra do Mar	semar	11 413 471	11 413 471	100%	8%
São Francisco	sfran	12 940 866	10 715 533	83%	9%
<b>TOTAL</b>		<b>148 194 638</b>	<b>139 584 893</b>	<b>94%</b>	<b>100%</b>

965

\* Percentage of mapped area for each BSR in relation to total mapped area

Table 2. Landscape metrics used to analyze the Atlantic Forest configuration.

<i>Index</i>	<i>Explanation</i>	<i>Classes or rules</i>
<i>Fragment size distribution</i>	Number of fragments and percentage of forest cover for different size classes	Fragment size classes(ha): <50, 50-100, 100-250, 250-500, 500-1 000, 1 000-2 500, 2 500-5 000, 5 000-10 000, 10 000-25 000, 25 000-50 000, 50 000-100 000, 100 000-250 000, 250 000-500 000 and 500 000-1 200 000
<i>Edge area</i>	Percentage of area submitted to edge effects for different edge widths	Edge widths (m): <50, 50-100, 100-250, 250-500, 500-1 000, 1 000-2 500, 2 500-5 000 and 5 000-12 000
<i>Connectivity</i>	Area of functionally connected fragments considering different distance rules for fragment linkage	Linkage distances (m): 0, 100, 200, 300, 400, 500, 1 000 and 1 500
<i>Mean isolation</i>	Mean isolation of random points to the nearest forest fragment. To analyze the effect of small fragments in estimating isolation, the smallest fragments were successively removed.	Size of the small fragments removed (ha): 0 (i.e., no fragment removed), <50, <100, <150, <200, <350 and <500
<i>Distance from Nature Reserves</i>	Distance of any given forest pixel to the nearest nature reserve	Distance classes (m): 0 (i.e., inside a Nature Reserve), <200, 200-600, 600-1 000, 1 000-2 000, 2 000-5 000, 5 000-7 500, 7 500-10 000, 10 000-25 000, 25 000-50 000 and >50 000

Table 3: Remaining Atlantic Forest in each biogeographical sub-region (BSR), with its area in ha and percentage. Data were obtained by superposing the map generated by SOS Mata Atlântica/INPE (2008) and the boundaries of BSRs adapted from Silva and Casteleti (2005).

BSR	Remaining Forest		Remaining Restinga/ Mangrove		Total remaining Atlantic Forest	
	Area (ha)	% *	Area (ha)	% *	Area (ha)	% *
	Araucaria	3 202 134	12.6			3 202 134
Bahia	2 047 228	16.7	115 059	0.9	2 162 287	17.7
Brejos Nordestinos	13 656	16.0			13,656	16.0
Diamantina	1 109 727	13.5			1 109 727	13.5
Interior	4 807 737	7.0	32 451		4 840 188	7.1
Pernambuco	360 455	11.5	19 363	0.6	379 818	12.1
Serra do Mar	3 678 534	32.2	491 263	4.3	4 169 797	36.5
São Francisco	499 866	4.7			499 866	4.7
<i>TOTAL</i>	<i>15 719 337</i>	<i>11.26</i>	<i>658 135</i>	<i>0.47</i>	<i>16 377 472</i>	<i>11.73</i>

975 \* Percentages are in relation to the BSR area.

Table 4: Protected area and forest under protection for the Atlantic Forest domain, and within seven biogeographical sub-regions (all BSRs except “Brejos Nordestinos”) adapted from Silva & Casteleti (2005).

BSR	Area of sub-region (a)		Protected area		Remaining forest (c)	Protected remaining forest (d)	Protected forest in relation to remaining forest within sub-regions (d)/(c)	Protected forest between sub-regions (di)/S(d)	Protected forest in relation to original forest within sub-regions (d)/(a)
	(ha)	(ha)(b)	%						
				(b)/(a)					
Araucaria	25 379 316	164 651	0.65%		3 202 134	98 121	3.1%	6.7%	0.39%
Bahia	12 241 168	113 447	0.93%		2 047 228	86 053	4.2%	5.9%	0.70%
Diamantina	8 200 259	151 412	1.85%		1 109 727	12 451	1.1%	0.9%	0.15%
Interior	68 417 731	561 381	0.82%		4 807 737	325 261	6.8%	22.2%	0.48%
Pernambuco	3 132 167	4 314	0.14%		360 455	3 731	1.0%	0.3%	0.12%
Serra do Mar	11 413 471	1 201 848	10.53%		3 678 534	926 184	25.2%	63.3%	8.11%
São Francisco	10 715 533	63 297	0.59%		499 866	11 823	2.4%	0.8%	0.11%
<i>TOTAL</i>	139 499 644	2 260 350	1.62%		15 705 681	1 463 622	9.3%	100.0%	1.05%

925 **Figures Heads**

Figure 1. Biogeographical sub-regions (BSRs) based on the main areas of endemism of birds, butterflies and primates as proposed by Silva and Casteleti (2005). Abbreviations for Brazilian states names are: AL= Alagoas, BA= Bahia, CE= Ceará, ES= Espírito Santo, GO= Goiás, MA= Maranhão, MG= Minas Gerais, MS= Mato Grosso do Sul, PE= Pernambuco, PB= Paraíba, PI= Piauí, PR= Paraná, RN= Rio Grande do Norte, RS= Rio Grande do Sul, SC= Santa Catarina, SE= Sergipe, SP= São Paulo, TO= Tocantins.

935 Figure 2. Remaining forest in the Brazilian Atlantic Forest region (source: SOS Mata Atlântica/INPE, 2008). See Fig. 1 for the abbreviations of Brazilian states names.

Figure 3. Distribution of remaining forest fragment sizes in the full extent of the Atlantic Forest region. %A: percentage of total area; %NP: percentage of number of fragments.

940

Figure 4. Cumulative (A) and per class (B) area under edge effect at different depths for the remaining Brazilian Atlantic Forest. Edge depths of 100 and 250 m are highlighted in (A).

945

Figure 5. Expected cluster size (mean functional size; ha) for functionally connected forest fragments estimated across varying functional linkage distances (m), for the Brazilian Atlantic Forest region.

950 Figure 6. Highest functionally connected forest cluster (% of total remaining forest) estimated across varying functional distances (m), for the Brazilian Atlantic Forest region.

Figure 7. Influence of the smallest fragment size (ha) on the mean isolation (m) between  
955 fragments, for the Brazilian Atlantic Forest region, and for its biogeographical sub-regions (BSRs). See Table 1 for BSRs abbreviations. Smallest fragments sizes: 0 ha (all fragments), 50 ha, 100 ha, 150 ha, 200 ha, 350 ha and 500 ha.

Figure 8. Nature reserves in the Brazilian Atlantic Forest region (source: MMA, 2007).

960

Figure 9. Remaining forest (area and percentage) within nature reserves (NR) and amount of forest per class of distance from nature reserves (m) for the Brazilian Atlantic Forest region.

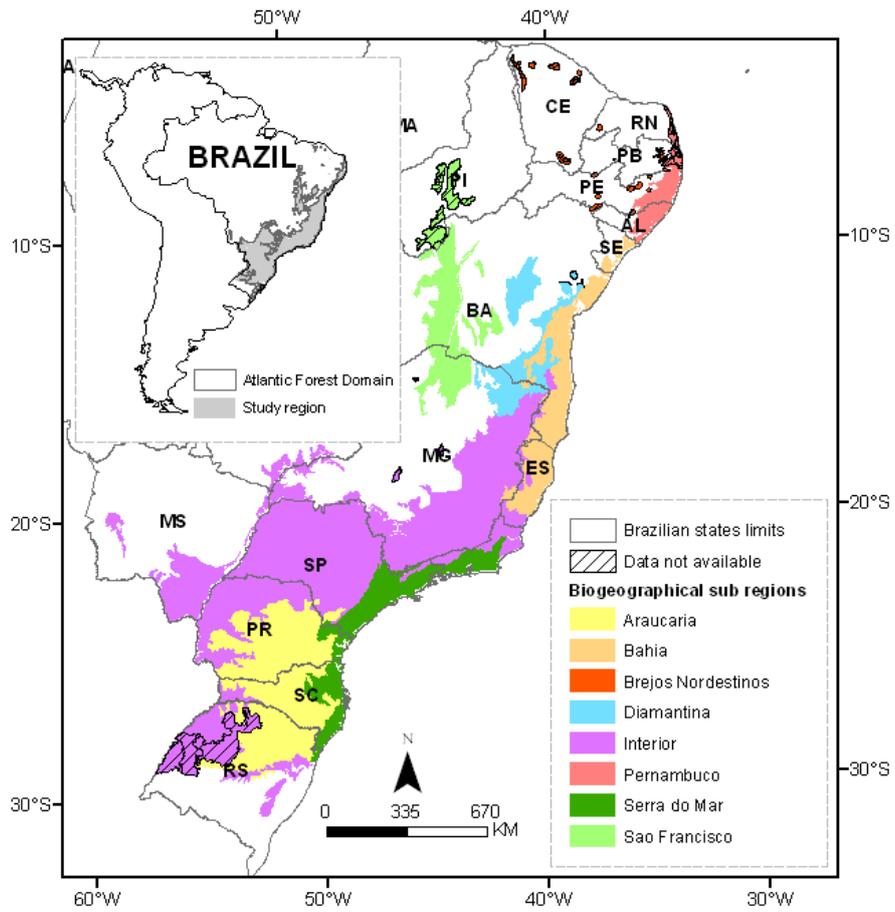


Figure 1:

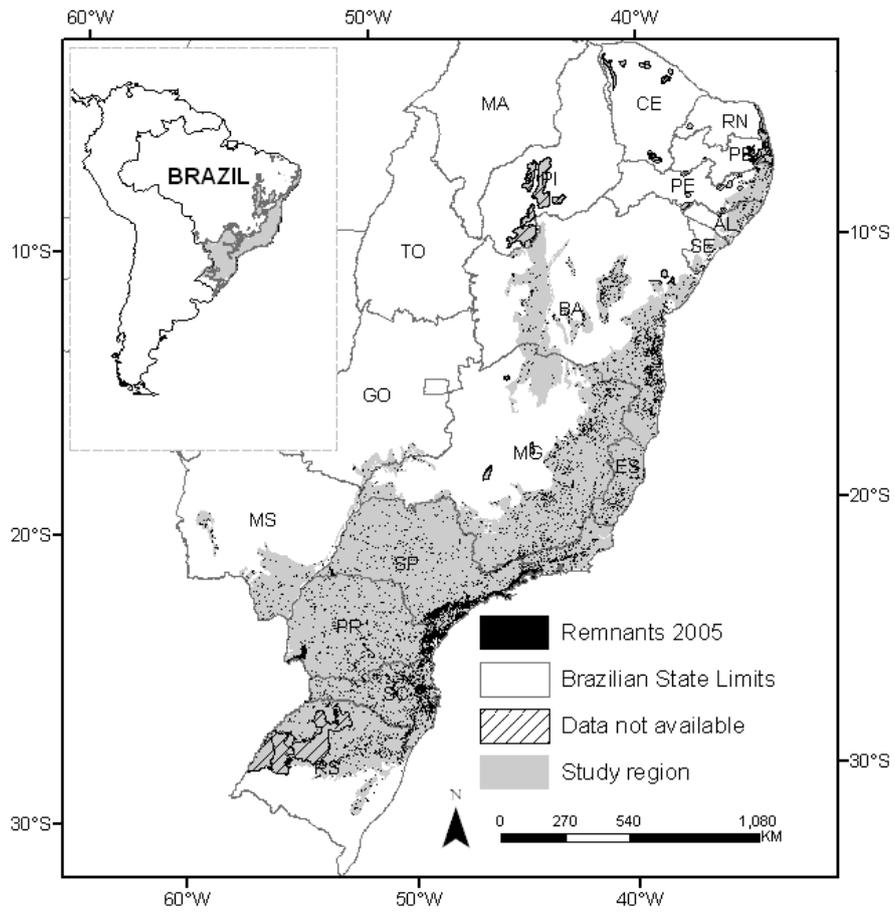


Figure 2

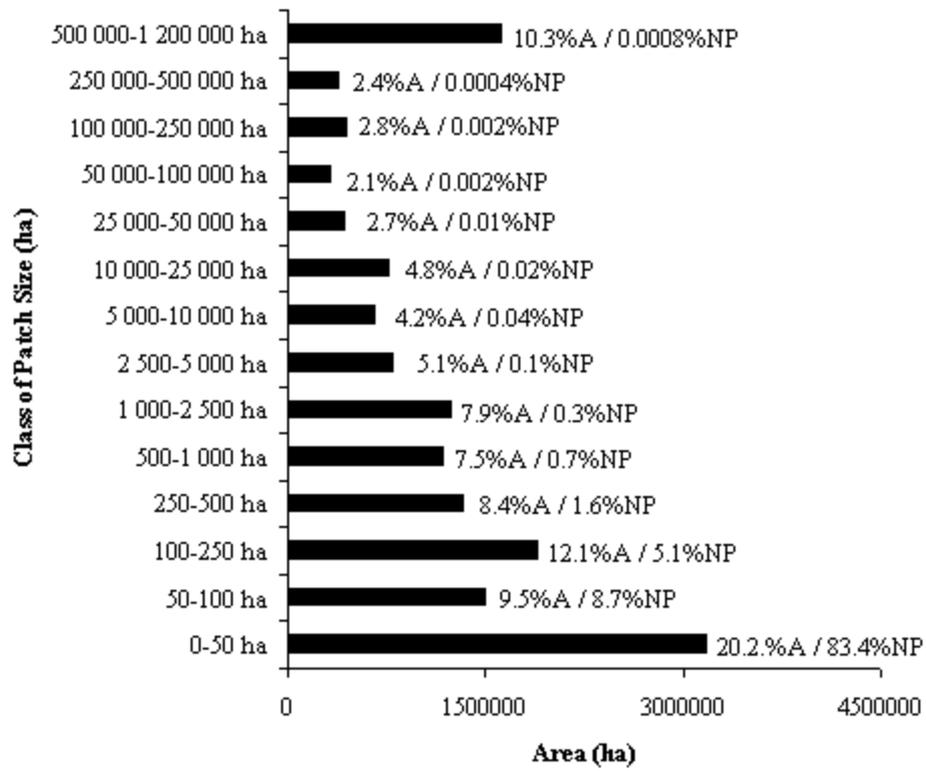


Figure 3

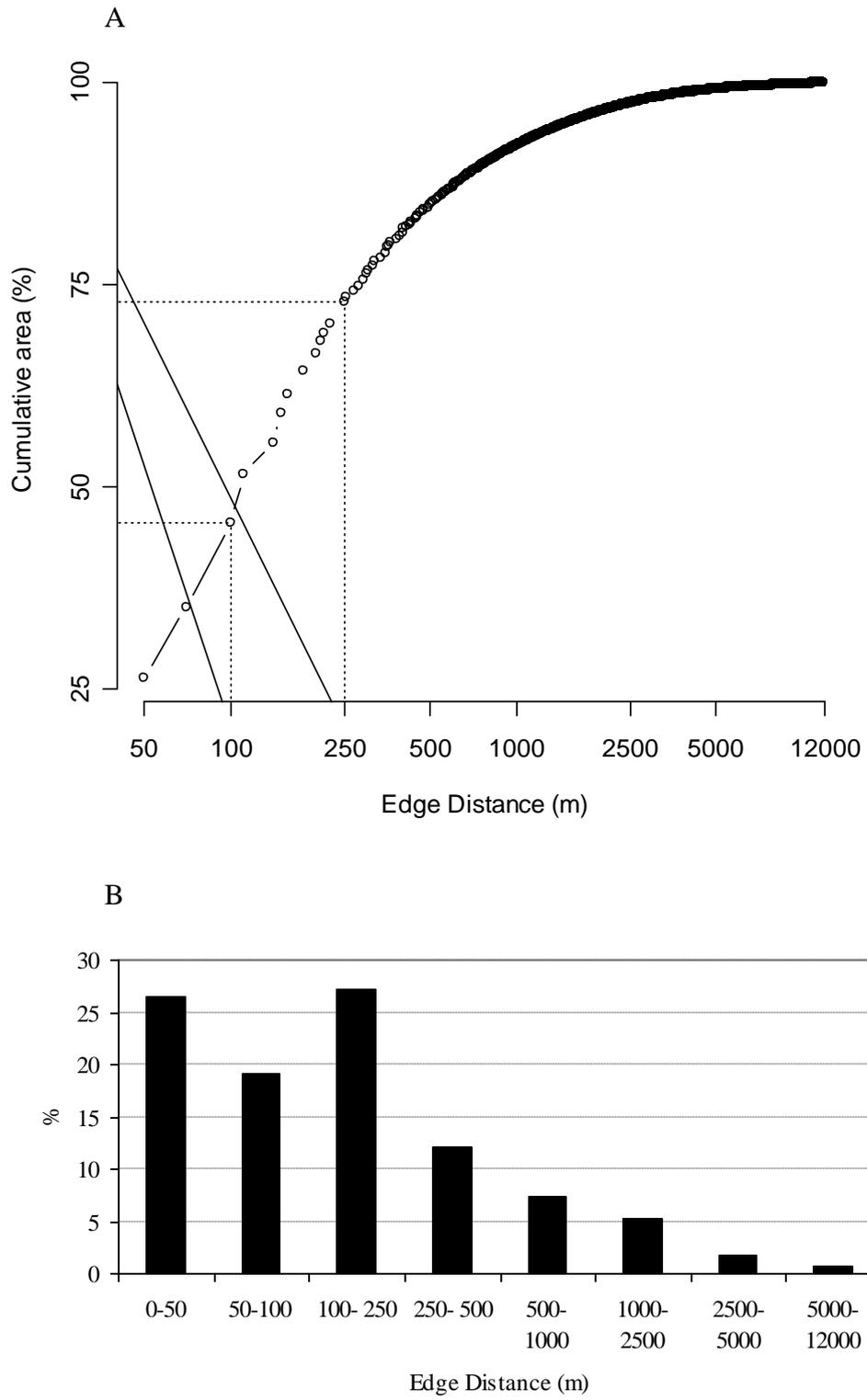


Figure 4

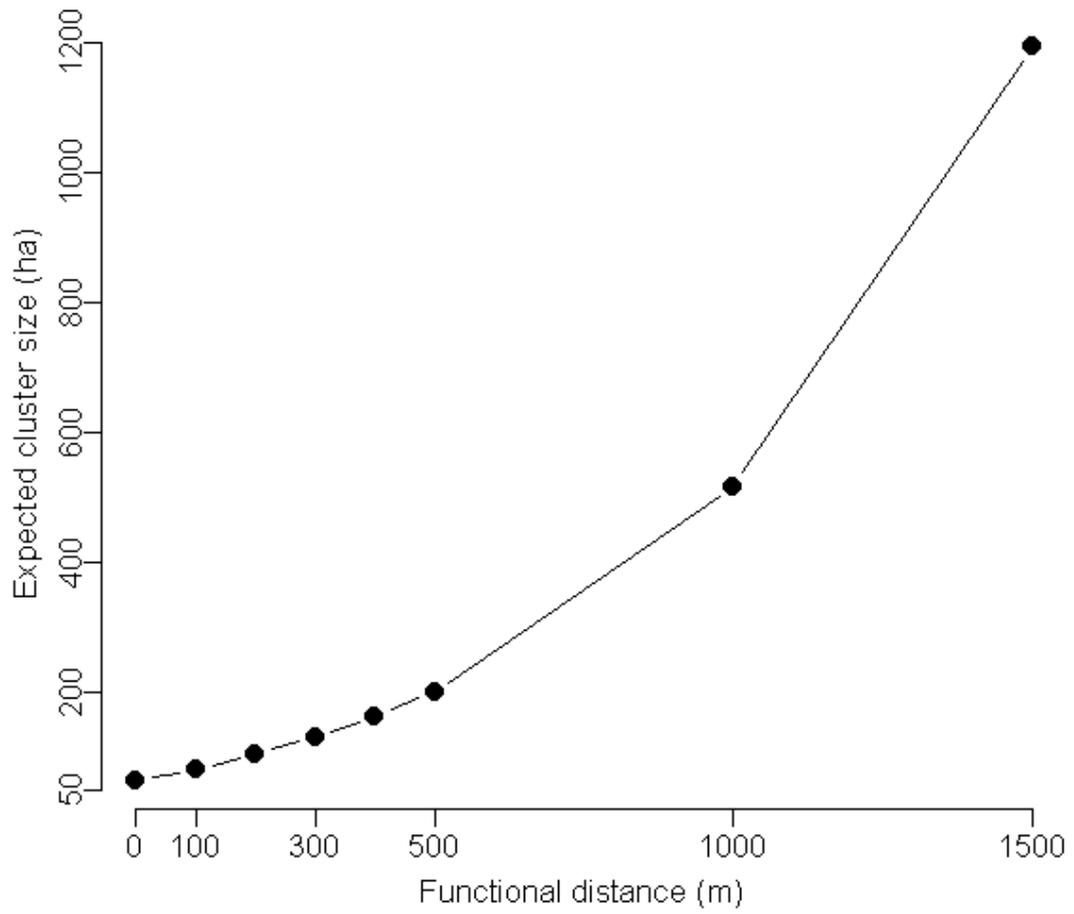


Figure 5

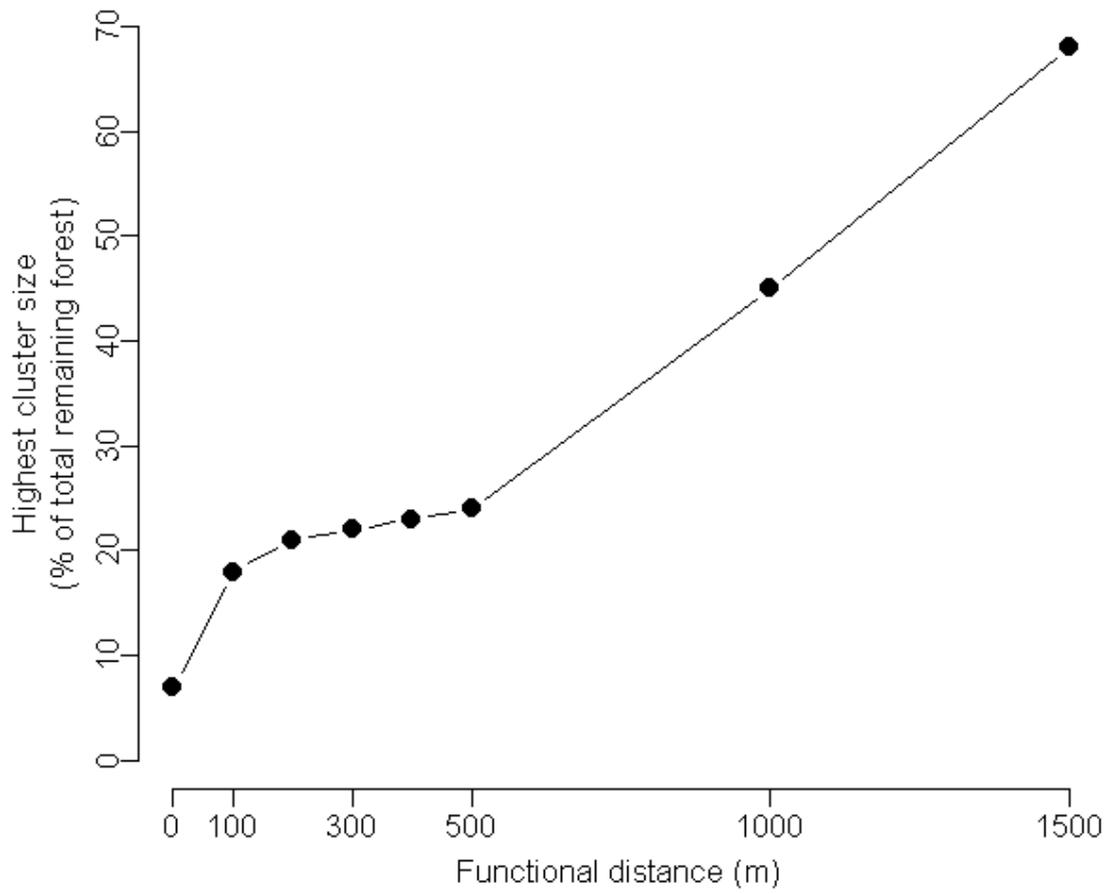


Figure 6

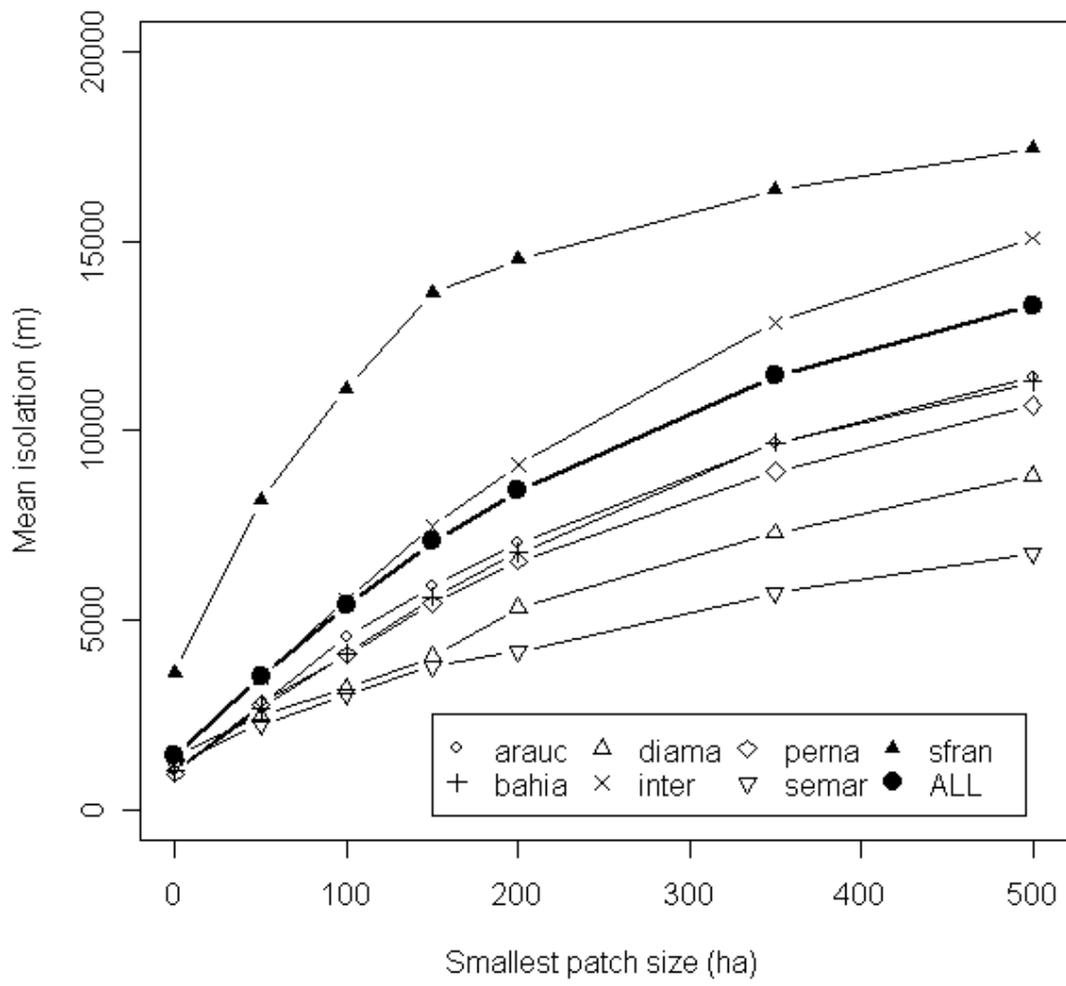


Figure 7

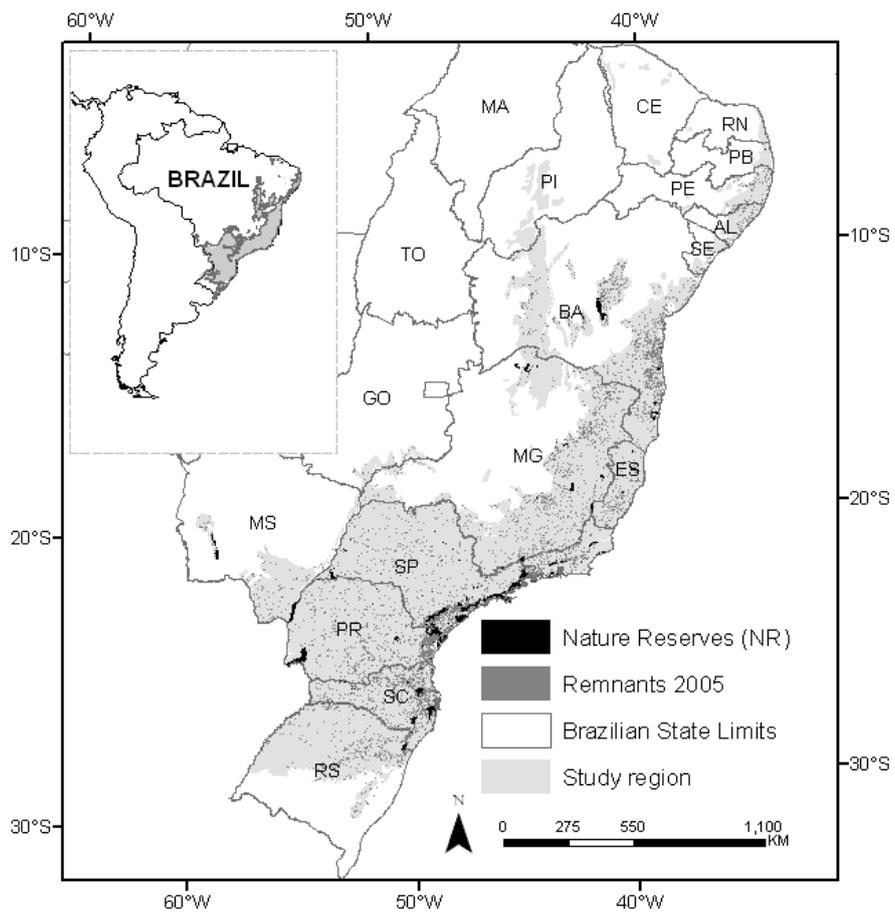


Figure 8

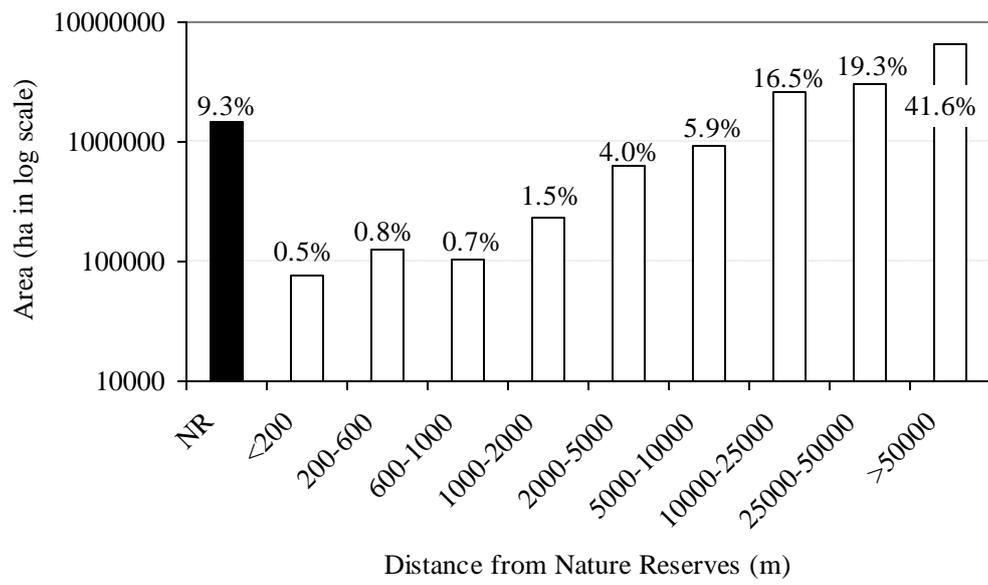


Figure 9

## Supplementary online material

Table 1S: Assessment of accuracy of the SOS Mata Atlântica/INPE (2008) map of remaining forest for the year 2005. The G statistics is the percentage of pixels correctly classified (i.e., forest and matrix). Standard deviation (sd) for Kappa's statistics are shown. Forest omission error is the percentage of forest on the reference map that was mapped as matrix on the map used for the analysis. Forest commission error is the percentage of matrix on the reference map that was mapped as forest on the map used for the analysis.

Reference map	Forest					
	Area (ha)	Cover	Map accuracy		% Forest Error	
			G**	Kappa (sd***)	Omission	Comission
Caucaia, SP	10 413	31%	78%	0.425 (0.010)	54%	5%
Itirapina, SP	151 858	18%	84%	0.322 (0.003)	72%	2%
Jurupara, SP	11 141	49%	77%	0.529 (0.008)	38%	5%
Morro Grande, SP	10 838	93%	77%	0.764 (0.011)	3%	1%
Ibiuna, SP	18 284	34%	76%	0.388 (0.007)	63%	3%
Pontal, SP	874 749	9%	97%	0.818 (0.001)	18%	1%
Nordeste Parana, PR	748 533	15%	87%	0.245 (0.002)	83%	1%
Ribeirao Grande, SP	10 800	11%	90%	0.167 (0.013)	89%	0.2%
São Paulo state, SP*	248 03013	12%	93%	0.648 (0.001)	36%	3%
Quadrilátero Ferrifero, MG	143 917	36%	80%	0.554 (0.002)	33%	8%

\* not including brazilian savanna cover class

\*\* G= overall accuracy (i.e. % of pixels classified correctly)

\*\*\* standard deviation for Kappa's statistic

## SUPPLEMENTARY FIGURE LEGENDS

Figure 1S: Remaining forest in each biogeographical sub-region (BSR) of the Brazilian Atlantic Forest region: (a) Araucaria, (b) Bahia, (c) Diamantina, (d) Interior, (e) Pernambuco, (f) Serra do Mar and (g) São Francisco. Source of map: SOS Mata Atlântica Foundation, 2005.

Figure 2S: Size distributions of remaining forest fragments within each biogeographical sub-region (BSR) of the Brazilian Atlantic Forest region.: (a) Araucaria, (b) Bahia, (c) Diamantina, (d) Interior, (e) Pernambuco, (f) Serra do Mar and (g) São Francisco. %A: percentage of total area; %NP: percentage of number of fragments.

Figure 3S: Amount of forest habitat under variable depth of edge effect for the biogeographical sub-regions (BSRs) of the Brazilian Atlantic Forest region. The area is cumulative, and the largest amount for each region represents the total remaining forest cover of that region. Edge depths of 100 and 250 meters are highlighted. See Table 1 for BSR abbreviations.

Figure 4S: Largest cluster size of functionally connected habitat forest fragments (ha) for varying functional distance linkages (m), for each biogeographical sub-region of the Brazilian Atlantic Forest region.

Figure 5S: Remaining forest (area and percentage) under conservation protection (nature reserves, NR) and amount of forest per class of distance from nature reserves, within biogeographical sub-regions of the Brazilian Atlantic Forest region: (a)

Araucaria, (b) Bahia, (c) Diamantina, (d) Interior, (e) Pernambuco, (f) Serra do Mar and (g) São Francisco.

Figure 6S: Land use and land cover map for the Brazilian Atlantic Forest region. We generated an up to date land use map for the entire region using existing official land use maps. Sources: (a) Remnants 2005: SOS Mata Atlântica/INPE (2008); (b) Sugar Cane: [www.dsr.inpe.br/canasat](http://www.dsr.inpe.br/canasat); (c) *Eucalyptus* spp. plantation for the state of São Paulo: Konkra et al. (2005); (d) other classes: Probio/MMA project, <http://mapas.mma.gov.br>. See Fig. 1 for the abbreviations of Brazilian states names.

# Araucária

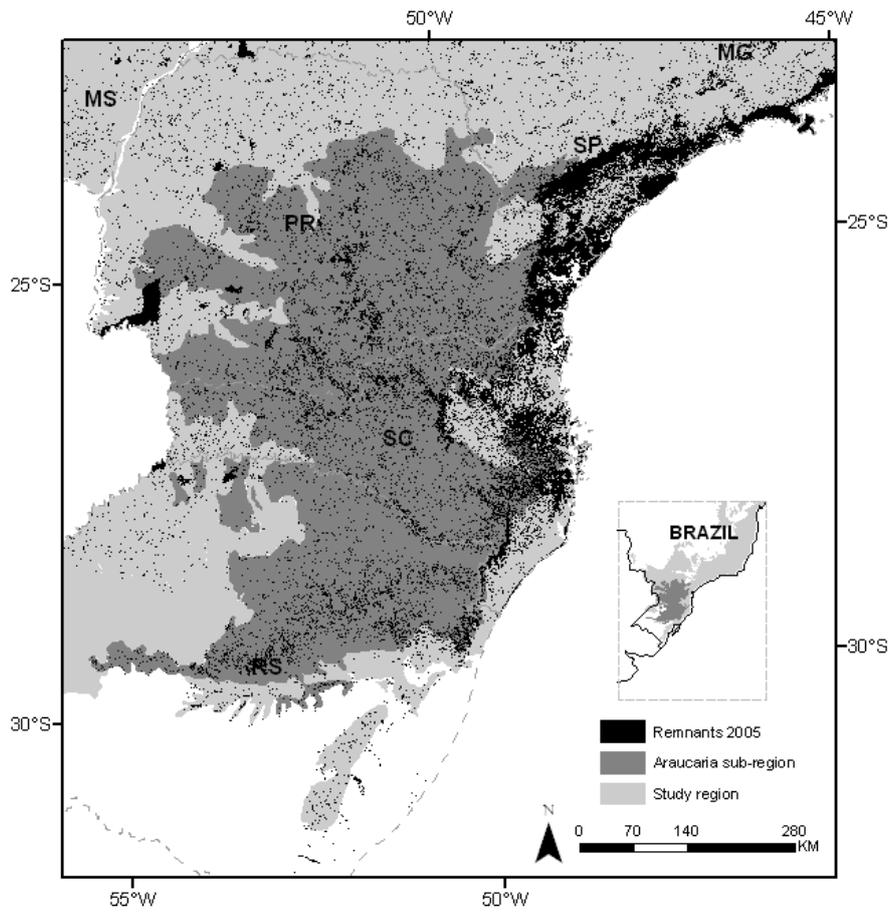


Figure 1S(a)

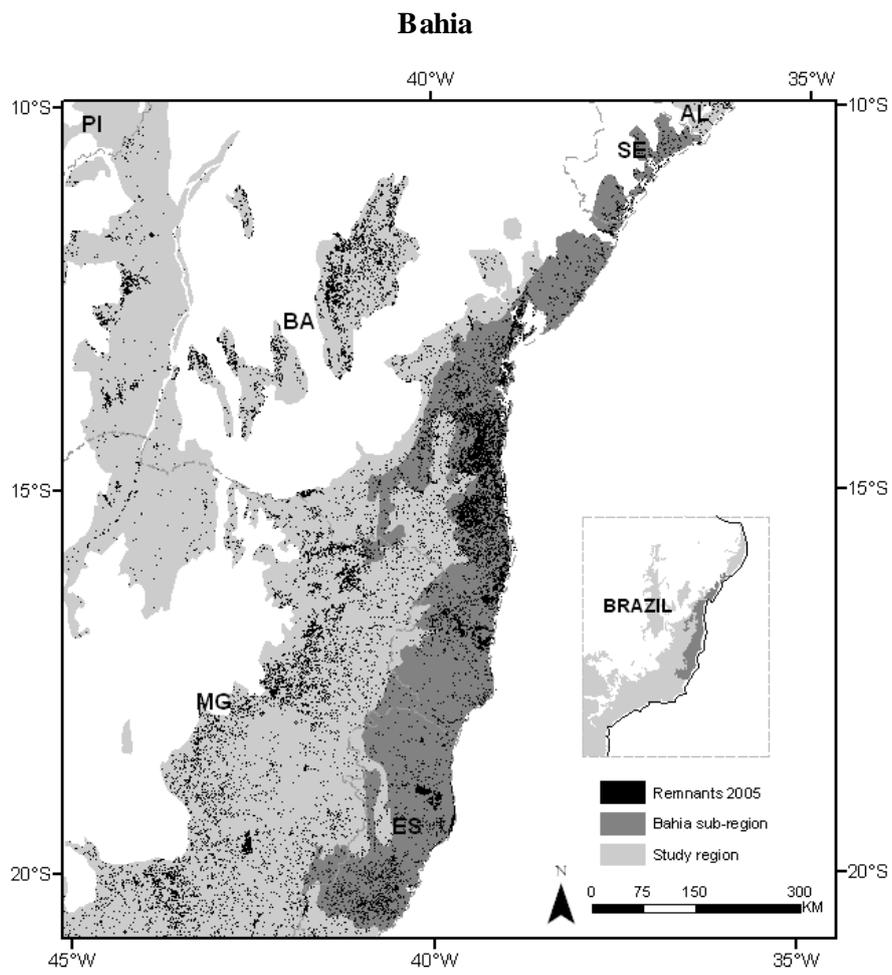


Figure 1S(b)

# Diamantina

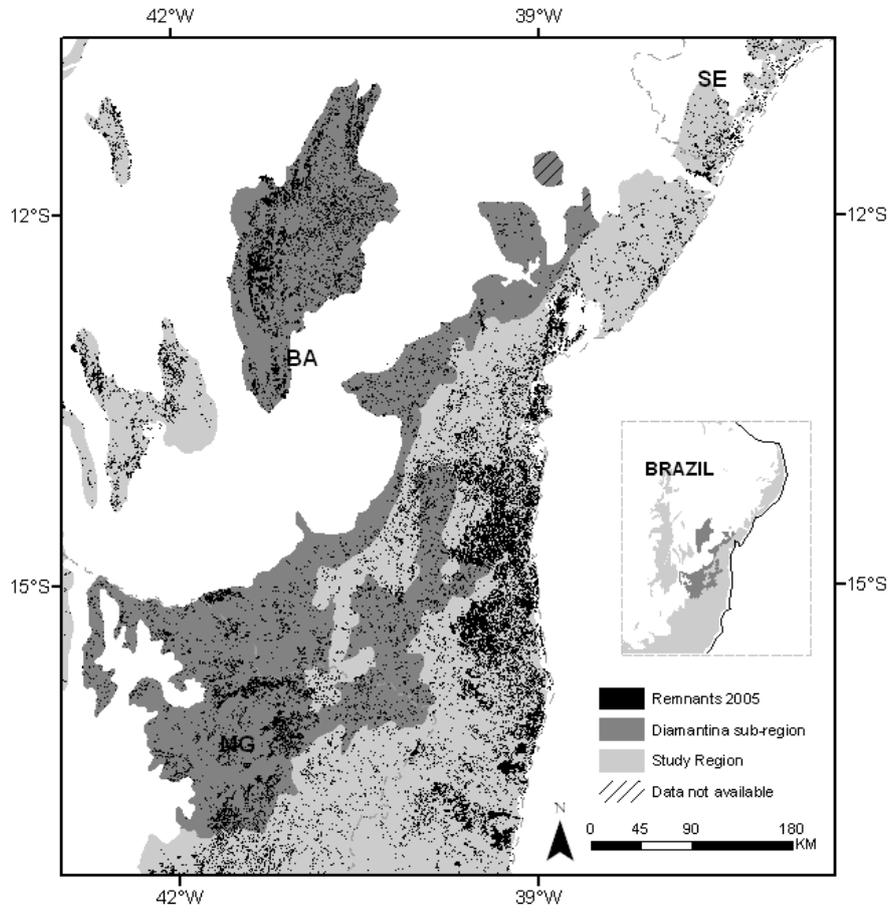


Figure 1S(c)

### Interior

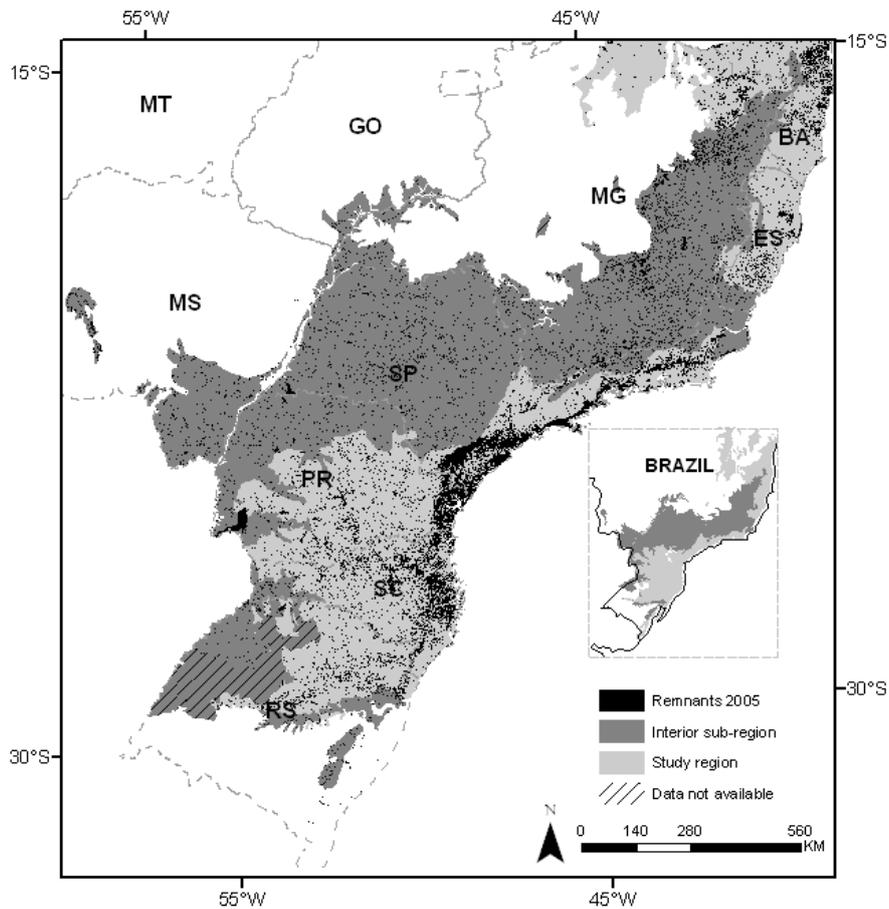


Figure 1S(d)

# Pernambuco

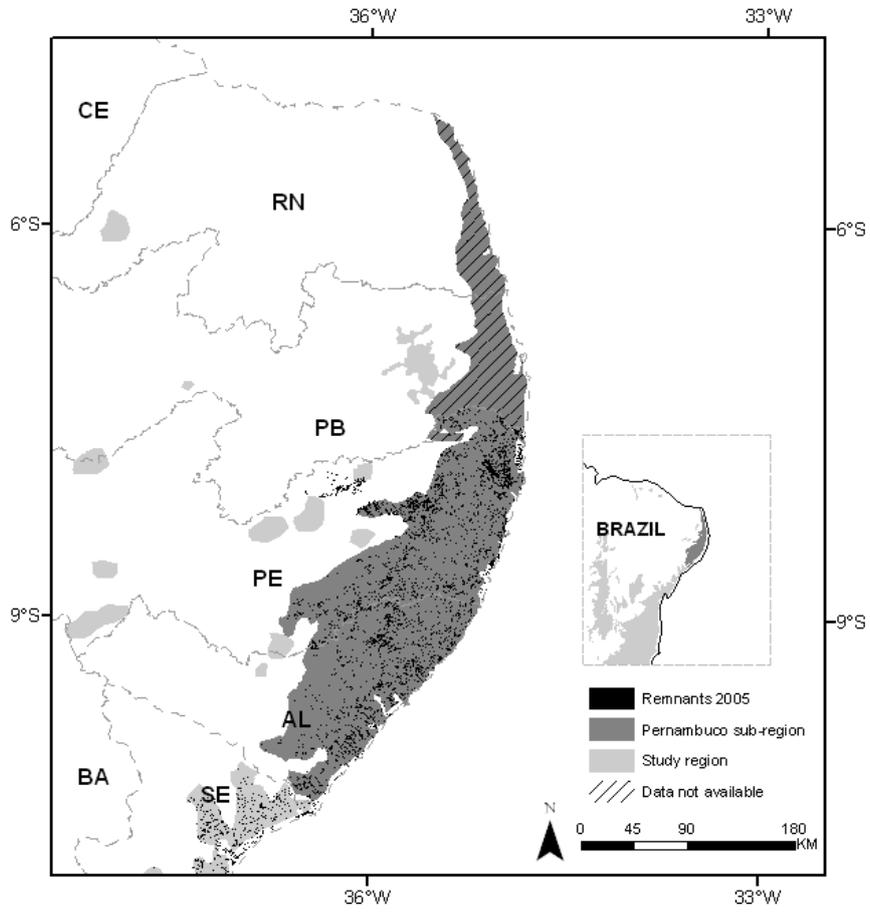


Figure 1S(e)

# Serra do Mar

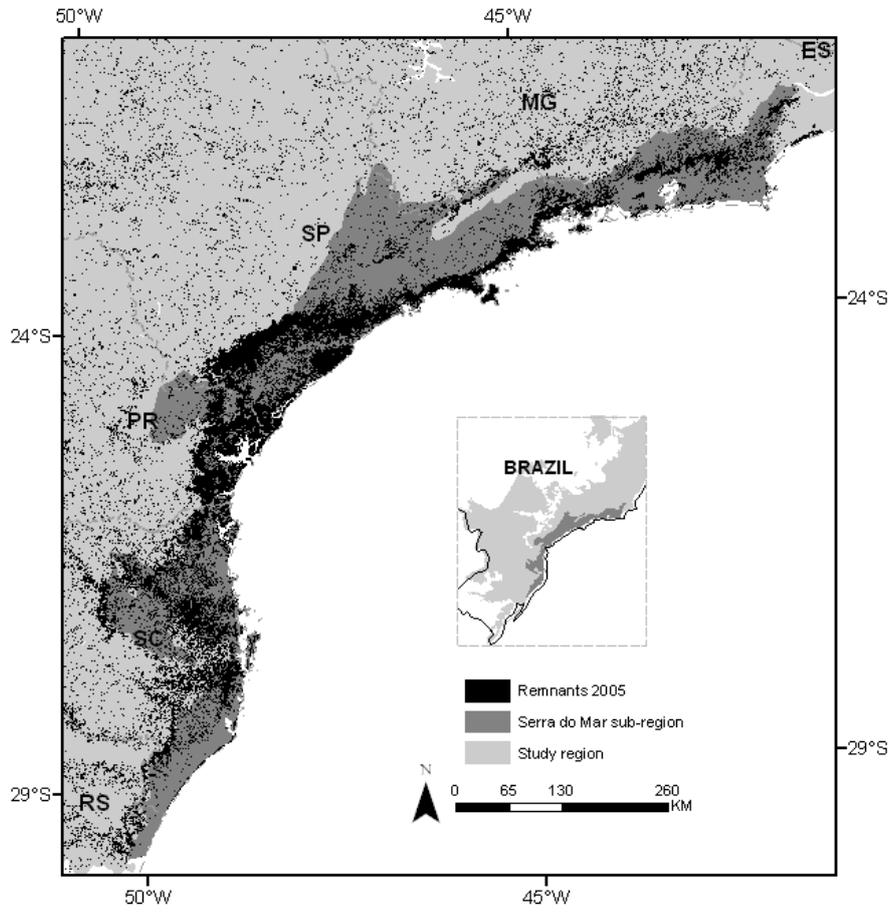


Figure 1S(f)

### São Francisco

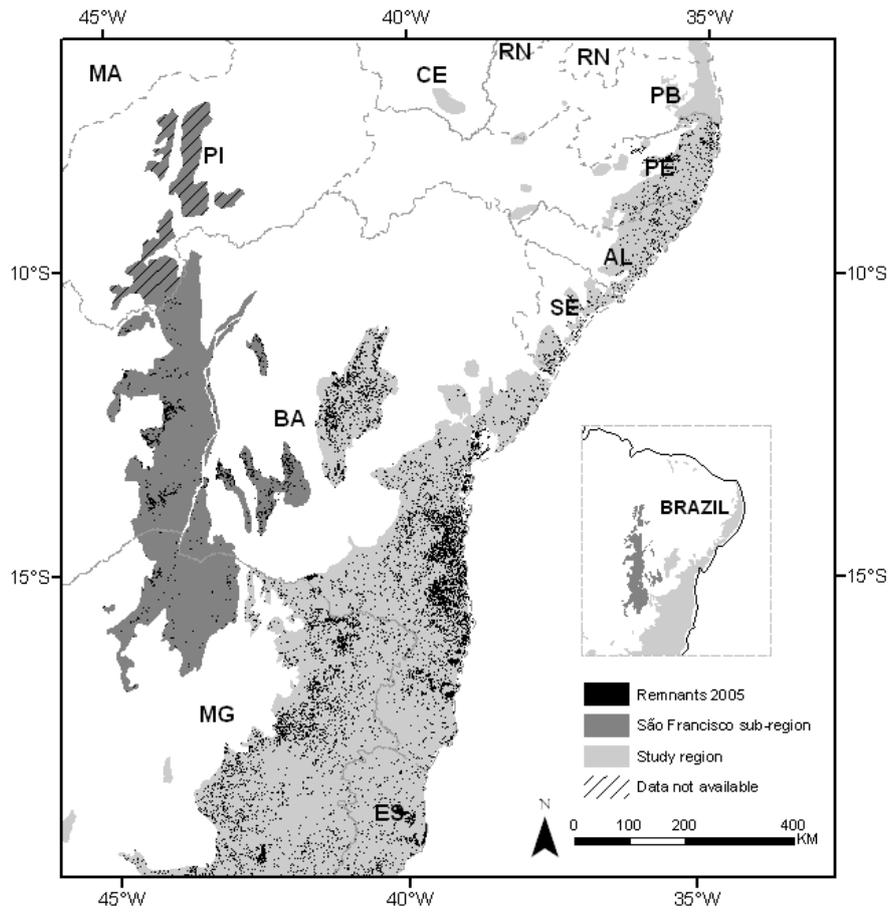


Figure 1S(g)

## Araucaria (arauc)

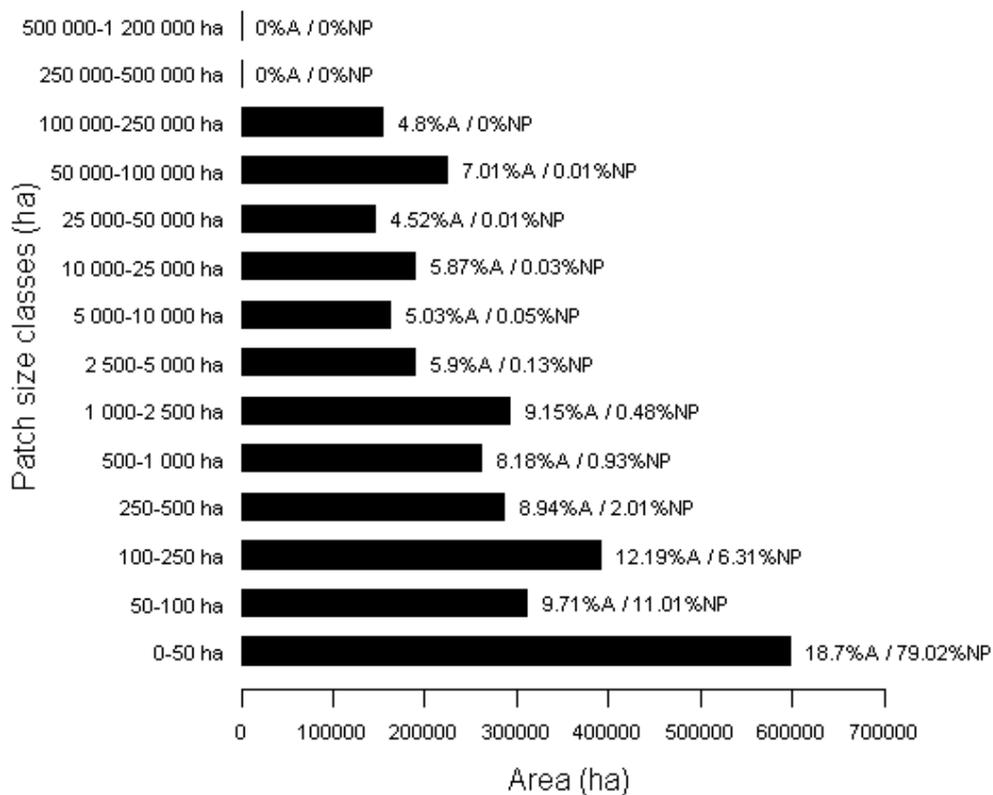


Figure 2S(a)

## Bahia (bahia)

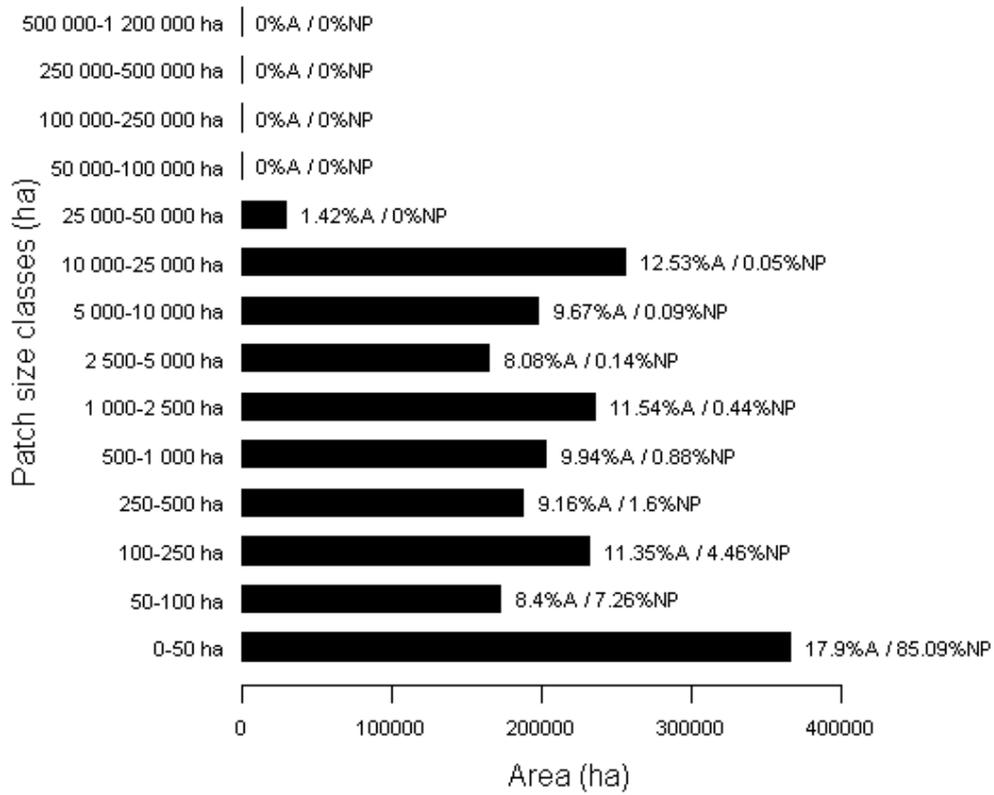


Figure 2S(b)

## Diamantina (diama)

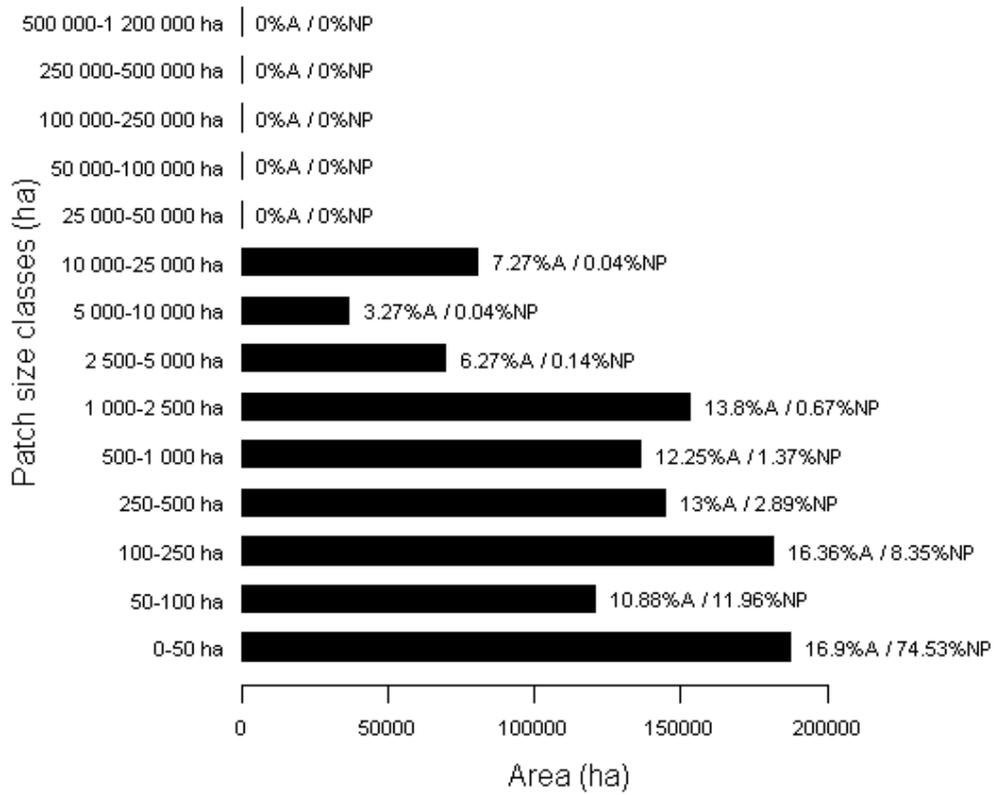


Figure 2S(c)

## Interior (inter)

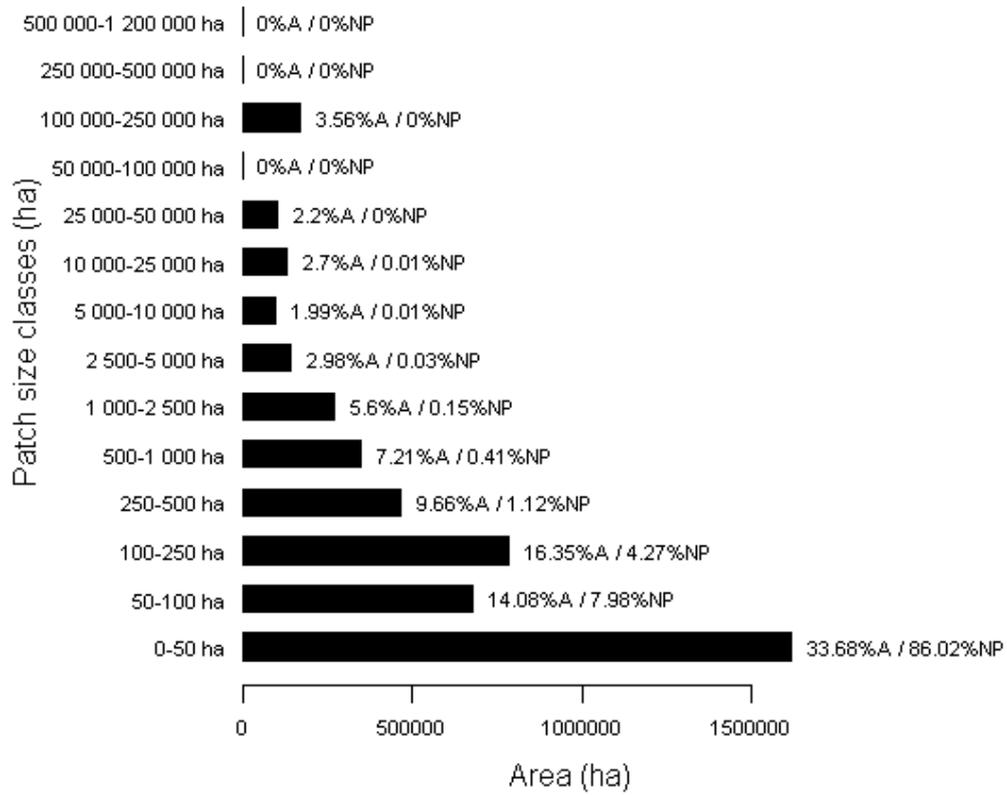


Figure 2S(d)

## Pernambuco (perna)

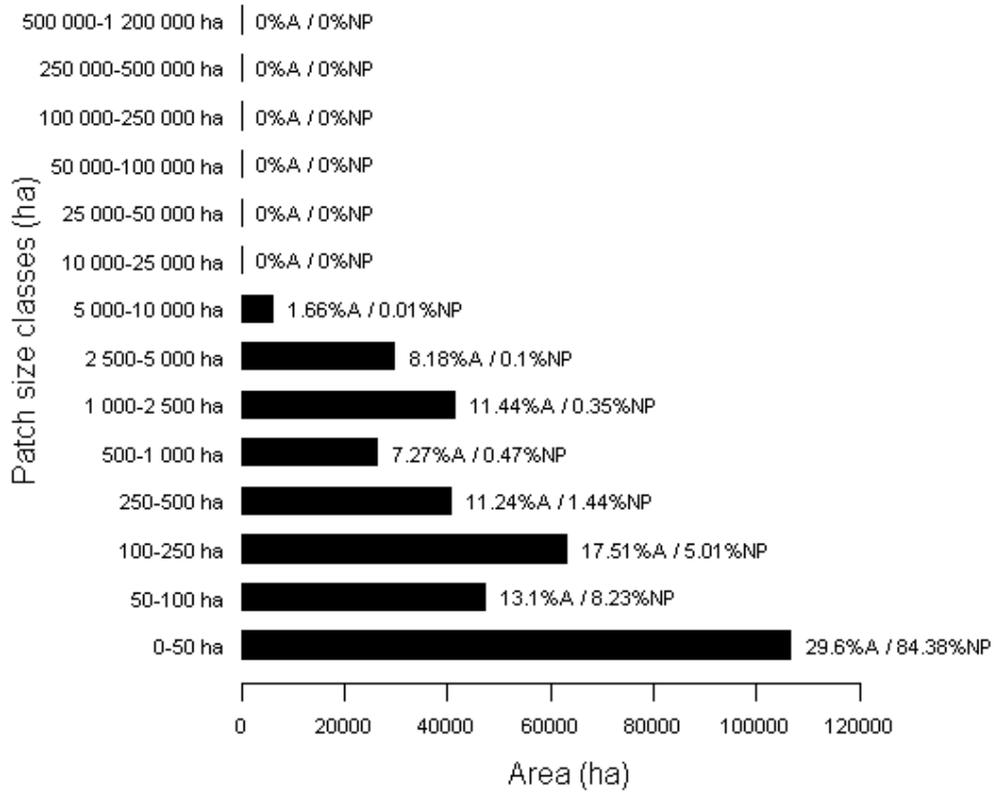


Figure 2S(e)

## Serra do Mar (semar)

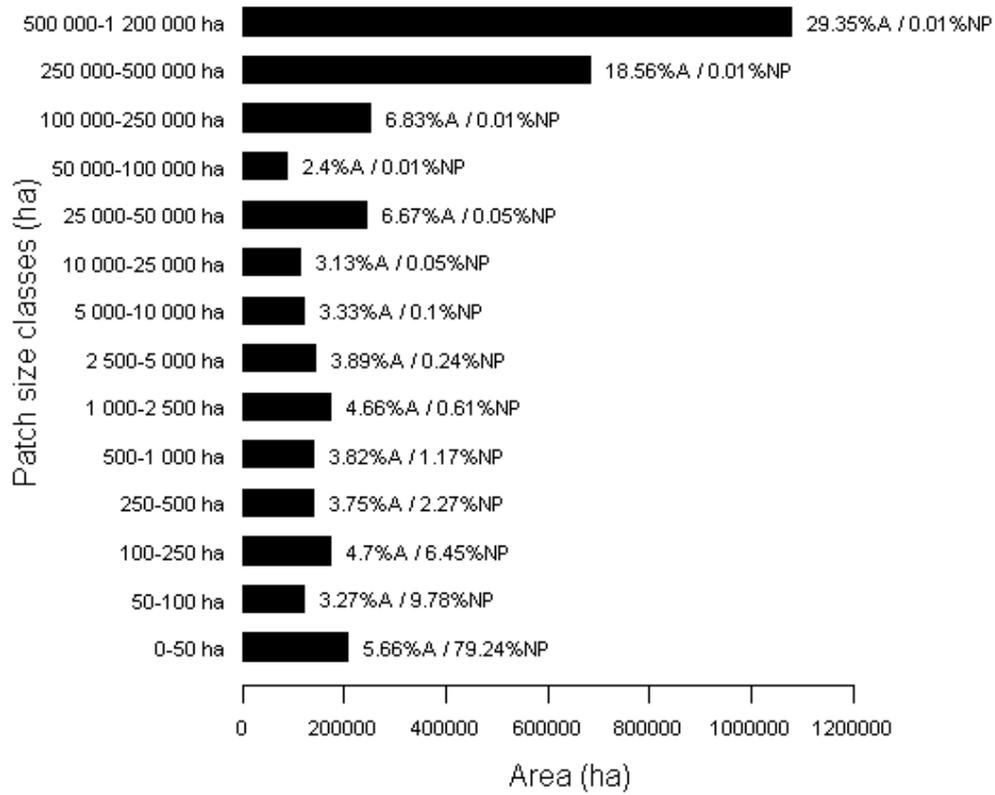


Figure 2S(f)

## Sao Francisco (sfran)

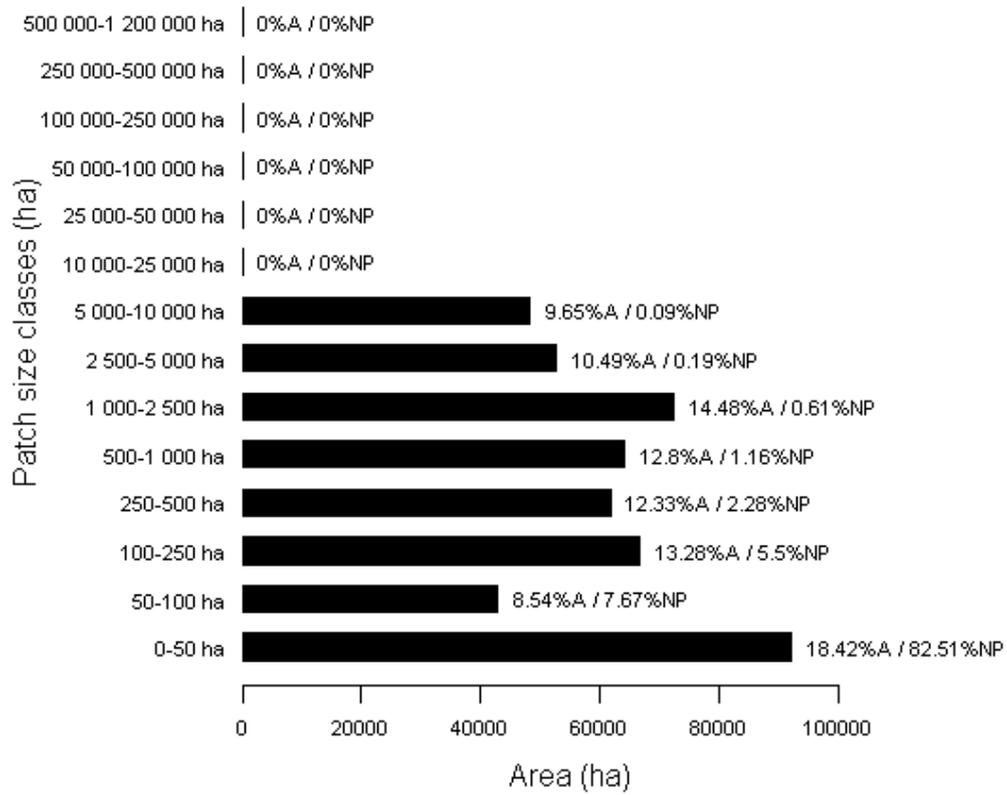


Figure 2S(g)

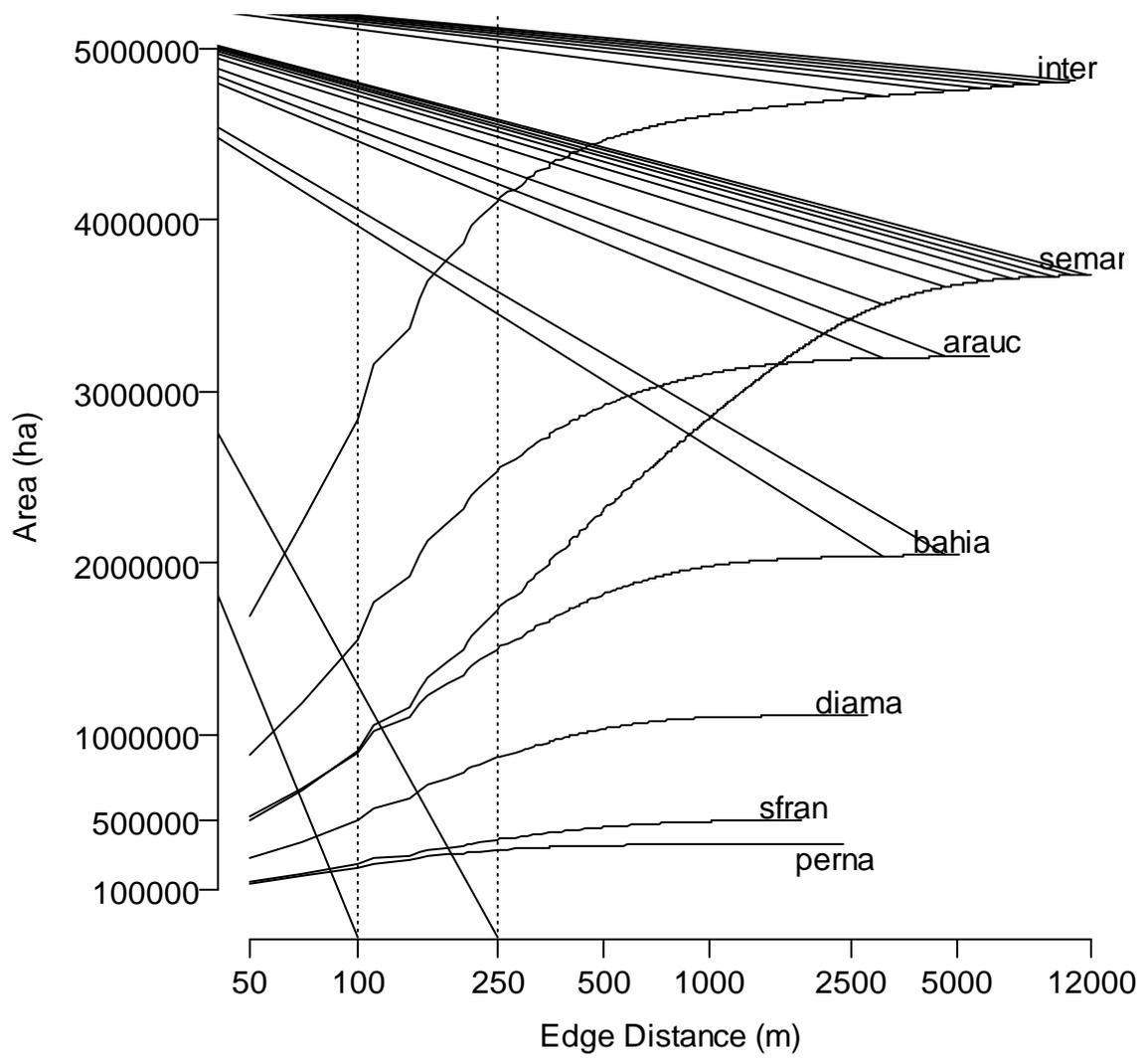


Figure 3S

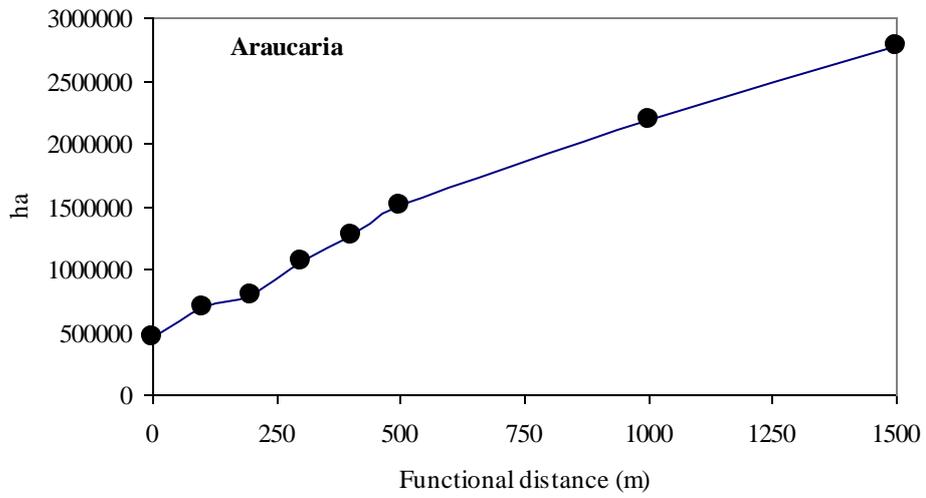


Figure 4S(a)

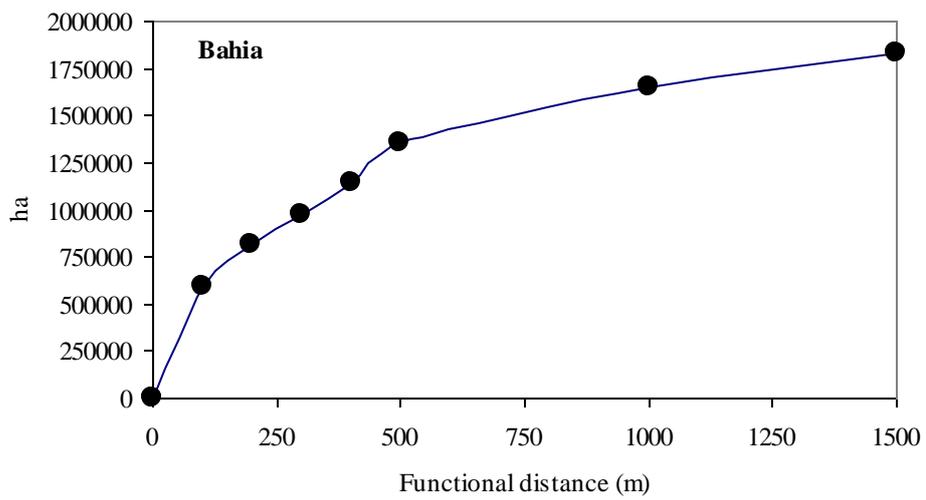


Figure 4S(b)

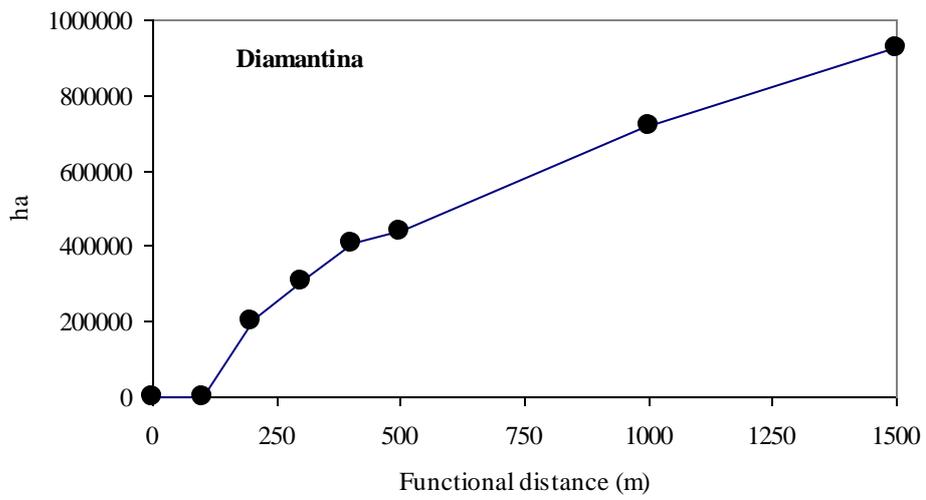


Figure 4S(c)

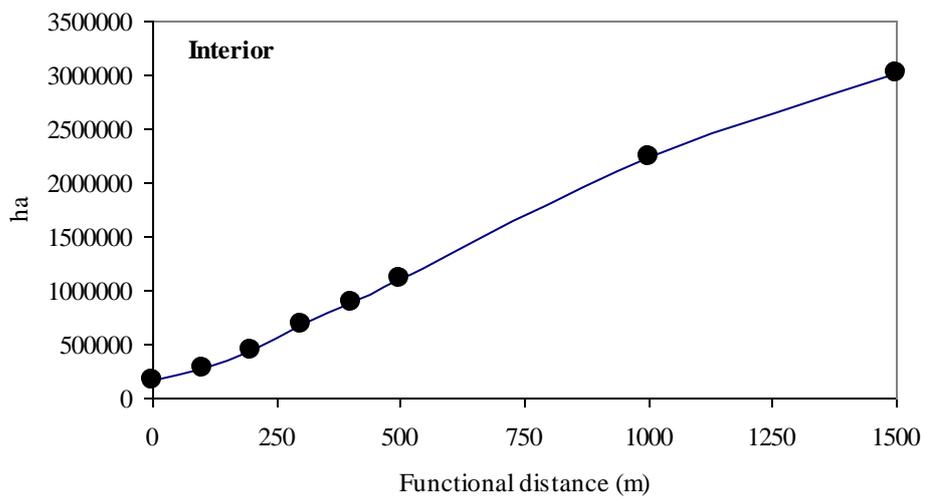


Figure 4S(d)

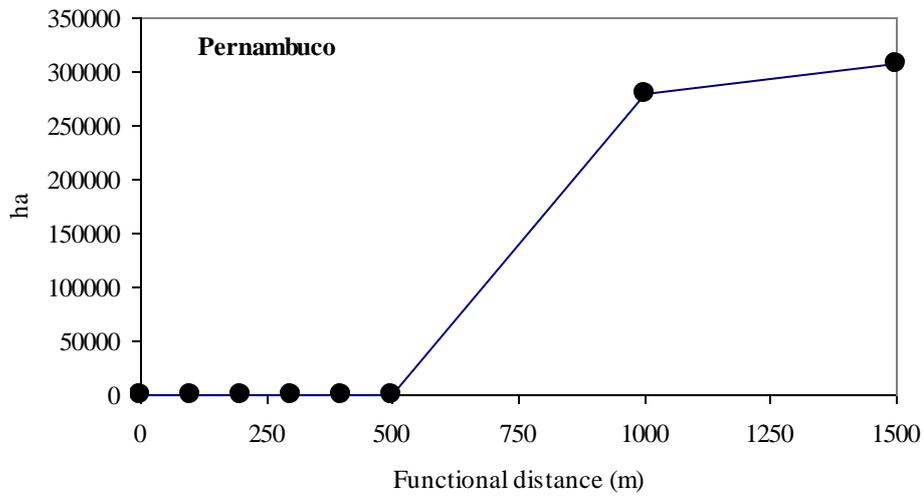


Figure 4S(e)

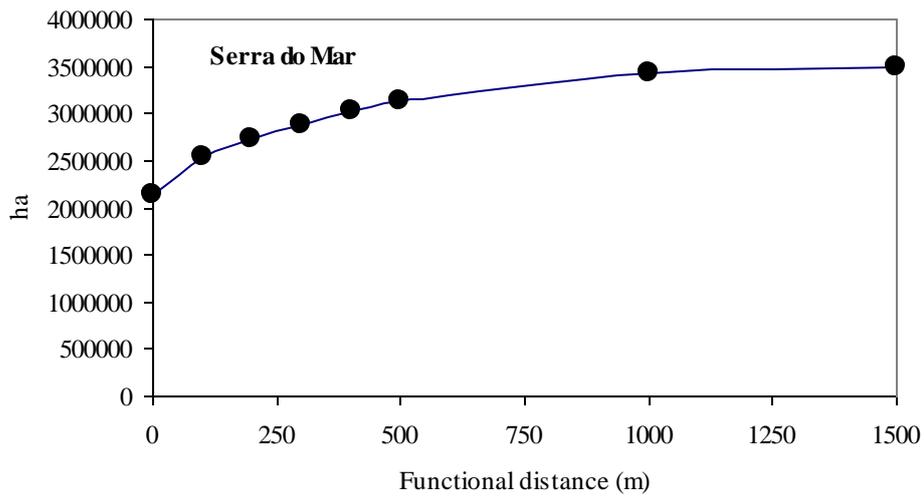


Figure 4S(f)

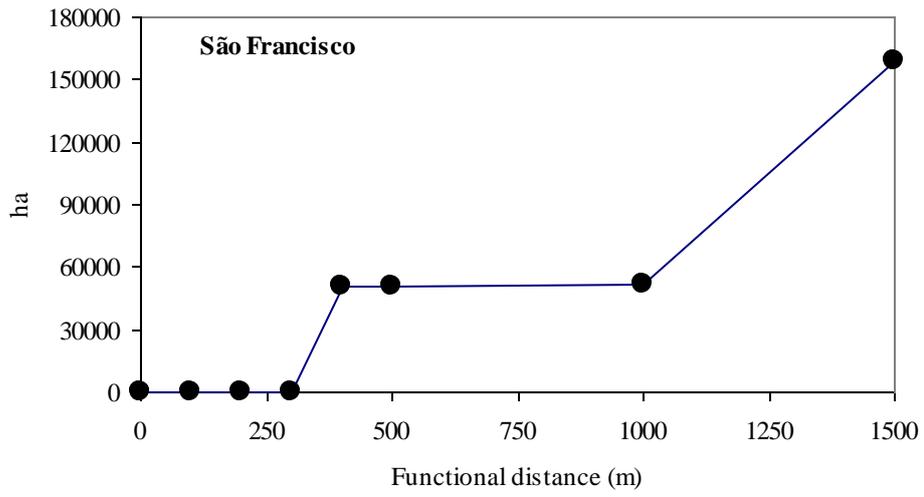


Figure 4S(g)

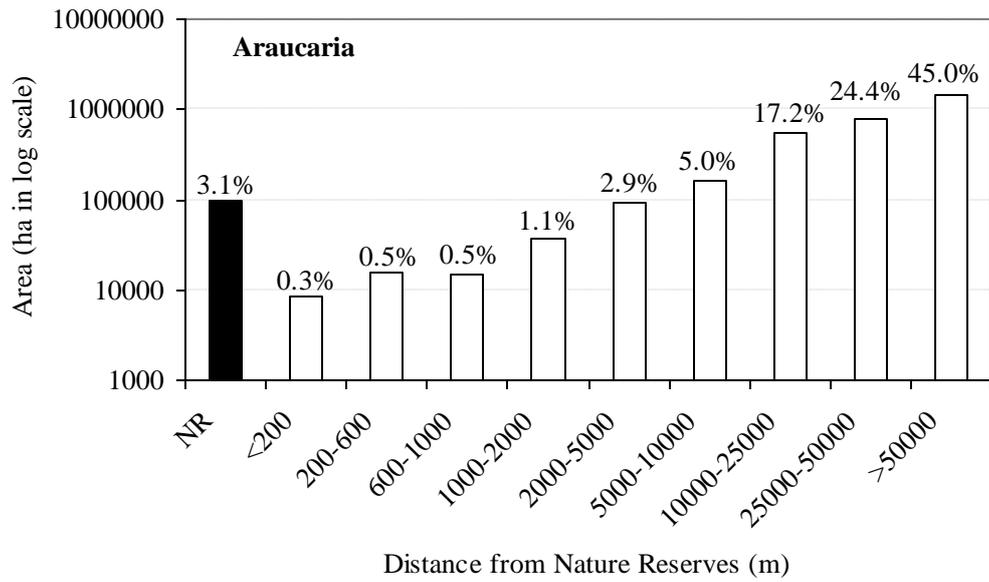


Figure 5S(a)

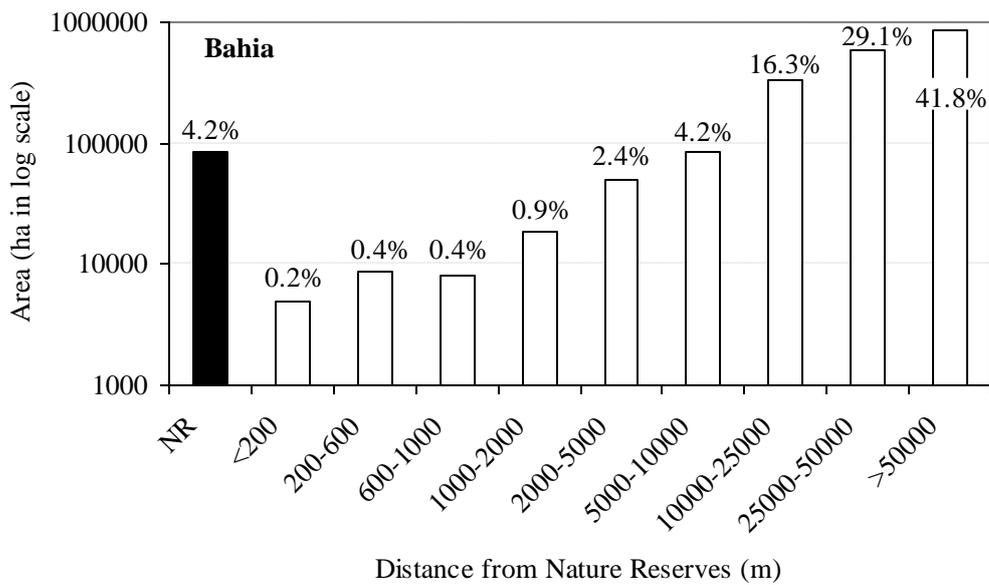


Figure 5S(b)

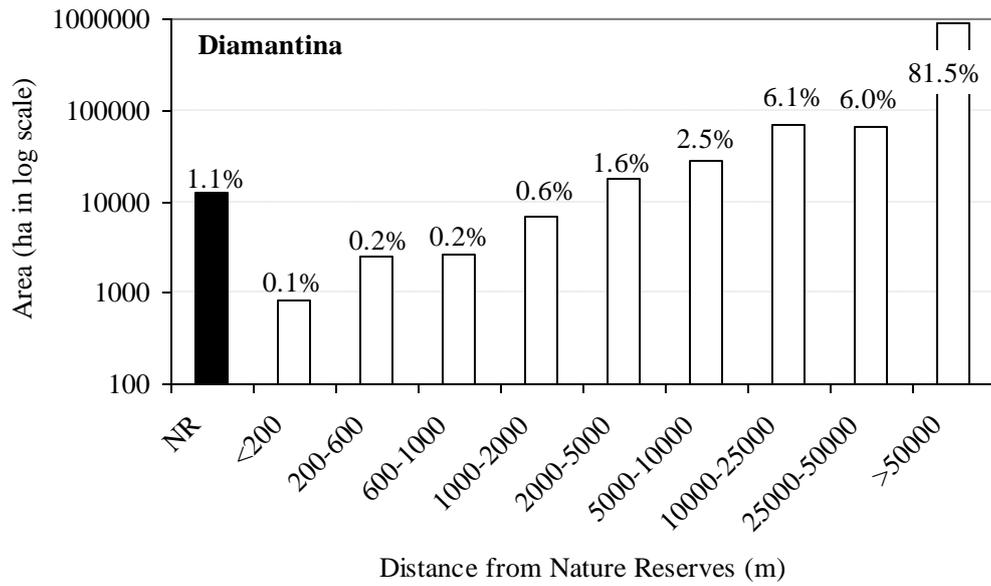


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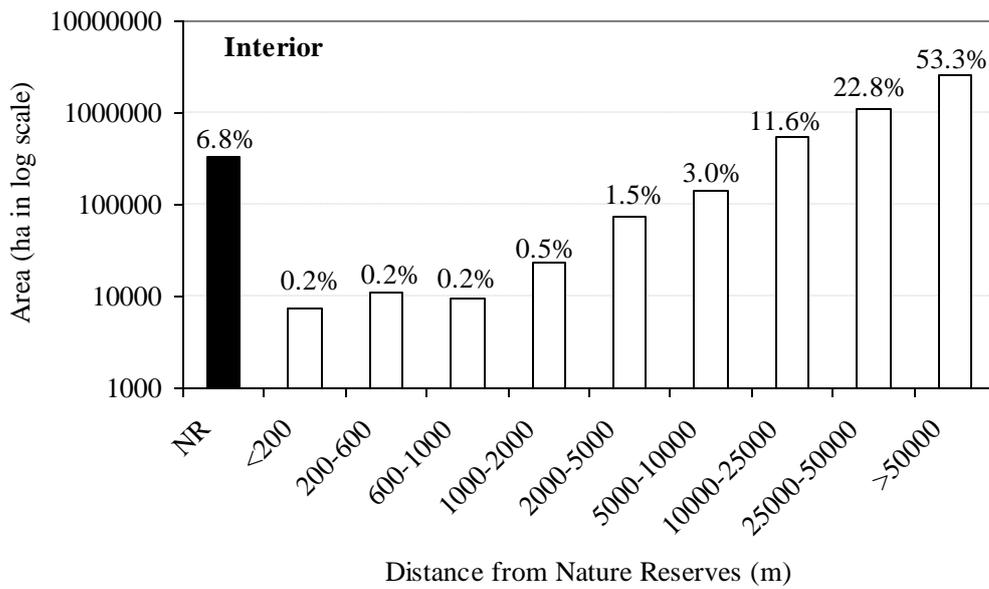


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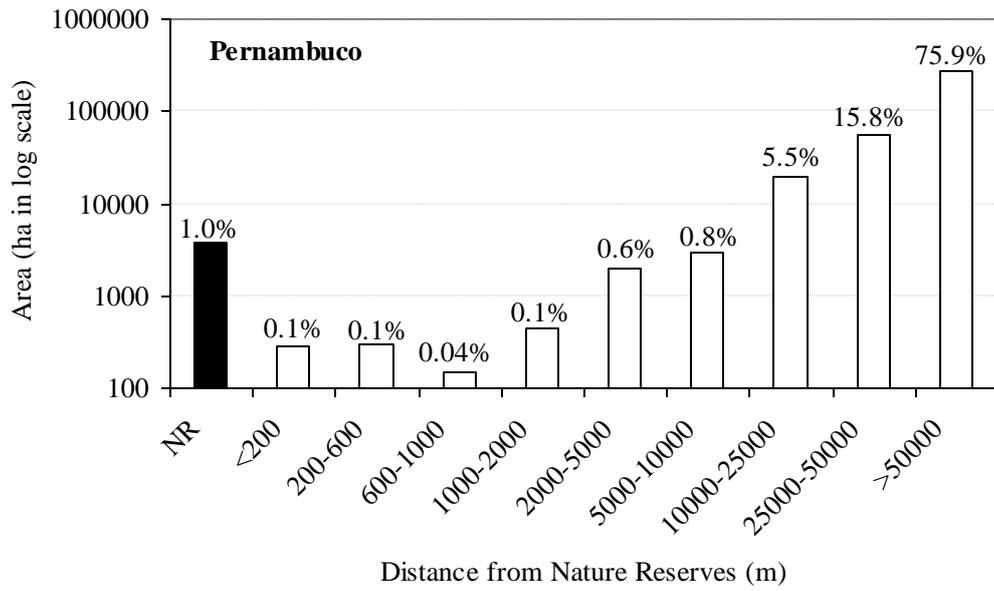


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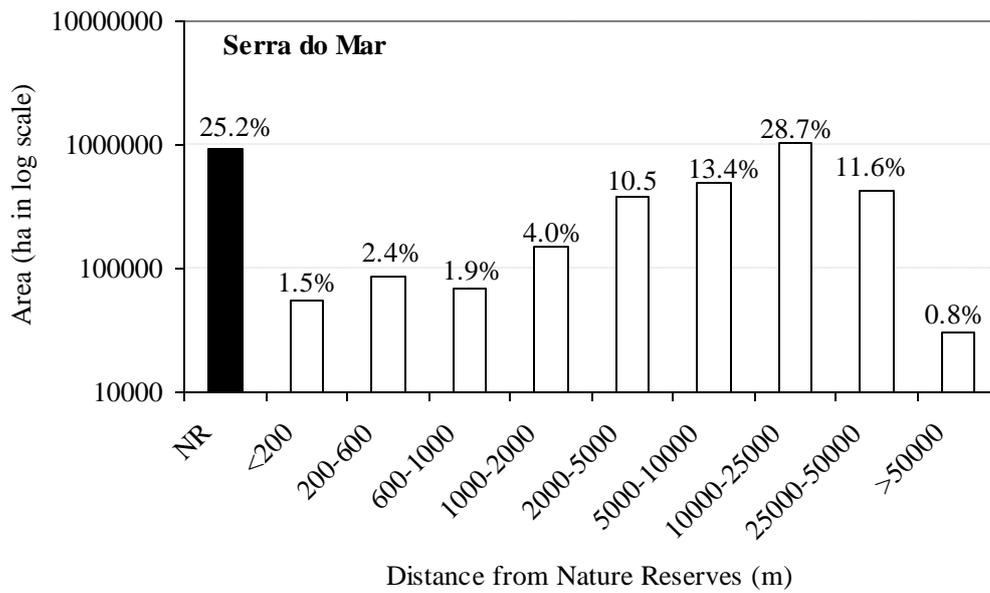


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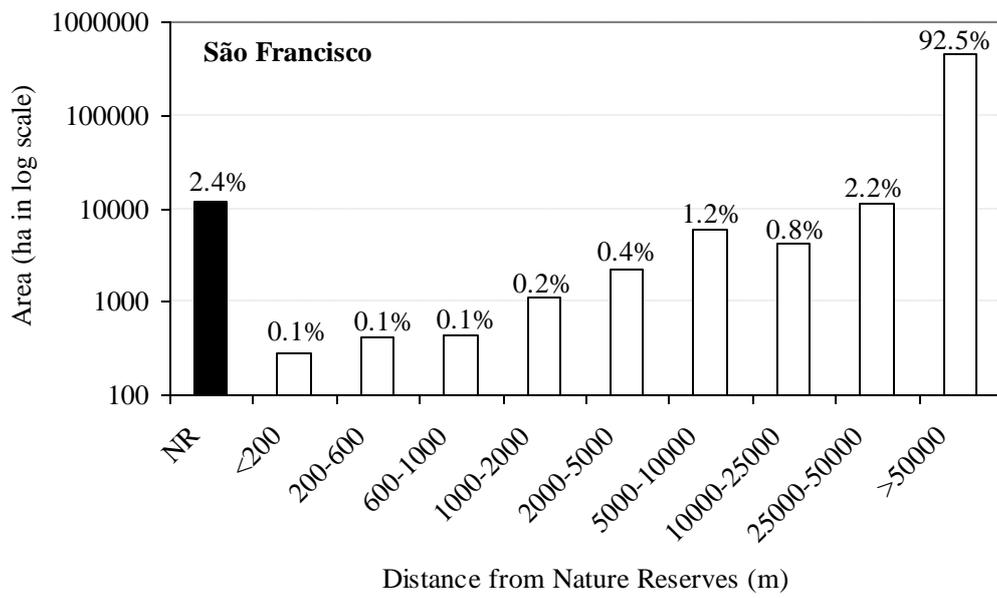


Figure 5S(g)

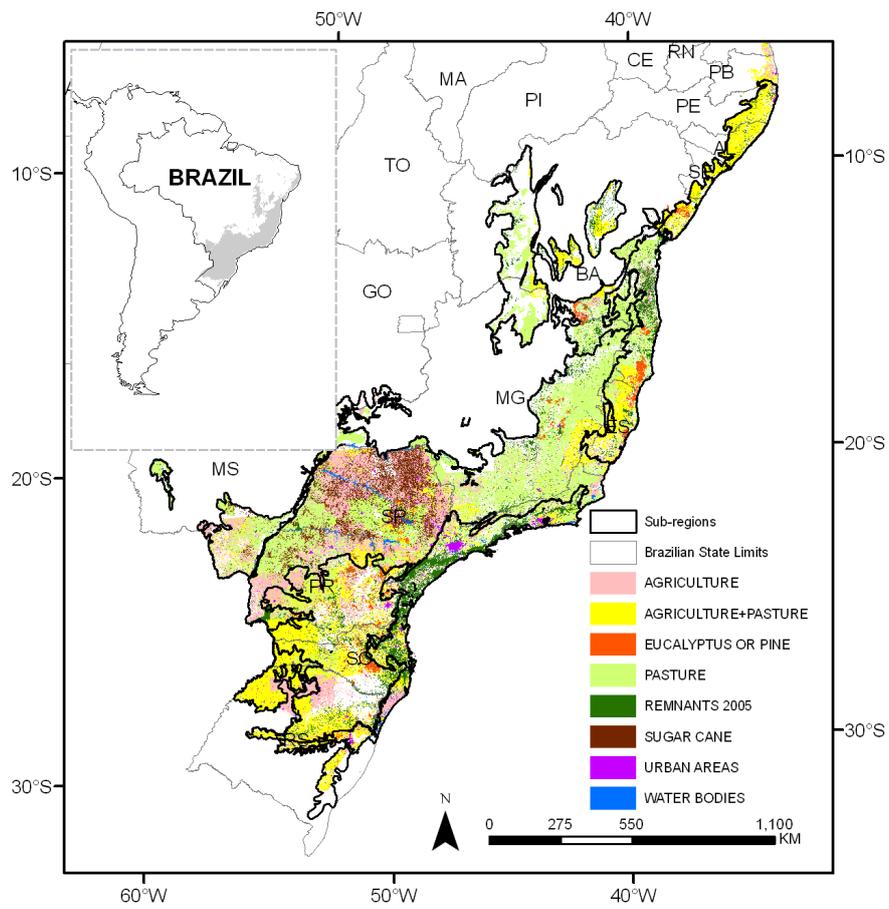


Figure 6S

# CAPÍTULO III

*The Brazilian Atlantic Forest: a shrinking biodiversity hotspot.*

Milton Cezar Ribeiro, Alexandre Camargo Martensen, Jean Paul Metzger, Marcelo Tabarelli e  
Fabio Scarano

Artigo submetido para publicação no livro **Biodiversity Hotspots**, a ser editado pela *Springer* sob organização de Frank E. Zachos e Jan Christian Habel. O artigo foi submetido em março de 2010, sendo aceito com revisões menores em junho de 2010.

## The Brazilian Atlantic Forest: a shrinking biodiversity hotspot

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### Abstract:

The Neotropical Atlantic Forest is one of the top biodiversity hotspots on the planet. Originally the forest extended over 1.5 million km<sup>2</sup> along the South American Atlantic coast, covering tropical and subtropical climates across highly heterogeneous relief conditions, which led to outstanding levels of endemism and species richness of the biota. Unfortunately, the Atlantic Forest has been historically altered by many human disturbances, particularly habitat loss and fragmentation. The forest cover is now reduced to less than 12% of its original extent, including regenerating areas and degraded forests. As a result, many species are currently threatened with global extinction, with populations collapsing on local to regional scales. In this chapter, we review the present state of knowledge of Atlantic Forest biodiversity and point out the main findings by several research groups in recent decades. Additionally, we (1) propose a new subdivision of biogeographical sub-regions into 55 sectors including 2,650 sub-watersheds, using niche theory and bioclimate data; (2) describe the original and present distribution of the Atlantic Forest; and (3) relate the forest distribution to elevation and geomorphometric information (aspect and terrain position). Brazilian legislation, forest protection and restoration efforts, and potential ecosystem services are also examined as key topics driving the future of the Atlantic Forest biodiversity.

## 1. Introduction

The Atlantic Forest is the second-largest rain forest on the South American continent. It once covered more than 1.5 million km<sup>2</sup> along the Brazilian coast, and extended westward into smaller, inland areas of Paraguay and Argentina (Galindo-Leal and Câmara 2003; Ribeiro et al. 2009). Stretching over extensive latitudinal (3°S to 30°S), longitudinal (35°W to 60°W), altitudinal (0- 2900 m a.s.l.), and soil-climate gradients (e.g., 1000-4200 mm annual rainfall), the Atlantic Forest is extremely heterogeneous and encompasses large blocks of evergreen to semi-deciduous forests (the bulk of Atlantic Forest habitat), but also mangroves, swamps, *restingas* (coastal forest and scrub on sandy soils), inselbergs, high-altitude grasslands (*campo rupestre* and *campo de altitude*), and mixed *Araucaria* pine forests (Scarano 2002; Câmara 2003). This diversified mosaic of habitats is currently the home of nearly 20,000 species of plants and 263 mammal, 936 bird, 306 reptile, and 475 amphibian species (Mittermeier et al. 2005). Moreover, outstanding levels of endemism make the Atlantic Forest one of the most distinctive biogeographical units in the entire Neotropical Region (Müller 1973; Prance 1982).

The evolutionary history of the Atlantic Forest has been marked by periods of connection with other South American forests (e.g., the Amazon and Andean forests), resulting in biotic interchange, followed by periods of isolation that led to allopatric speciation (Silva et al. 2004). As a consequence, its biota is composed of both old (pre-Pliocene) and young (Pleistocene-Holocene) species (Silva and Casteleti 2003), which probably evolved within forest refuges that persisted in isolation during periods of drier climates (Silva et al. 2004). This dynamic evolutionary history produced a distinct biota consisting of five well-defined species centers (Silva and Casteleti 2003), with endemism rates ranging from 30% in birds to 44% in plants (Mittermeier et al. 2005). Additionally, the high level of species endemism combined with environmental heterogeneity has allowed the Atlantic Forest to sustain exceptionally high levels of alpha and beta diversity in many groups, including plants, mammals, and butterflies (Brown and Freitas 2000; Costa et al. 2000; Oliveira-Filho and Fontes 2000).

Despite its extraordinary biodiversity and immense endemism rate, the Atlantic Forest has experienced relentless habitat loss since the arrival of European colonists in the 16<sup>th</sup> Century. A massive agricultural expansion in the colonial period, followed by industrialization and urban development, have profoundly affected the Atlantic Forest biota, which is now confined to only ~11.7% (163,377 km<sup>2</sup>) of its original extent in Brazil (Ribeiro et al. 2009), 24.9% (11,618 km<sup>2</sup>) in Paraguay (Cartes and Yanosky 2003; Huang et al. 2007, 2009), and ~38.7% (9,950 km<sup>2</sup>) in

northern Argentina (Chebez and Hilgert 2003; De Angelo 2009). Furthermore, habitat loss has reached more than 90% in some centers of endemism (Ribeiro et al. 2009), making the Atlantic Forest a global priority for biodiversity conservation, i.e. a biodiversity hotspot sensu Mittermeier et al. (2005). Overall, the Atlantic Forest has been converted into human-modified or anthropogenic landscapes, which are typically agro-mosaics with a dynamic combination of small old-growth forest remnants, early- to late-secondary forest patches on abandoned cropland or pasture, small patches of assisted regenerating forests, agroforestry patches, and managed plantations of exotic trees such as *Pinus* and *Eucalyptus*. Forest clearing is frequently associated with other human disturbances (e.g., hunting, logging, collection of non-timber forest products), which has driven a fraction of the Atlantic Forest's unique biodiversity to nearly complete extinction (Tabarelli et al. 2005). In fact, few tropical biodiversity hotspots are "hotter" than the Atlantic Forest in terms of both existing threats and conservation value (Laurance 2009). Its 700 presently protected areas (Galindo-Leal and Câmara 2003) cover only 1.62% of the total original forest (Ribeiro et al. 2009).

In this chapter, we first document the environmental variability across the Atlantic Forest region, in order to better delimit the distribution of bioclimate over its original extent. We superimposed bioclimate data and the biogeographical sub-regions (Silva and Cateleti 2003), and propose a refinement a new sub-division considering the environmental variability within 2,650 subwatersheds. Land use and historical and current habitat cover is examined at the biome scale in terms of both ecological/geographical distribution and landscape structure. We analyze the historical and present relationship between elevation and geomorphometric parameters (aspect and relief position) and forest distribution. Forest conservation efforts, including Brazilian legislation, are summarized, as well as key topics regarding ecosystem services and forest restoration. Finally, we examine potential perspectives, threats, and opportunities for Atlantic Forest conservation, and offer some general insights into the prospects for the persistence of biodiversity in human-modified tropical forest landscapes worldwide.

## **2. Refining the biogeographical division of the Atlantic Forest using bioclimate data**

To characterize the Atlantic Forest region and refine the already well-established biogeographical division of the Atlantic Forest (Silva and Castelelli 2003), we used bioclimate and elevation data. Using data on bird, butterfly, and primate distributions, Silva and Cateleti (2003) proposed a partition of Atlantic Forest into eight biogeographical sub-regions (hereafter

BSR), five as centers of endemism (Bahia, Brejos Nordestinos, Pernambuco, Diamantina, and Serra do Mar) and three as transition zones (São Francisco, Araucaria, and Interior Forests; see Figure 1). Although this sub-division documents the major patterns of biodiversity distribution, with clear consequences for conservation planning, here we advocate for its refinement.

Humboldt and Bonpland (1807) recognized the importance of climate for species and biodiversity distribution. This recognition later merged with the ecological niche concept (Grinnell 1917), defined as the range of ecological conditions in which a species can occur spatially. Hutchinson (1957) clarified how species and environment are interrelated, using his multi-dimensional “hyper-volume” theory. Specifically, his concept merged autecology and predictive geographical modeling. Ecological niche models basically depict the relationship between species records and a set of environmental conditions, building mechanistic models that allow the extrapolation of potential biodiversity patterns and species occurrences (Guisan and Zimmermann 2000; Guisan and Thuiller 2005).

Environmental or spatial subdivisions can be determined at different spatial and temporal scales (Fortin and Dale 2005; Wagner and Fortin 2005). For macro-regional (> 1 million ha) and continental scales, several datasets are now available from the Internet, particularly related to bioclimate information. The most commonly used database is WORDCLIM 1.4 (<http://biogeog.berkeley.eu>, Hijmans et al. 2005; Ramirez and Jarvis 2008), which covers the entire globe with a ~900 m spatial resolution. Although the main applications of these map databases are in modeling species distributions, we used the bioclimate information to refine the biogeographical divisions of the Atlantic Forest. We searched for a unique congruence of climate conditions that could disclose some particular environmental circumstance that might be distinct within the biogeographical region. Based on the results, we proposed to fine-tune the Atlantic Forest subdivision.

#### *Proposed subdivision for BSRs*

We used 19 environmental layers of WORDCLIM 1.4 (Hijmans et al. 2005; Ramirez and Jarvis 2008), and an elevation map to characterize the environmental niche amplitude of the region, as was previously used to model species distribution in the Atlantic Forest (Durães and Loiselle 2004; Acosta 2008; Torres et al. 2008; Murray-Smith et al. 2009; Fernandez et al. 2009; Marcelino et al. 2009; Siqueira et al. 2009; Loiselle et al. 2010). Because of the high colinearity between the environmental and elevation maps, we conducted a PCA analysis to reduce

dimensionality (for details of the method, see Loiselle et al. 2010). The first four PCA axes accounted for 92% of the variance, with the first two axes covering 71%. Axis 1 was mainly correlated with the annual mean temperature and the mean temperature in the coldest quarter of the year, while axis 2 was more influenced by elevation, precipitation in the wettest month, precipitation seasonality, and precipitation in the wettest quarter. Axes 3 and 4 (accounting for 21% of the explained variance) were mainly correlated with annual precipitation, precipitation in the warmest quarter, and the annual temperature range.

To map different environmental gradients (see Figure 1b,c, and d for PCs 1, 2, and 3, respectively), we plotted the bioclimate-derived PCA axis on a 5<sup>th</sup>-order sub-watershed division (hereafter SWS; Pfafstetter, 1987). The SWS is important in this process because it allowed us to divide the entire Atlantic Forest into ~ 2,650 parcels, with a size range varying widely between the extremes of fine size for modelling and management (38% of the parcels are < 10 000 ha, and 60% < 50 000 ha). Few SWS ( $n=25$ ) are > 500 000 ha in size. The most common classes of SWS (<50 000 ha) are ideal for regional planning, mainly because this size allows the incorporation of landscape-level features that are important for conservation and restoration planning. Several studies across the world (Australia: Radford et al. 2005; Canada: Polakowska 2010; Brazil: Pardini et al. 2005, Martensen et al. 2008, Barreto et al. 2010; US: Urban and Keitt 2001; Tasmania: Whiteley 1999) have adopted 10 000 ha as the size of the study region or the grid-cell subdivision. Therefore, we superimposed the SWS with PC axes on the BSRs proposed by Silva and Casteleti (2003), and produced scatter-plots of paired PC1 to PC4. Although the BSRs can be clearly identified as forming groups, Figure 2 shows that there is considerable overlap between the analyzed BSRs on the bioclimate (PCs) space

Because our objective in this analysis was to generate a more detailed sub-division of the Atlantic Forest, we combined the cluster analysis with the BSRs suggested by Silva and Casteleti (2003). The results of this superposition are shown in Figure 3. We divided the Atlantic Forest into 55 small sectors, and the number of divisions were proportional to the sizes of the BSR (Table 1), which means that the BSRs contain similar heterogeneity within them.

Only two subdivisions have more than 45% of natural vegetation, one in the Araucaria subregion and one in Serra do Mar (Table 2). All others have less than 25% of forest cover, and only four of them have more than 20%, one in Bahia, one in Diamantina, one in Serra do Mar and another one in the Araucaria BSR. Most of the sub-divisions have less than 10% of forest, which below the minimum percentage for biodiversity conservation (Secretariat of the

Convention on Biological Diversity 2002). In the Araucaria Forest most of the sub-divisions are covered by mixed forest, while in the Serra do Mar and Bahia, most of the forests are dense forests (Table 2). In the Interior Forest BSR, most of sub-divisions semidecidual forest are predominant, while in Diamantina and São Francisco BSRs the decidual forest is more common. In the Pernambuco semidecidual forests and open forests are the more common, as well as the restingas close to the ocean. The drier sub-divisions are located in the Diamantina and São Francisco regions, presenting less than 800mm per year, whereas the wettest subdivisions are located in Araucaria, reaching as much as 1900mm per year and also in the Serra do Mar and Interior Forest BSRs. In the Bahia and Pernambuco BSRs, the average annual rain fall is above 1200 mm. In the interior Forest, some of the sub-divisions present average temperature below 20oC, while all in Serra do Mar and in Araucaria Forest presented averages below 20oC. In all other subdivisions, the average temperature is above 20°C.

This new sub-division allows a better representation of the Atlantic Forest region considering not only the biogeographical data of Silva and Casteleti (2003), but also information on bioclimate and altitude. Field studies should now be conducted to understand the amount of biodiversity variation between subunits, to properly categorize the Atlantic Forest biota in order to support conservation plans.

### **3. Altitudinal ranges and geomorphometric parameters across the Atlantic Forest distribution**

Deforestation is recognized worldwide as a process that follows non-random patterns (Seabloom et al. 2002). Soil fertility, economic interests, and proximity to urban settlements and roads are important factors that drive forest loss and fragmentation in tropical regions (Laurance et al. 2001; Gardner et al. 2009). In the Atlantic Forest, deforestation and regeneration processes are clearly influenced by topography, land use, and urban areas (Silva et al. 2007; Teixeira et al. 2009; Freitas et al. 2010). Silva et al. (2007) also found that forest cover in part of the Atlantic Plateau of São Paulo was positively correlated with steeper slopes and higher altitudes (> 932 m), but was not influenced by slope orientation.

#### *Elevation ranges*

Recently, Tabarelli et al. (2010) quantified the original and present forest distribution across elevation ranges for the entire Atlantic Forest. Originally, more than 80% of the forest

occurred at elevations from 200 to 1200 m, and particularly between 400 and 800 m (Figure 4). The original trends of the proportion of forest distribution between elevation ranges are still perceptible in the present remnants, but the percentage of forest remaining within each elevation range has changed dramatically (Figure 4). Higher altitudes (>1200 m) retain more than 20% of the original cover, up to 40% for elevations above 1600 m; whereas at altitudes from 400 to 800 m, only about 10% of the original forest still exists.

### *Relief position*

Relief position is important because it influences both species distribution (Kappelle et al. 1995; Burnet et al. 1998) and land cover (Silva et al. 2007; Teixeira et al. 2009; Freitas et al. 2010; Silva 2010), and it can have different effects on the biodiversity. We divided the Atlantic Forest into four relief positions, using a Shuttle Radar Topographic Mission elevation map with 90-m spatial resolution (SRTM/NASA; <http://www2.jpl.nasa.gov/srtm>). The relief positions were the following: channel zones which corresponds to the areas close to the rivers, flat terrains (slope <12% of inclination), hillside (slope >12% of inclination), and mountain ridges. Overall, the steeper relief (hillside) was predominant (61%) in the original Atlantic Forest distribution, containing the largest amount of remaining forest (88,020 km<sup>2</sup>), including more than half of the total remnants (Figure 5). Ridge areas represent only 4% of today's Atlantic Forest, while channel zones and flat terrain cover 16% and 19% respectively. After the long deforestation process, we now only record 7.6% and 10.6% of remaining forest on flat land and hillsides (Figure 5). In contrast, the ridges are the best-protected areas, with 33% of the original habitat cover (Figure 5), and also include some non-forest physiognomies (campo rupestre and campo de altitude). However, as previously stated, ridges cover only a small proportion of the total Atlantic Forest, even in its original distribution.

### *Relief aspect orientation*

Aspect is a circular landform parameter that varies between 0 and 360° and indicates the flow-line direction (Hengl and Evans 2009; Olaya 2009). This parameter is obtained from digital elevation models, and could be a good surrogate for solar energy irradiance, net primary production, biomass accumulation (Lu et al. 2002), and species richness (Silva et al. 2008; Silva 2010). Since biodiversity is related to vegetation biomass and energy intake, understanding the spatial distribution of a forest in different terrain aspects can help to comprehend forest

dynamics, as well as to support restoration programs. As seen above, the Atlantic Forest relief is not equally distributed, and the aspect parameters vary widely along the biome. Here, we analyzed how the original and present Atlantic Forest remnants are distributed, with respect to terrain aspect. We extracted the terrain aspect parameter from the SRTM 1.4 data. We reclassified the original aspect data according to the eight cardinal directions, and quantified the amounts of original and present forest cover. We also combined this information with elevation data

The terrain aspect for the original Atlantic Forest distribution varied from 11% to 16% among the eight directions (Figure 6A). No directional trend was observed for the original forest (Rayleigh test,  $t=0.0076$ ;  $p=0.9445$ ), although the observed distribution was slightly skewed toward the West. In contrast, the remaining forest differs from the original one (Rayleigh test,  $t=0.5842$ ;  $p=0.000162$ ) by having 20% less deforestation in the South compared to the average in the Atlantic Forest. The Southeast and Southwest respectively show 14% and 9% lower deforestation rates than in the entire Atlantic Forest on average, corroborating the pattern of less deforestation southward (Figure 6B). These results are influenced by the Serra do Mar continuum (more than 1 million ha), which has a large fraction of its terrain facing South and Southwest. This reflects a land-use pattern that avoids the south-facing slopes (Mello 2009), given the lower light intensity, which is less favorable for agricultural production (Silva et al. 2007).

Superimposing the present remaining forest, the terrain aspect, and the elevation zones, the South to Southwest orientations were the most represented for the two elevation ranges that include more forest (401-800 m and 801-1600 m; Figure 7). In contrast, the elevation range of 0-100 m showed a slight tendency to include more forest in the West aspect direction. This elevation range is largely composed of coastal lowlands with mountains to the west that shade them in the evenings, particularly from the central part of the state of Rio de Janeiro toward the southern part of the Atlantic Forest. Other ranges of elevation did not show a predominant direction of terrain aspect (see Figure 7).

#### **4. The remaining forest and its spatial distribution**

The Atlantic Forest of eastern Brazil is essentially a complex mosaic of different ecosystems, each of them with a distinct species pool and patterns of human occupation, requiring different conservation and restoration efforts. This complexity and idiosyncrasies need

to be clearly considered when conservation measures are to be taken, since precise actions will be extremely beneficial in terms of time and financial needs.

A shortcut to consider these particularities is to analyze the landscape structure, which has been widely used as a biodiversity surrogate in conservation planning (Williams et al. 2002; Lindenmayer et al. 2008), especially where inventory data and ecological information are not available (Fairbanks et al. 2001). Here we review the available literature on the landscape structural patterns of Atlantic Forest remnants, particularly based on the findings of Ribeiro et al. (2009). We added new analyses and local examples to determine the importance of considering the fine scale in defining regional conservation and restoration planning (Ranta et al. 1998; Teixeira et al. 2009; Barreto et al. 2010). We mainly focused on describing the distribution of forest habitat patches.

### *Forest amount*

Although the overall amount of forest in the entire region is only around 12%, in some regions such as the São Francisco BSR and the Transition Forests the remaining habitat is very limited, as little as 4.7% in the case of the São Francisco (Table 3). In contrast, the Serra do Mar BSR has 36.5% of its original extent covered by forests, which makes it by far the best-protected BSR. All the other areas have 12 to 18% forest cover (Table 3).

Overall the percentage of forest within the 5<sup>th</sup>-order SWS is particularly low (Figure 8). SWS with larger proportions of forest (>55%) are found along the coastal mountain ranges of the state of São Paulo, and particularly in the south-coastal region of São Paulo and the coastal region of Paraná. Outside the Serra do Mar region, only a few highly forested SWS occur on the south coast of Bahia, in the Iguaçú region in the Interior Forests, and also in the state of Rio de Janeiro (Figure 8).

Landscapes with small amounts of forests (< 15%) have been suggested to have biodiversity patterns that are more related to the size of the forest fragments, since the overall connectivity is generally too low to allow forest species to move among the fragments (Martensen 2008). Therefore we expect that in most of the SWS, forest-fragment size would be a good surrogate for species diversity, and the larger patches should be a clear conservation priority. Regions with intermediate proportions of forests (~ 30%) have been shown to be highly influenced by connectivity patterns (Martensen et al. 2008). Such regions should therefore be targeted to increase connectivity, particularly between large remnants and the surrounding

smaller forest fragments. Riparian forests, which are legally protected, are especially important and have proved to effectively protect riverine systems (Silvano et al. 2005; Roque et al. 2010) as well as terrestrial ones (Lees and Peres 2008).

### *Land-use types*

Sugarcane was the first crop to be planted extensively in the Atlantic Forest, beginning early in the 16th Century and starting an intensive forest-conversion process. Later, coffee plantations in the states of Rio de Janeiro, São Paulo, and Paraná pushed the logging frontier forward. Today, large properties of sugarcane plantations and *Eucalyptus* and *Pinus* plantations share the landscapes that were formerly covered by Atlantic Forests and small patches of agriculture of smallholders, producing large social modifications.

Since the early cycles in Brazil, the general agricultural pattern has been based on large monoculture properties. Even today, this pervasive system continues and land concentration is still enormously high, with 15% of the properties covering more than 75% of the country's farmland (IBGE 2006). Large landowners usually occupy the best farmland, flat or gently sloping (< 15%), leaving the steep hills for the small farming families (Altieri 2009a, b). Small farms comprise more than 84% of the properties, but cover only around 24% of the farmland in the country (IBGE 2006). Although they occupy less than one-fourth of Brazilian farmland, small family properties are responsible for a significant proportion of the country's food base, producing 87% of the manioc, 70% of the beans, 46% of the corn, 38% of the coffee, 34% of the rice, 58% of the milk, 59% of the pork, 50% of the poultry, 30% of the beef, and 21% of the wheat; but only 16% of the soybeans (IBGE 2006). However, in flat areas where mechanization is possible, sugarcane plantations have taken over the land for biofuel (Lapola et al. 2010), which should actually be termed agrofuel (Altieri 2009a, b).

Following this general deforestation pattern, different types of matrix (i.e., non-forest; Gascon et al. 1999) were established in the Atlantic Forest region (Figure 10). Cattle ranching and farming are the two predominant matrices found in the biome, and cover a large part of the Interior Forest sub-region. In the Araucaria and southern Bahia sub-regions, forestry plantations (*Pinus* and *Eucalyptus*; Fonseca et al. 2009; see also Figure 10) are among the most important types of matrix, although farming and ranching are predominant. The state of São Paulo is covered by a mixture of sugarcane plantations (Rudorff and Sagawara 2007; Nassar et al. 2008), farming, ranching (Brannstrom 2001; Durigan et al. 2007), and a growing number of *Eucalyptus*

plantations. The Pernambuco sub-region is also dominated by ranching and farming, with a particular dominance of sugarcane plantations (Trindade et al. 2008; Kimmel et al. 2010; Silva 2010).

Large sugarcane plantations have the greatest impact on the environment. Traditional sugarcane harvesting was based on burning the crop, which causes problems of air pollution and also from the accidental spread of fire into the surrounding forest fragments (Durigan et al. 2007). The mechanization of sugarcane harvesting, although it has reduced previous impacts including the employment of workers in subhuman conditions, which caused severe health problems and even deaths (Silva 2008), has also reduced the connectivity between forest fragments, since isolated trees have been cut down to facilitate mechanical harvesting. Isolated trees considerably increase the connectivity between fragments (Harvey et al. 2004), and thus their loss should be properly compensated by additional connectivity features such as corridors, which can compensate the homogenization caused by sugarcane plantations, especially in the state of São Paulo. Similar recommendations for conservation can be made elsewhere, especially when forest fragments are already interspersed among the plantations.

Adding more complexity to this social dimension, vast *Eucalyptus* plantations are gaining ground, based on huge well-capitalized corporations from other fields that possess the financial power to acquire vast landholdings. These corporations have focused on acquiring the cheap small hilly properties, as forestry technologies evolve to operate on steeper terrain. This process has contributed to urban growth through intensifying migration to urban areas. Forestry has proved to be the “beauty” in some cases where good ecological management practices are employed (Fonseca et al. 2009). In other cases, unfortunately more commonly, forestation is the “beast”, where management is focused only on high productivity, often to the detriment of social and environmental aspects (Zurita et al. 2006).

Another large fraction of farmland in Brazil and in the Atlantic Forest is covered by pastures (Figure 9). Most of them are lightly managed, and still contain scattered trees that sometimes form small forest patches in different early successional stages. Intense debate is continuing about the conversion of these areas into intensively managed fields, especially sugar cane, with claims that this will allow higher production and economic gains. Besides the clear positive financial advantages of these proposals, negative aspects such as decreasing matrix permeability, increasing dependency on non-renewable resources, and increasing the use of chemical products, as well as the far-reaching social impacts of these agricultural practices will

occur in the Atlantic Forest region, while the benefits will be felt mostly elsewhere, such as lowering habitat conversion in the Cerrado and Amazon, since habitat conversion in the Atlantic Forest is already low. From another side, cattle ranching causes large impacts in riparian forests and riverine systems, which could reduce their potential to promote corridor connections between fragments, thus complicating the problem.

#### *Number of forest fragments and their patch size*

The Atlantic Forest is patchily distributed in 245,173 forest fragments of varying size. Although some large fragments still exist, such as those that extend along the coastal mountains of southeast Brazil, especially in the states of São Paulo, Paraná, and Santa Catarina, most of the forest fragments (83.4%) consist of patches smaller than 50 ha, which is expected to severely compromise biodiversity conservation (Lindenmayer et al. 2006; Laurance et al. 2007). Only 77 fragments (0.03% of the total fragments) are larger than 10,000 ha, which highlights the very poor conservation condition of the unique Atlantic Forest biota.

In all BSRs, small fragments (< 50 ha) were by far the most numerous of the remnants. The only distinct pattern occurs in the Serra do Mar region, which in addition to having the largest fraction of fragments smaller than 50 ha, similarly to the other regions, has more than half of its forests in large fragments (>50,000 ha). Moreover, this region is the only one that contains a forest fragment larger than 1 million ha, and also contains the second- and third-largest fragments of the entire remaining Atlantic Forest. In all other regions, the largest fragments are < 250,000 ha, and only the Araucaria Forest (n=4) and the Interior Forest (n=1) also contain fragments > 50,000 ha, respectively the inland forests of Santa Catarina, including the São Joaquim National Park, and the Iguaçú National Park in Paraná. In the Bahia BSR, the largest patch has approximately 29,000 ha, while in the São Francisco and Pernambuco no patch exceeds 10,000 ha, and in Diamantina none is larger than 25,000 ha.

#### *Forest core and edge area*

Land-use patterns in the Atlantic Forest region have generated intensive fragmentation, resulting in an impressive amount of forest edges. Today at least 73% of the remaining forest is located less than 250 m from any forest edge, and 46% is less than 100 m from any edge. Only 7.7% is located farther than 1000 m, and around 12 km is the longest distance that one can penetrate into the forest from any edge. The pattern is similar for every BSR, again with the

exception of the Serra do Mar. Whereas all BSRs have edge forests (100 m from edges) in amounts of at least 40% to as high as 60% in Pernambuco, Serra do Mar has only 25% of its remaining forest less than 100 m from forest edges. This relatively small edge effect is reflected in the higher proportion of core areas, i.e., more than 256,000 ha farther than 2.5 km and almost 57,000 ha farther than 5 km from edges. The largest block in the Atlantic Forest is located in the Serra de Paranapiacaba, in the state of São Paulo, Serra do Mar BSR, which together with the Iguaçú National Park in the Interior BSR are the only two fragments that have forests deeper than 12 km from any edge.

### *Connectivity patterns*

The capacity of a species to cross open areas is directly associated with its potential to maintain sustainable populations in the present fragmented conditions of the Atlantic Forest. Species that are not able to cross open areas, *i.e.* obligate forest species, have a functionally connected mean area of only 64 ha, while a species that are capable of crossing 50 m have a mean functional area of around 200 ha. The largest functionally connected cluster for species capable of crossing 100 m is comprised of the largest fragment of the Serra do Mar and the nearby fragments. This cluster totals more than 2.8 million hectares (18% of the remaining forest), and stretches from the state of Rio de Janeiro all the way south to Rio Grande do Sul, comprising the largest “corridor” of the Atlantic Forest. In the Bahia region, species that can cross short gaps such as 100 m can reach a functional area of 50,000 ha (17% of the remaining forest in the region). In the other BSRs, the distances to reach a functionally connected area of this size are always large, up to 400 m in the São Francisco and more than 500 m in the Pernambuco region.

The mean distance between fragments in the entire Atlantic Forest is around 1441 m, but of course this varies widely. The importance of the small fragments in reducing isolation is enormous. For example, when fragments < 50 ha are excluded, the mean isolation increases to 3532 m, and when fragments smaller than 200 ha are excluded, the mean isolation reaches more than 8,000 m, which highlights the immense importance of these fragments in sustaining viable populations in the region. This is vital in all regions, but is particularly important in the São Francisco and in the Interior Forest, although less so in the Serra do Mar, since most of the remains are clumped in one or a few large fragments.

### *The role of nature reserves in protecting Atlantic Forest biodiversity*

Brazil and South America have the world's largest proportion of land in protected areas (Brockington et al. 2008). However, the rapid increase in the proportion of protected land took place during the last two decades, when the Atlantic Forest biome had already been turned into a myriad of fragments of varying sizes. Thus, the total protected area of the Atlantic Forest today is approximately 2.26 million ha, which represents only 1.62% of the original cover, well below the 10% recommended by the Global Strategy for Conservation (Secretariat of the Convention on Biological Diversity 2002; Rodrigues et al. 2004). Nature reserves encompass 14.4% of the remaining Atlantic Forest, but protect only 9.3% of the remaining forest, since other types of land cover also occur within the reserves. All regions have a small amount of their forest under protection. The Serra do Mar region has around 25% of its remaining forests under some type of restriction, followed by the Interior Forests (6.8%) and Bahia (4.2%). All other regions have less than 4% of the remaining forest under protection. Today, restrictive legislation protects all the Atlantic Forest remnants (*Lei da Mata Atlântica*); however, law enforcement is lax even in the Conservation Units.

The largest amount of forest under some degree of restricted use is located in the Serra do Mar, which alone represents 63% of the protected area, followed by the Interior Forests (22%). Today, only 1.05% of the original forest is protected, and in all regions, with the sole exception of the Serra do Mar, the percentage is below 0.8%. In spite of the relatively large amount of conservation units in the central Serra do Mar, which protect 8.11% of its original cover, it still falls below the 10% target for biodiversity conservation (Secretariat of the Convention on Biological Diversity 2002; Rodrigues et al. 2004).

Some reserves are contiguous, and thus we could identify seven large protected regions with areas around 100,000 ha. Five of them are in the Serra do Mar region: (1) Serra do Mar State Park, SP and Bocaina National Park, SP/RJ; (2) the former Jacupiranga State Park, SP, which today is a mosaic of Integral Protection and Sustainable Development units, and Superagui National Park, PR; (3) the Paranapiacaba continuum, composed of the PETAR State Park, Intervales State Park, Xituê Ecological Station, and Carlos Botelho State Park, all in the state of São Paulo; (4) the Serra do Tabuleiro State Park, SC; and (5) the Juréia mosaic, composed of the Banhados de Iguape Ecological Station, Juréia-Itatins Ecological Station, Itinguçu State Park, and Prelado State Park (SP). Recently, this last region has been the focus of intense debate between stakeholders, local communities, conservationists, and people involved in

urban development who have exerted great pressure on the process. The conservation units might be reshaped in the near future, to accommodate the different interests in the region. The two other regions of large blocks of Nature Reserves are in the Interior Forest, the Iguaçu National Park (PR), the most important remnant of the interior forests; and in the Diamantina region, where the Chapada Diamantina National Park encompasses a considerable mosaic of open habitats, more related to the Cerrado biome, and some forest blocks. Together these large blocks of Nature Reserves encompass 1,212,800 ha, which comprises 53.6% of all protected areas. Moreover, 17 reserves range in size from 20,000 to 60,000 ha, also a considerable size, and represent an additional 26% of the total forest under protection; these reserves are particularly located in the Interior, Serra do Mar, Bahia, and Araucaria centers. The remaining forest under protection (~20%) is scattered in small reserves in all the Atlantic Forest regions.

Of the remaining forest outside the conservation units, only 22.6% is located within 10 km of nature reserves, whereas 61% is farther than 25 km. The patterns within the biogeographical regions are similar, again with the Serra do Mar as the sole exception. In most of the regions, a small amount of forest lies within 10 km from conservation units, whereas the larger fraction is farther than 50 km. In contrast, in the Serra do Mar, almost 60% of the remaining forest is less than 10 km from conservation units, which provides these forest fragments with some connectivity to a large block of preserved forest.

## **5. Conservation of marginal habitats**

On previous occasions, it has been shown that, for conservation purposes, the Atlantic Forest should be treated as a whole, including both rainforest and non-rainforest cover (Scarano 2002, 2009). Marginal habitats are extensions of the core rainforest and also serve as a buffer zone for it, because of the intimate floristic relationships that they maintain and also the animal transit between them, despite marked fragmentation. Since the history of a landscape affects the present distribution pattern of species in fragmented landscapes, this history should be considered in conservation planning (Metzger et al. 2009). Interestingly, as seen in the above data, there is also a strong bias in the distribution of conservation units between forest and non-forest habitats of the Atlantic Forest biome. Rock outcrops, above the tree line or on inselbergs, are mostly well protected and maintain a fauna and flora that is often relict and highly endemic, but has many close relatives within the neighboring rainforest. Lowlands, conversely, are poorly protected. Restinga vegetation is often replaced by housing and touristic complexes, because of

the obvious attractiveness of the Brazilian coast. Swamp forests have been widely affected by drainage, either due to replacement by agriculture or efforts to eradicate tropical diseases in the early 20th Century. The fact that these types of habitats have lower species richness and lower rates of endemism than the core rainforest does not help either, and makes them less of a priority particularly when the conservation currency is merely quantitative, counting the number of species and the number of endemics. Restingas and swamps are geologically younger, and most species found in these areas originate from the rainforest. However, the stressful nature of these habitats has promoted the expression of plastic types of the original rainforest species, which are living evidence of what is perhaps the rainforest's main treasure: its genetic diversity (Scarano 2009).

A sad example of the failure of the legal system to treat the Atlantic rainforest as a whole, *i.e.* to include non-rainforest vegetation types, has been reported by Sá (2006). The peculiar coastal dry forest found in Búzios municipality in the state of Rio de Janeiro is relict vegetation that much resembles physiognomically the *caatinga* vegetation found in the semiarid region of the Brazilian northeast. Previous efforts at classifying Brazilian vegetation types have labeled Buzios dry forest as *caatinga*. As a result, this highly attractive region for tourism is not covered by the law protecting the Atlantic rainforest, since it is supposed to be *caatinga*. However, Sá (2006) has shown that the floristic similarity between the dry forest and the rainforest is over 80%.

We propose three recommendations for a conservation strategy that is more inclusive of marginal habitats: 1) laws must be enforced and government must lead in providing good examples. Brazil has a sad record of not compensating landowners when their lands are seized for protected areas; 2) private protected areas have a successful history in the Atlantic Forest biome, and should be further supported; 3) the design of future protected areas and of future restoration initiatives should aim to promote connectivity not only along the forest-forest axis, but also along the forest-sea axis.

## **6. Ecosystem services and forest restoration**

Beyond the conservation of species richness and endemism, the interactions among species and between the species and the abiotic environment support, regulate, and provide the services and cultural benefits that people derive from biodiversity (McNeely et al. 2009). For instance, although not much is left of the Atlantic Forest biome, the existing remnants safeguard

freshwater, climate, and food production, among other securities. The potable water available for the nearly 50% of the Brazilian population that lives in coastal regions, including large cities such as Rio de Janeiro and São Paulo, either springs from or is bordered by Atlantic Forest. The emerging carbon market indicates that these remnant forests not only ameliorate local climate in an otherwise fully urban landscape, but might also contribute significantly to the global carbon balance. Pollination, pest control, and erosion regulation are all provided by natural remnants of the Atlantic Forest. Furthermore, most of the cities are surrounded by forest fragments, and people use these natural areas for recreation.

Of course, reduced and fragmented as it is now, the provisioning of all such essential services for human well-being is under serious threat. Most of the Atlantic Forest is less than 200 m from any forest edge (Ribeiro et al. 2009), and therefore 200 m from a land-use area. More than 100 million people live in the region formerly covered by Atlantic Forests, in both rural and urban areas, including more than 3,000 cities and extensive farmed fields and grazing land. Moreover, most of the remaining Atlantic Forest was already clear-cut or severely altered by humans, some parts even before European colonization. Finally, almost all of the remaining forests are located on private land; some of them have people living there or somehow related to the area. All of these reasons make it imperative to consider the human perspective in any conservation plan for the Atlantic Forest region.

Recently, Ribeiro et al. (2009) exposed the precariousness of the Conservation Unit System in the Atlantic Forest, which protects around 1% of the original vegetation. The need to expand this system is obvious. However, the efficiency of the existing units is already questionable, since most of them have problems in reaching their conservation targets. The several reasons for this include problems with unit protection and management, and also with the relationship with the surrounding human communities. Moreover, indigenous peoples have been moving to Conservation Units (Cardoso Island State Park and Intervales State Park in the state of São Paulo are two examples), since they are the only places remaining where the native Americans can maintain at least some of their original culture and is not private land. This evolution has posed a challenge to conservationists, to modify their ways to deal with traditional peoples inside conservation units, since both groups have similar goals.

Presently, more than 90% of the remaining forests, including almost all the deforested areas, are located on private land. Therefore, conservation management must be adapted to these conditions. Forest restoration has been suggested as one of the key actions to be implemented in

order to achieve Atlantic Forest conservation (Ribeiro et al. 2009; Rodrigues et al. 2009). However, effective means to engage people in landscape management and forest restoration are still lacking (Rodrigues et al. 2009). The estimated amount of forest that must be restored merely to comply with current Brazilian environmental legislation is immense, and 15 million ha is expected to be restored up to 2050 (<http://www.pactomataatlantica.org.br>). Except for a few large (hundreds of hectares) restoration projects (see examples and different experiences recounted by Rodrigues et al. 2009), most of the experiments are small and locally focused, and have not published their results and/or properly monitored their programs. This lack of information makes it more difficult to reach appropriate conclusions to help with future restoration actions (Rodrigues et al. 2009). An important rural economy could be enhanced by a massive restoration program in the Brazilian Atlantic Forest, since seed collection (see example in Instituto Refloresta, formerly Ecoar Florestal, [www.refloresta.org.br](http://www.refloresta.org.br)), sapling production in community nurseries, and restoration implementation and maintenance could be conducted by small local farmers as a source of supplementary income. Large landowners who produce agricultural commodities that are largely exported to Europe and North America as well as used in the local economy, should be obligated to comply with the environmental regulations, including taxation and moratoriums on products that excessively impact the environment. The Amazon Soy Moratorium appears to have had some relative success, and could be even more efficient in regions where the land-use patterns are better established. Small landowners should receive governmental incentives to environmentally improve their properties, including payment for environmental services, abundant technical and financial support for forest restoration, and relaxation of the laws regulating agro-ecological activities in key areas, in situations where these areas are not yet forested. In both cases a massive campaign should be conducted, using all means of communication, to sensitize the community to the importance of restoring important areas for Atlantic Forest conservation. Areas along the rivers are a main priority, and can link fragments, allowing populations to maintain themselves in functionally connected fragments (Martensen et al. 2008); as well as protecting river systems (Silva 2003).

Conservation of the remaining Atlantic Forest can only be accomplished by incorporating the human dimension into conservation projects, under a generally recognized community pact for Atlantic Forest conservation.

## 7. Agroecology: Opportunities for Atlantic Forest conservation?

Agroecology, now at the fore of the conservation debate, has proved to enhance food production, biodiversity conservation, and poverty alleviation (Jose 2009). Tropical countries in general are particularly favorable for agroecological production, because of their particular social and environmental aspects. Steeper and higher areas usually have larger amounts of forest (see above), and are usually occupied by family farms. These areas should be the focus of governmental efforts to make production in agroecological systems viable. The possibility of realizing profits from the multiple gains of this type of system should be explored. For example, ecosystem services such as those related to maintenance of water quality and quantity, minimization of erosion, and biodiversity conservation (reviewed by Jose 2009) must be evaluated. Also, some effort must be made to realize better values from the forest products, which are largely free of chemicals and could be produced with low impact.

In the Atlantic Forest there are many examples of agroforest systems in every region, which stand out as good examples of highly productive systems with low environmental impact. Among the better-known are the “cabruças” on the south coast of Bahia (Alvim and Nair 1986; Schroth and Harvey 2007), where shade cocoa is planted and the environmental benefits over other production systems have been largely explored (Pardini et al. 2009). In the Ribeira Valley located in the Serra do Mar BSR in São Paulo (REBRAFE 2007), there are also some very good examples of highly diverse and productive systems, which produce many agricultural goods and fruits, as well as forest products. Examples in the Interior Forests are also abundant, such as in the Pontal do Paranapanema (Cullen Jr. 2004). In the Araucaria subregion, silvipastoral systems that mix trees, such as *Araucaria angustifolia*, and pastures, locally called “faxinais”, are widespread. Also in southern Brazil there are some examples that combine timber trees, perennial cash crops, and the South American holly (*Ilex paraguariensis*) (REBRAFE 2007). Some experiments have been indicating a good potential for the use of agroforests as elements to improve connectivity between fragments (Cullen Jr. et al. 2004; Uezu et al. 2008; Pardini et al. 2009), to decrease edge effects by functioning as buffer zones (Cullen Jr. and Fenimore 2002; Cullen Jr. et al. 2004), to reduce soil erosion (Franco et al. 2002), to increase soil fauna (REBRAFE 2007) and biodiversity in general (Schroth et al. 2004; McNeely and Schroth 2006; Jose 2009), and also to increase soil fertility (REBRAFE 2007). Vieira et al. (2009) emphasized the contribution of agroecology techniques as a transition phase that stimulates early forest restoration with a so called “agro-successional” restoration strategy, which has been used as a

means to induce landowners to restore tracts of forest. The social aspects of agroforest systems in the Atlantic Forest are also normally evaluated, and enormous benefits have been reported (Franzen and Mulder 2007; Vieira et al. 2009).

## 8. Conclusions

The Atlantic Forest region is one of the top world hotspots for biodiversity conservation, and should be a global target for conservation. In this chapter, we explored the characteristics of the biota and the distribution of the forest, and pointed out some weakness in its conservation. Most importantly, we presented clear objectives to aid in its conservation.

A great cause for concern is the rapid expansion of large monocultures, particularly sugarcane and *Eucalyptus* plantations, which could threaten the last forest remnants, in particular by decreasing connectivity between them and causing additional edge effects, especially the agricultural land uses. Moreover, the expansion of these systems has been the cause of extensive migration of people from rural to urban areas, which has had additional environmental impacts on urban areas, also formerly covered by Atlantic Forest.

One key point is that Atlantic Forest conservation is impossible without a clear consideration of the human role, since most of the remaining forest is located on private lands. An effective Atlantic Forest conservation plan should start with making the approximately 110 million people now living in the region aware of its global importance and its present fragile situation. Such a plan should target the preservation of the last large remnants, but should also incorporate agricultural land, within a fragmented-landscape management perspective. Small family farms are usually located in steeper areas where forest remnants are usually more abundant, and where low-impact agricultural production could be both socially and environmentally beneficial. Restoration should be a clear target, and an immense reforestation effort should be made, focusing on creating clusters of fragments that are functionally connected, particularly by riparian corridors, where additional benefits could be achieved. Ecosystem services should be rapidly implemented in certain key conservation regions, which should help with conservation on small properties.

Despite the unsatisfactory present state of conservation, the Atlantic Forest still harbors a huge amount of biodiversity, including many endemic species. Urgent conservation actions should be taken; focusing on clear targets, in order to promptly implement management plans

and avoid massive loss of biodiversity. Some steps are presented here, and we urge that they be taken sooner rather than later.

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Table 1: Summary area data for internal subdivisions proposed for the biogeographical sub-regions (BSRs; Silva and Casteleti 2003). The subdivisions were generated based on bioclimate (14 environmental layers of Worldclim 1.4) and altitudinal variation data for the Brazilian Atlantic Forest.

Biogeographical sub-region	Number of subdivisions	Area in ha			
		minimum	mean	s.d.	maximum
Araucária	9	823 781	2 926 777	9 193 929	9 379 519
Bahia	6	200 941	2 223 135	2 197 306	5 575 259
Diamantina	3	1 645 058	3 598 382	1 691 630	4 577 447
Interior	25	50 713	2 848 668	3 309 680	14 805 211
Pernambuco	2	281 664	1 798 296	2 144 842	3 314 928
São Francisco	5	291 418	2 508 833	2 236 126	5 934 037
Serra do Mar	5	820 619	2 610 988	3 586 569	9 018 947

Table 2: Characterization of the proposed sub-divisions within each Biogeographical Subregion (BSR). BSRs are ordered from north to south, and sub-divisions within each of them, were ordered by their sizes. Predominant vegetation cover of each subdivision was obtained from vegetation map available from IBGE (2004). Elevation was obtained from SRTM DEM. Mean annual precipitation, mean annual temperature and precipitation seasonality were obtained from Worldclim database.

Biogeog. Sub-regions*	Sub-divisions	Vegetation	Area km <sup>2</sup>	Forest %	Elevation m		Precipitation mm		Temperature °C		Precipitation seasonality %
					mean	s.d.	mean	s.d.	mean	s.d.	
Perna	PE-Mata pernambucana	Semidecidual forest/Open forest	33 149	14.5	245	215	1384	363	23.5	1.3	60
Perna	PE-Alagoas	Semidecidual forest/Restinga	2 817	6.9	105	71	1107	202	24.6	0.5	66
Bahia	BA-Sul baiano	Dense forest	59 561	20.7	153	126	1209	198	23.9	0.6	32
Bahia	BA-Salvador	Dense forest	40 867	18.4	173	177	1466	336	23.7	1.3	36
Bahia	BA-Linhares	Dense forest	12 423	18.8	459	397	1223	91	22.0	2.3	52
Bahia	BA-Aimorés	Dense forest	11 020	9.2	375	276	1210	52	22.8	1.6	61
Bahia	BA-Itambé	Dense forest	7 459	10.2	638	202	864	94	21.5	1.3	48
Bahia	BA-Sergipe	Savanna/ Restinga	2 009	10.4	70	60	1101	182	25.2	0.4	63
S.Fran	SF-Bom Jesus da Lapa	Decidual forest	59 340	6.8	589	187	873	93	24.1	1.3	89
S.Fran	SF-Januária	Decidual forest	36 025	2.2	559	107	891	93	23.8	0.8	94
S.Fran	SF-Barra	Semidecidual forest/Ecological transitional zones	20 904	3.2	526	133	855	101	24.6	0.9	87
S.Fran	SF-Guanabi	Decidual forest	9 172	9.6	852	272	783	121	21.6	1.6	81
Diam	DI-Seabra	Decidual forest/ Semidecidual forest	45 726	20.2	666	232	794	102	21.8	1.3	47
Diam	DI-Jequitinhonha	Decidual forest	45 590	12.6	659	252	857	78	21.9	1.3	71
Diam	DI-Jequié	Decidual forest	16 451	6.8	448	260	853	202	21.9	1.5	36

Biogeog. Sub-regions*	Sub-divisions	Vegetation	Area km <sup>2</sup>	Forest %	Elevation m		Precipitation mm		Temperature °C		Precipitation sazonality %
					mean	s.d.	mean	s.d.	mean	s.d.	
Inter	IF-Ribeirão Preto	Semidecidual forest/ Ecological transitional zones	145 235	4.9	540	196	1308	135	22.0	1.3	70
Inter	IF-Bauru	Semidecidual forest/ Ecological transitional zones	67 022	4.8	645	218	1327	132	20.2	1.3	59
Inter	IF-Vale do Rio Doce	Semidecidual forest	60 740	10.6	552	267	1268	141	21.8	1.7	78
Inter	IF-Zona da Mata/Viçosa	Semidecidual forest	42 484	9.9	530	331	1288	147	21.1	1.8	71
Inter	IF-Porto Alegre	Semidecidual forest	42 109	5.0	81	101	1425	104	18.8	0.7	12
Inter	IF-Vale Mururi	Semidecidual forest	41 885	12.9	519	248	1034	112	22.6	1.3	63
Inter	IF-Sul de Minas	Semidecidual forest	41 880	6.6	993	175	1525	103	19.2	1.2	75
Inter	IF-Dourados	Semidecidual forest	38 979	4.8	372	93	1471	100	22.8	0.5	39
Inter	IF-Toledo	Semidecidual forest	34 091	9.0	395	119	1643	156	20.1	1.0	24
Inter	IF-Pontal	Semidecidual forest	30 817	5.6	414	92	1259	73	21.6	0.9	43
Inter	IF-Sul goiano	Semidecidual forest	21 158	5.2	554	126	1392	112	24.0	0.9	78
Inter	IF-Cianorte	Semidecidual forest	18 865	4.9	413	114	1381	87	20.8	1.0	31
Inter	IF-Itapemirim	Ecological transition zones	18 187	7.1	634	88	1246	88	19.5	0.8	48
Inter	IF-Três Passos	Decidual forest	16 944	6.0	363	137	1844	76	19.8	0.6	10
Inter	IF-Juíz de Fora	Semidecidual forest	12 358	16.0	608	302	1440	109	20.4	1.6	72
Inter	IF-Iguatemi	Semidecidual forest	11 774	5.5	350	59	1569	47	21.9	0.2	30
Inter	IF-Cerro Largo	Decidual forest	10 814	3.0	294	108	1800	35	20.1	0.6	11
Inter	IF-Rio brilhante	Semidecidual forest/ Ecological transitional zones	10 455	5.0	345	42	1435	26	23.5	0.2	42
Inter	IF-Oliveira	Semidecidual forest	8 761	8.0	936	112	1444	58	20.0	0.7	82
Inter	IF-Quadrilátero	Semidecidual forest	8 027	17.1	955	156	1426	65	20.1	1.1	86
Inter	IF-Seberi	Decidual forest	6 908	8.1	433	139	1823	40	19.6	0.6	10
Inter	IF-Itararé	Ecological transition zones	6 358	4.9	671	132	1261	49	19.5	0.9	42

Biogeog. Sub-regions*	Sub-divisions	Vegetation	Area km <sup>2</sup>	Forest %	Elevation m		Precipitation mm		Temperature °C		Precipitation sazonality %
					mean	s.d.	mean	s.d.	mean	s.d.	
Inter	IF-Macaé	Semidecidual forest/Restinga	5 404	8.2	20	44	1083	41	23.2	0.3	48
Inter	IF-Vale do Paraíba	Semidecidual forest	5 341	13.1	630	300	1467	162	19.8	1.7	70
Inter	IF-Bodoquena	Decidual forest	5 214	14.8	278	183	1276	45	24.4	1.1	52
S.Mar	SM-Contínuo da Serra Mar	Dense forest	88 594	45.5	418	378	1636	333	19.9	2.3	43
S.Mar	SM-Tubarão	Dense forest	12 850	20.0	143	198	1442	89	19.0	0.9	21
S.Mar	SM-Ibúna	Dense forest	10 384	17.8	826	91	1622	347	17.5	0.7	54
S.Mar	SM-Bragança	Dense forest	8 910	9.1	941	252	1476	166	17.7	1.4	65
S.Mar	SM-Mantiqueira	Dense forest	8 206	14.1	776	270	1469	184	18.4	1.5	66
Arauc	AR-Araucária Centro Sul paranaense	Mixed forest	101 587	10.8	822	192	1632	179	17.5	1.2	23
Arauc	AR-Centro riograndense	Mixed forest/Decidual forest	56 696	15.3	540	277	1656	182	17.7	1.3	14
Arauc	AR-Oeste catarinense	Mixed forest	23 747	10.3	841	219	1907	170	16.8	1.4	13
Arauc	AR-Noroeste riograndense	Mixed forest	22 511	5.7	702	177	1726	104	17.6	1.4	13
Arauc	AR-Serrana	Estepe savanna	17 672	15.1	1033	191	1651	76	15.5	1.0	13
Arauc	AR-Telemaco Borba	Mixed forest	8 475	8.3	790	114	1438	66	18.4	0.6	27
Arauc	AR-Jaguariaiva	Mixed forest	8 238	8.9	851	166	1339	80	18.1	1.2	39
Arauc	AR-Rio do Campo	Mixed forest	7 460	46.8	679	202	1554	79	17.2	1.0	21
Arauc	AR-Ponta Grossa	Mixed forest	7 167	23.5	825	160	1498	144	18.0	1.0	32
Arauc	AR-Santa Maria	Decidual forest	5 875	8.8	290	92	1760	30	18.9	0.4	7

\*: BSR's abbreviation: Arauc=Araucária, Bahia=Bahia, Diam=Diamantina, Inter=Interior Forest, Perna=Pernambuco, S.Mar=Serra do Mar, S.Fran=São Francisco.

Table 3: Area of Atlantic Forest (ha and %) remaining in each biogeographical sub-region (BSR) according to Ribeiro et al. (2009).

<b>BSR</b>	<b>Remaining Forest</b>		<b>Remaining Restinga/ Mangrove</b>		<b>Total remaining Atlantic Forest</b>	
	<b>Area (ha)</b>	<b>% *</b>	<b>Area (ha)</b>	<b>% *</b>	<b>Area (ha)</b>	<b>% *</b>
Araucaria	3 202 134	12.6			3 202 134	12.6
Bahia	2 047 228	16.7	115 059	0.9	2 162 287	17.7
Brejos Nordestinos	13 656	16.0			13,656	16.0
Diamantina	1 109 727	13.5			1 109 727	13.5
Interior	4 807 737	7.0	32 451		4 840 188	7.1
Pernambuco	360 455	11.5	19 363	0.6	379 818	12.1
Serra do Mar	3 678 534	32.2	491 263	4.3	4 169 797	36.5
São Francisco	499 866	4.7			499 866	4.7
<i>TOTAL</i>	<i>15 719 337</i>	<i>11.26</i>	<i>658 135</i>	<i>0.47</i>	<i>16 377 472</i>	<i>11.73</i>

\* Percentages proportional to BSR area.

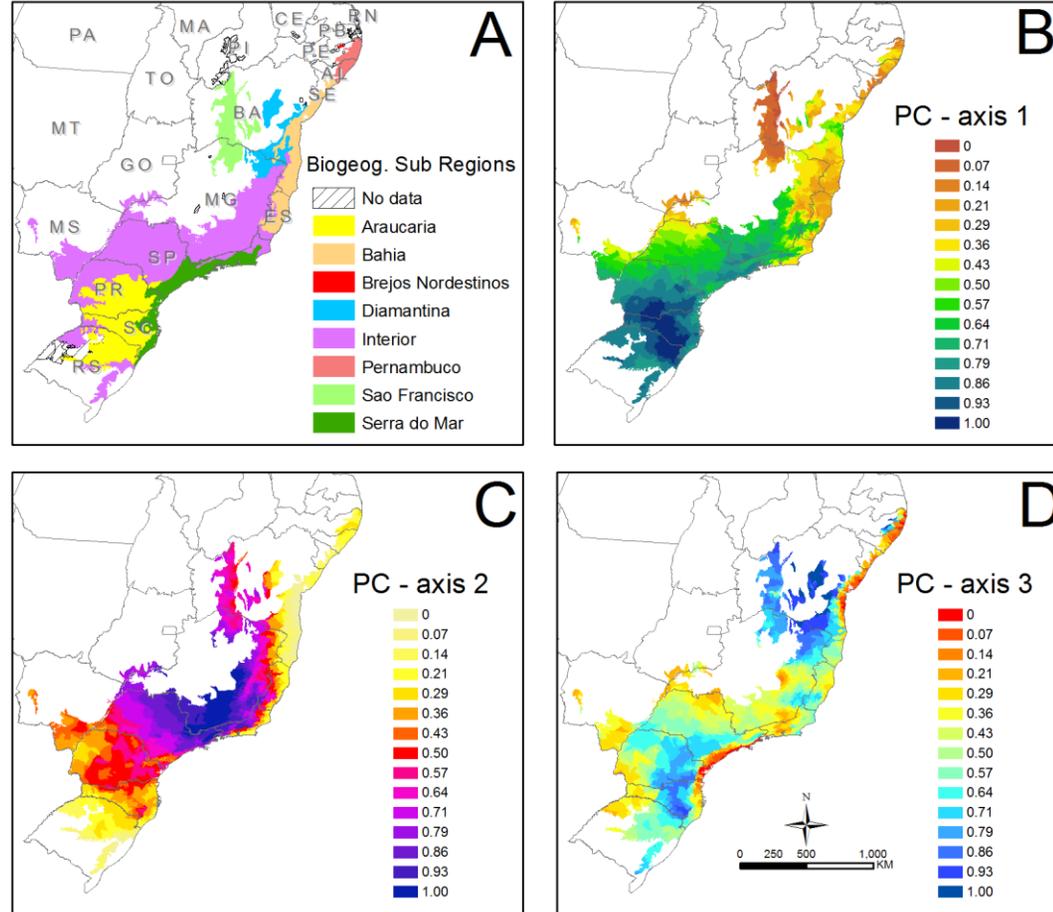


Figure 1: (A) Biogeographical sub-regions (BSRs) proposed by Silva and Casteletti (2003); (B), (C), and (D) are PC axes obtained from the analysis of 19 layers from Worldclim 1.4 and an elevation map. Axis 1 (B) was mainly correlated with annual mean temperature and mean temperature in the coldest quarter; the warmer colors represent higher annual mean temperatures. Axis 2 (C) was more influenced by elevation, precipitation in the wettest month, precipitation seasonality, and precipitation in the wettest quarter; the cooler (bluer) colors indicate higher elevations, while yellow represents the lower elevations. Axis 3 (D) was mainly correlated with annual precipitation and precipitation in the warmest quarter; warmer colors represent higher annual precipitation, and cooler colors represent lower annual precipitation.

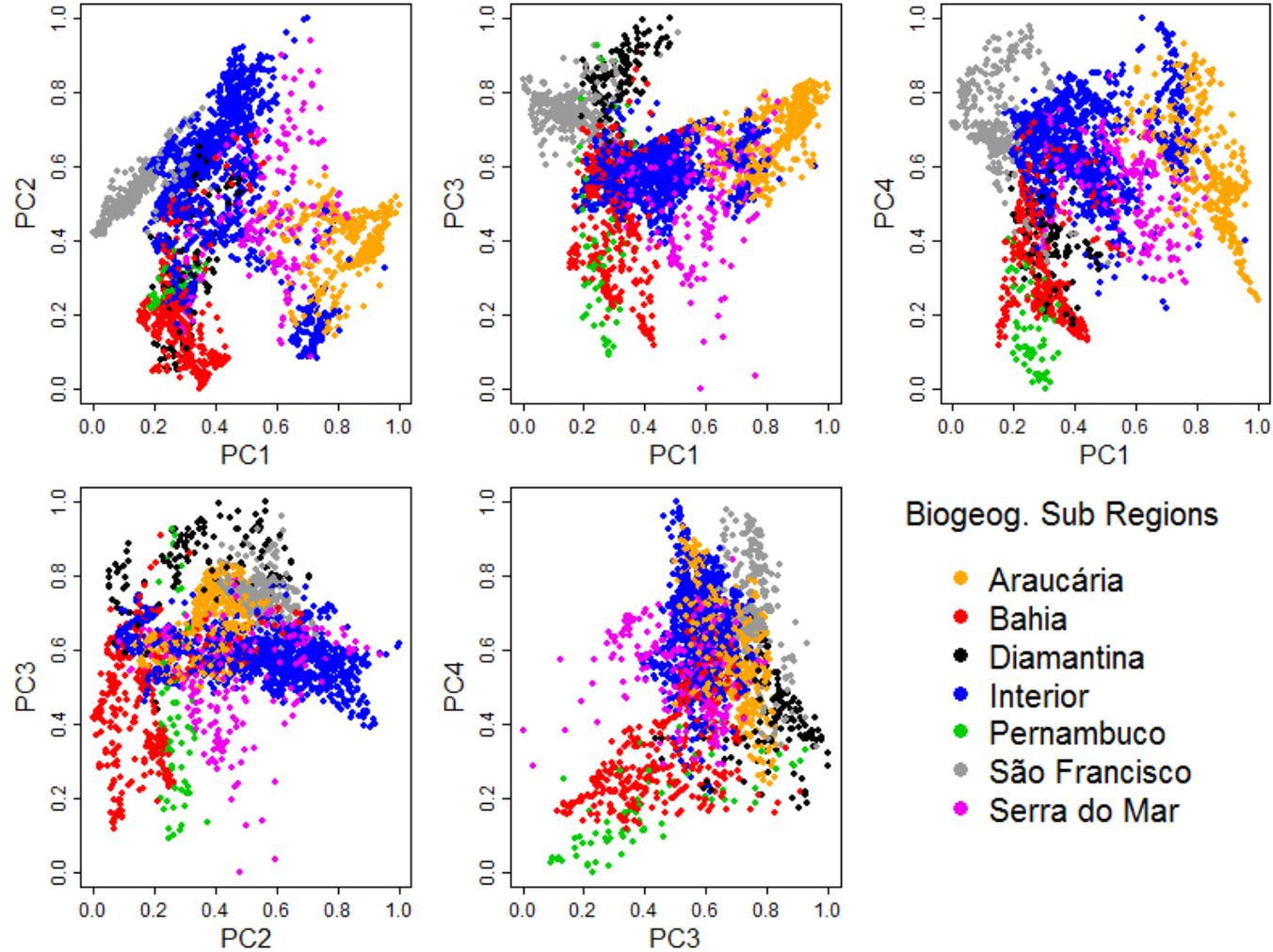


Figure 2: Standardized principal components (PCs) for the first four axes obtained from the analysis of 19 layers from Worldclim 1.4 and an elevation map, of the Brazilian Atlantic Forest bioclimate environmental space. Each point ( $n=2,650$ ) represents a different sub-watershed of order 5a. Biogeographical subregions are identified by colored dots.



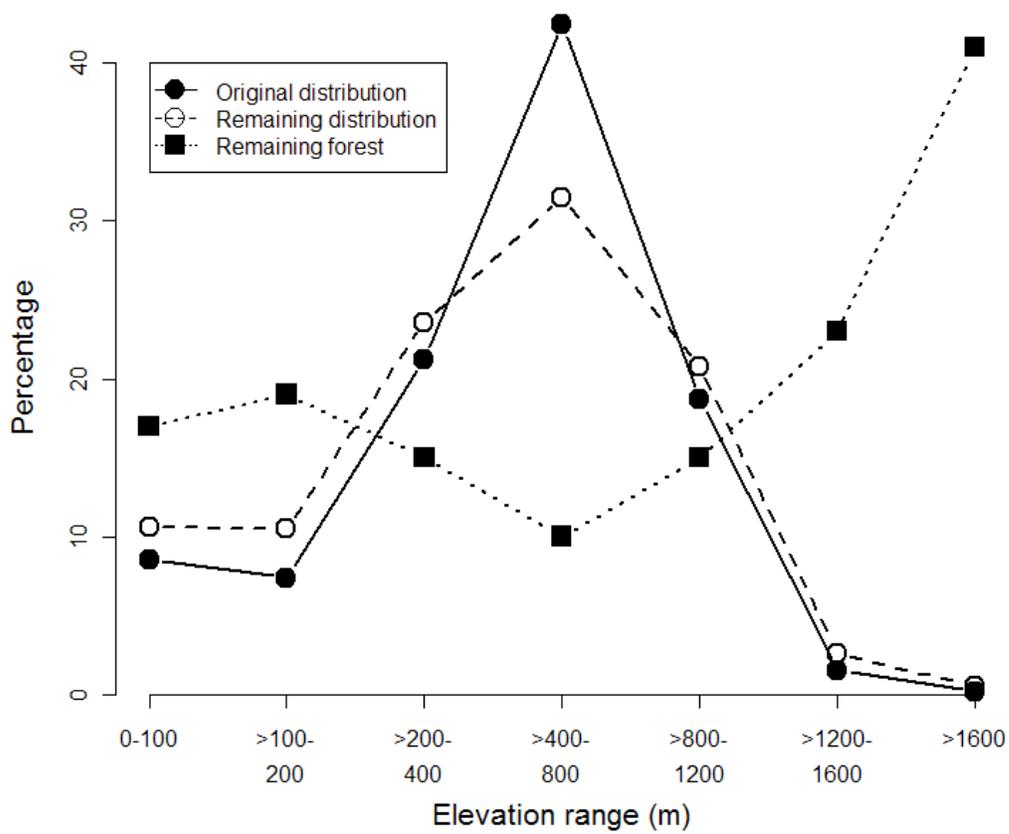


Figure 4: The circles indicate the percentages of original and remaining Atlantic Forest distribution across elevation ranges. Squares indicate the percentage of remaining forest within each elevation range.

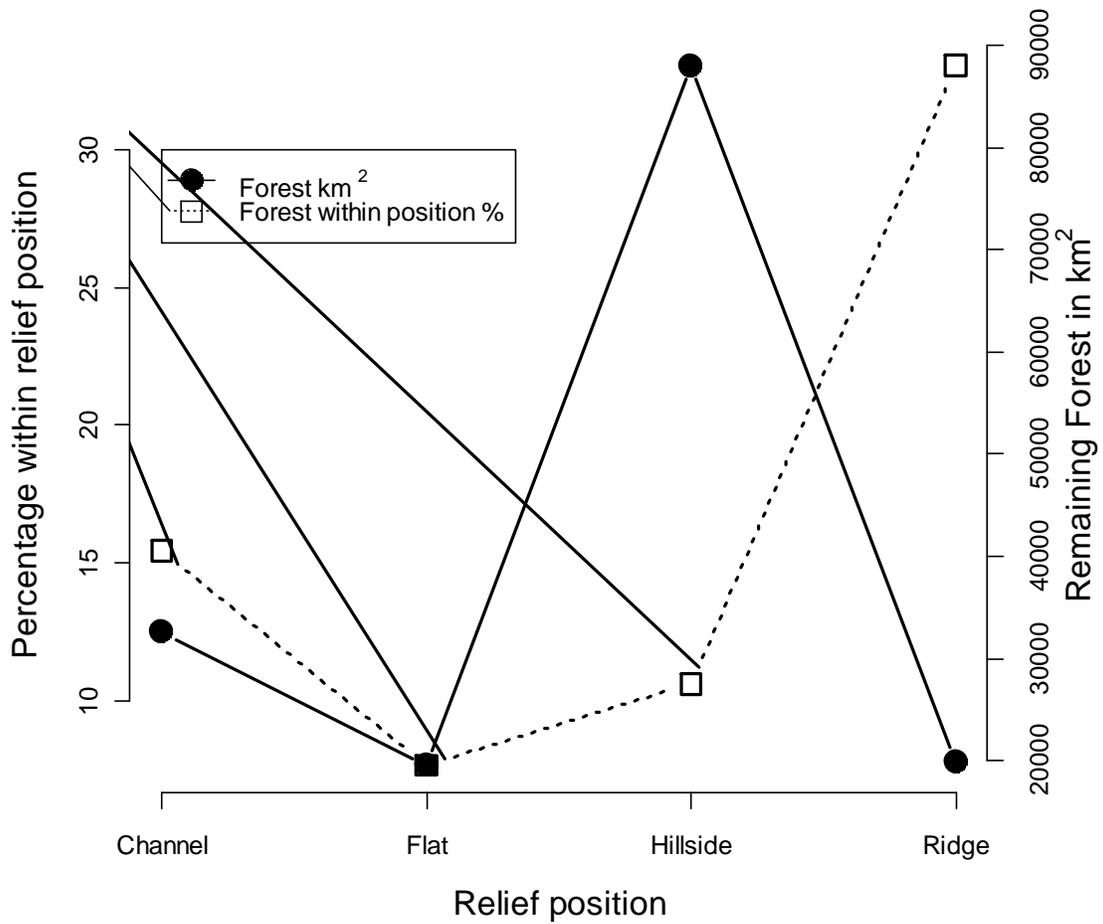
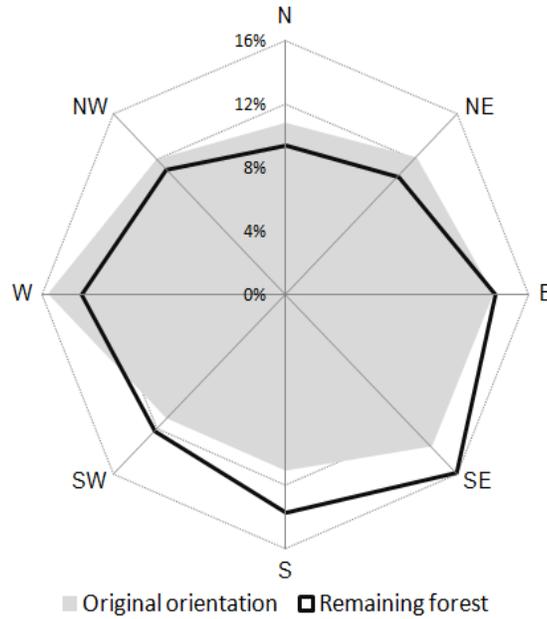


Figure 5: Percentage and amount (km<sup>2</sup>) of remaining Brazilian Atlantic Forest within each terrain position. Solid circles indicate area in km<sup>2</sup> for the entire region, and open squares indicate the percentage of forest within each type of terrain.

(A)



(B)

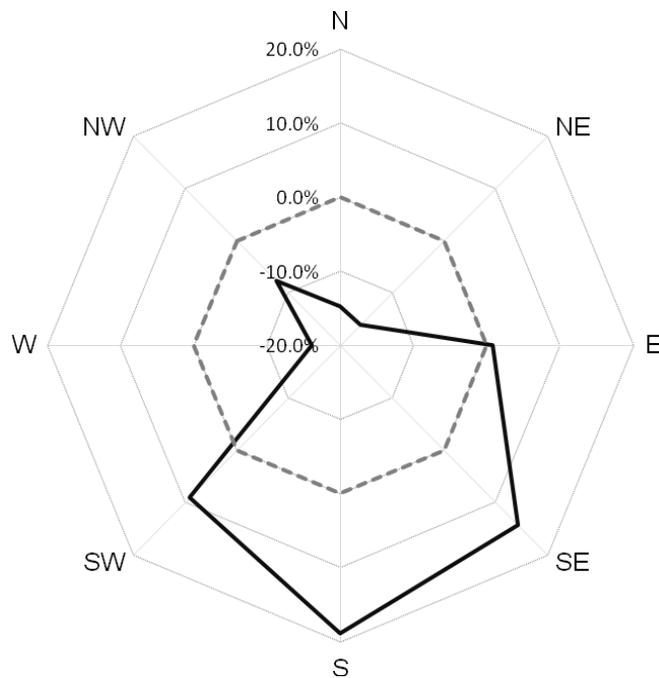


Figure 6: (A) Aspect orientation in percentage for the original (shaded gray) and remaining (solid line) Brazilian Atlantic Forest (summing to 100%). (B) difference (in %; solid line) between the original and remaining forest distribution within aspect orientation, where positive values indicate less deforestation and negative values more deforestation in relation to the original distribution. Dashed line in (B) indicates zero difference between the original and remaining forest aspect orientation. Radar graph axis legend: N=north, NE=northeast; E=east; SE=southeast; S=south; SW=southwest; W=west; and NW=northwest.

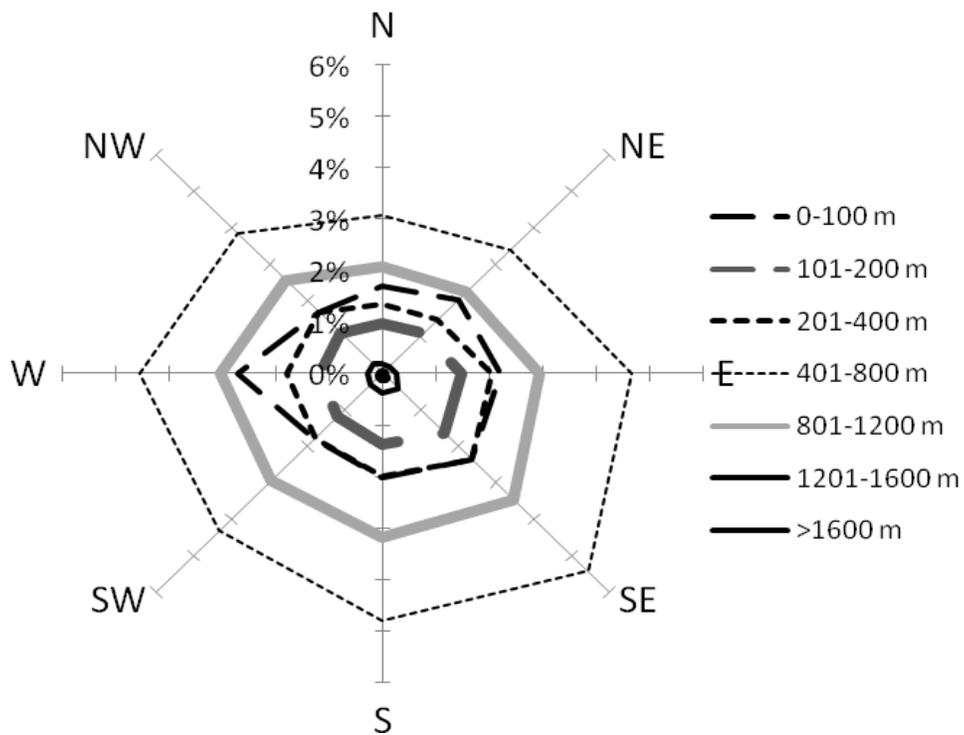


Figure 7: Aspect orientation in percentage of remaining forest in different elevation ranges for the Brazilian Atlantic Forest, summing to 100%. Radar graph axis legend: N=north, NE=northeast; E=east; SE=southeast; S=south; SW=southwest; W=west; and NW=northwest.

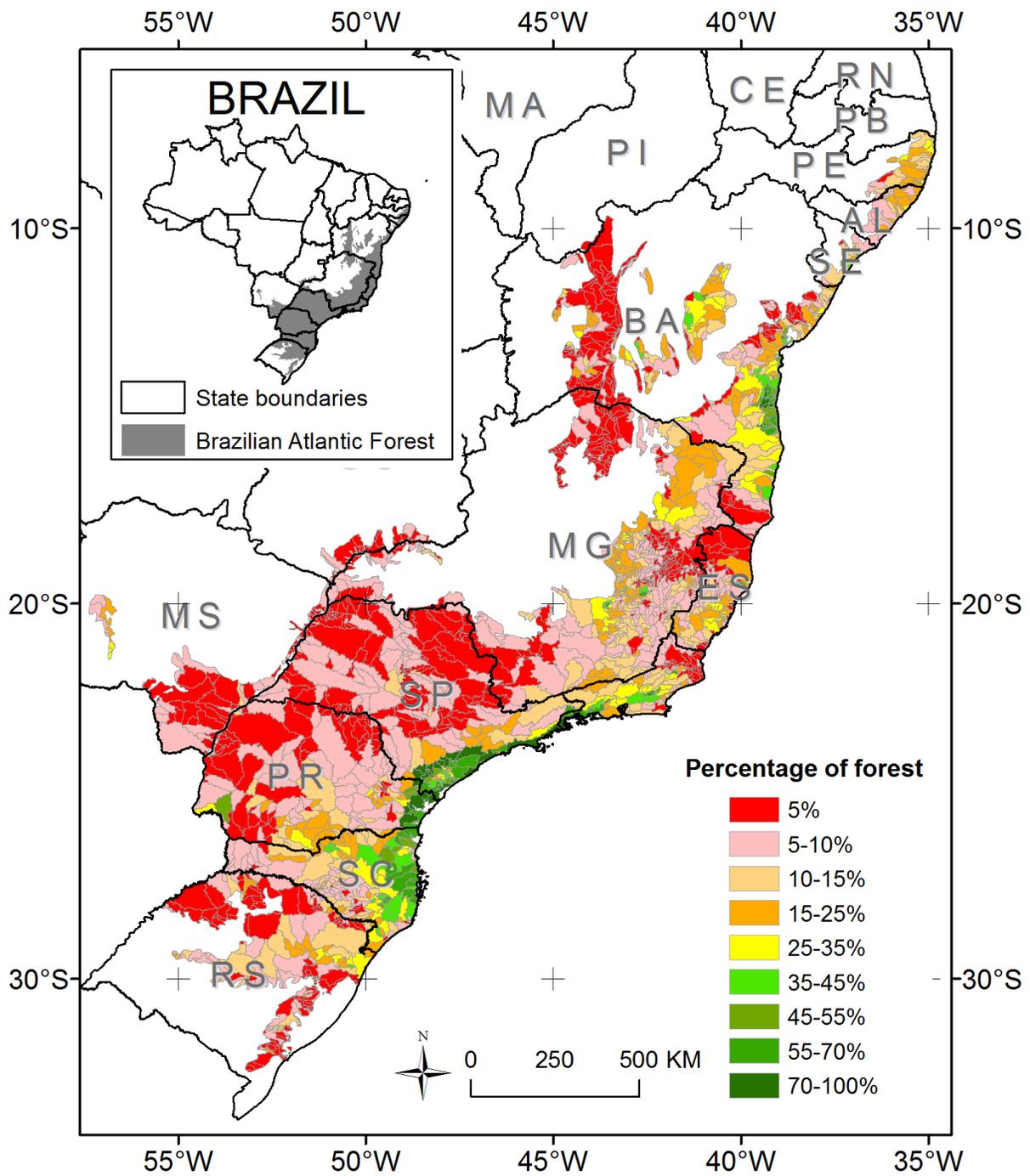


Figure 8: Percentage of remaining Brazilian Atlantic Forest within the sub-watersheds of order 5a, as proposed by Pfafstetter (1987).

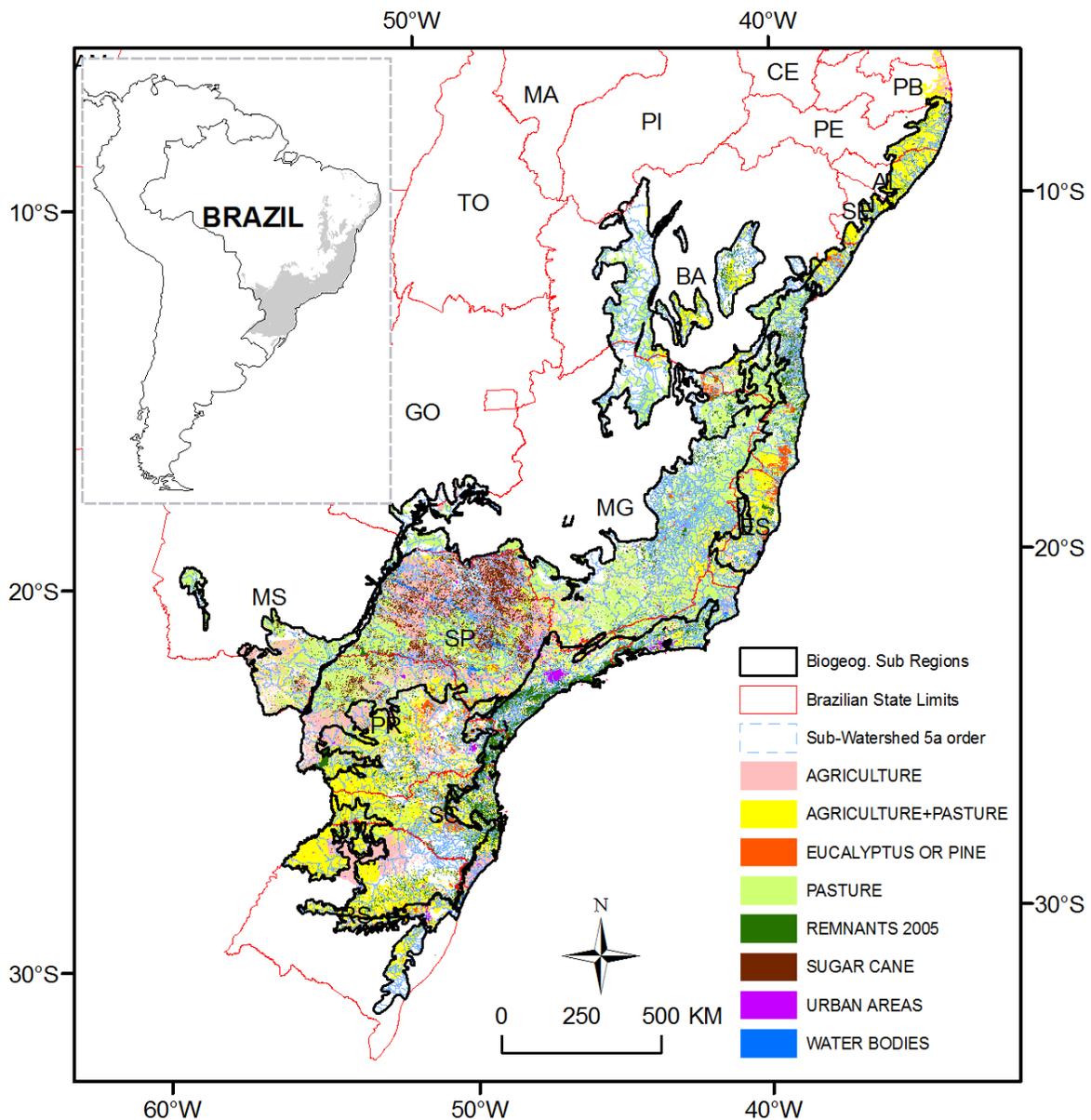


Figure 9: Land-cover map for the Brazilian Atlantic Forest region, generated for the entire region using official land-use maps. Sources: (a) Remnants 2005: SOS Mata Atlântica/INPE (2008); (b) Sugarcane: [www.dsr.inpe.br/canasat](http://www.dsr.inpe.br/canasat); (c) *Eucalyptus* spp. plantation for the state of São Paulo: Kronka et al. (2005); (d) all other classes: Probio/MMA project, <http://mapas.mma.gov.br>. Source: Modified from Ribeiro et al. (2009).

# CAPÍTULO IV

## *Assessing simulated bird species responses to habitat amount, aggregation, and quality: a spatially explicit model*

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1 **Assessing simulated bird species responses to habitat amount, aggregation,**  
2 **and quality: a spatially explicit model**

4 Running title:

5 *Simulating bird species movements in fragmented landscapes*

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24 **Abstract**

25 Habitat loss and fragmentation have been the focus of many conservation studies because of  
26 their detrimental effects on biodiversity. When the amount of habitat decreases below a given  
27 threshold, both habitat quality and spatial configuration play important roles in species  
28 persistence and biodiversity maintenance. To determine the relative contribution of habitat  
29 amount, habitat aggregation, and habitat quality on species' response patterns, we developed  
30 an ecologically scaled Individual Based Model (IBM), the BioDIM (*Biologically scaled*  
31 *Dispersal Model*). BioDIM was calibrated with data for Atlantic Forest bird species, allowing  
32 simulation of five species profiles, considering different levels of sensitivity to habitat  
33 disturbance and gap crossing capacity. Home-range sizes as well as routine and explorative  
34 movement distances were also included as species attributes. The model is density-dependent  
35 and overcrowding forces individuals to change their movement behaviour. This  
36 parameterization of BioDIM was run on 10 000 simulated landscapes to investigate the  
37 effects of habitat amount (5 to 70%), aggregation (from random to clumped), and quality  
38 (from 0.1 to 1.0) on four response variables: mortality rate, dispersal rate, movement  
39 variability, and movement cost. Univariate models suggested that the dispersal rate and  
40 movement costs were best explained by habitat amount while mortality rate and movement  
41 variability were explained by habitat aggregation. Analysis of the models combining two or  
42 more factors suggested that movement variability, mortality rate, and movement cost were  
43 best explained by habitat amount, aggregation, and their interactions, whereas dispersal rate  
44 was best explained by the model that included habitat amount, aggregation, and quality. Our  
45 ecologically scaled IBM allowed us to determine that, depending on the process of interest  
46 (here represented by our response variables), different sets of models could explain them.  
47 Habitat amount and aggregation continued to be the most important factors, but habitat  
48 quality also contributed to explain some response variables. BioDIM contributed to better  
49 understand the strength of influence of each factor, and can help us to simulate patterns that  
50 could contribute to the development of conservation and restoration planning at landscape  
51 scale.

52

53 *Key-words:* landscape simulation, habitat fragmentation, dispersal model, virtual species,  
54 Atlantic Forest, conservation, connectivity, IBM, ISEM2009.

## 55 **1. Introduction**

56 Habitat loss and fragmentation have been a main focus of conservation studies in recent  
57 decades, mainly because of their influences on biodiversity conservation (Fahrig 2003;  
58 Lindenmayer et al., 2008; Tabarelli et al., 2010). Assessing how different species respond to  
59 the amount, aggregation, and quality of habitat is essential for supporting conservation and  
60 restoration planning and for designing experiments with the best-testable hypotheses.  
61 However, it is still difficult to disentangle the effects of habitat amount from spatial  
62 arrangement (Fahrig, 2003). Additionally, the literature suggests that habitat quality plays an  
63 important role in species persistence and biodiversity maintenance in altered landscapes  
64 (Castellón and Sieving, 2005; Uezu et al., 2008; Hansbauer et al., 2009), which further  
65 complicates the problem.

66         The acquisition of empirical data to test the strength of influence factors such as  
67 amount, aggregation, and quality of habitat is costly in time and money, and thus simulation  
68 studies emerge as one of the best option to explore this question. Simulating virtual or  
69 hypothetical species with individual-based models (IBM; DeAngelis and Mooij, 2005) has  
70 been very helpful to assess how landscape structure can influence species responses to  
71 different factors (With and Crist, 1995; Tischendorf and Fahrig, 2000; Hilker et al., 2006).  
72 Birds are often one of the most interesting taxonomic groups to simulate with IBM, because  
73 many species are sensitive to habitat disturbance (Stotz et al., 1996; Develey and Stouffer,  
74 2001; Loiselle et al., 2010) and fragmentation (Desrochers and Fortin, 2000; Uezu et al.,  
75 2005; Martensen et al., 2008; Uezu et al., 2008; Boscolo and Metzger, 2009; Metzger et al.,  
76 2009; Banks-Leite et al. 2009).

77         Individual movements, both within and between habitat patches, can influence species  
78 persistence in fragmented landscapes (Lima and Zollner, 1996; Morales and Ellner, 2002;  
79 Morales et al., 2004). Dyck and Baguette (2005) suggested a definition for dispersal, as a  
80 three-stage process that includes (a) emigration (crossing habitat boundaries), (b) matrix  
81 transversing (or transit through a landscape with movements across non-habitat or resource-  
82 poor habitat), and (c) settlement (immigration or colonisation). They also classified  
83 movements as routine or dispersive. Routine movement occurs mainly within habitat patches,  
84 over short distances, following a nearly random pattern (Dyck and Baguette, 2005), or  
85 between functionally connected patches in daily or frequent movements (Boscolo et al., 2008;  
86 Martensen et al., 2008). Dispersal movements are longer with a more directional pattern

87 where individuals choose a dispersal route. This directional pattern can be described by a  
88 correlated-random-walk-like pattern (Morales et al., 2004, Dyck and Baguette, 2005).

89 When dispersing from one habitat patch to another, individuals experience poor-  
90 quality habitat (With and Crist, 1995; Rayfield et al., 2010), where mortality rates tend to be  
91 higher (Castellón and Sieving, 2005; Munkemuller and Johst, 2006; Rayfield et al., 2010).  
92 Thus, the propensity of an individual to cross open areas depends on overcrowding of the  
93 original patch (Dyck and Baguette, 2005), but also on species' capability to cross the  
94 inhospitable matrix and the distance to be traveled between habitat patches (With and Crist,  
95 1995; Castellón and Sieving, 2005; Awade and Metzger, 2008; Boscolo et al., 2008).  
96 Species' sensitivity to edge proximity (Lyra-Jorge et al., 2009) has also been suggested to  
97 influence an individual to undertake dispersive movement. That is, the intensity of  
98 movements between habitat patches decreases the more sensitive species are to edge  
99 conditions (Hansbauer et al., 2008a; Hansbauer et al., 2009; Lyra-Jorge et al., 2009) and  
100 overcrowding can be a major factor in forcing individuals to disperse (Dyck and Baguette,  
101 2005). Most bird species have a territorial behaviour while nesting, thus it is therefore  
102 important to account for this behaviour. Individual home-range sizes can be used as a clue for  
103 estimating both carrying capacity (Morris and Diak, 2002; Moorcroft and Lewis, 2006) and  
104 population size (Hansbauer et al., 2008b). The larger the home-range sizes, the smaller the  
105 population size that can be supported by a given habitat patch (Moorcroft and Lewis, 2006).

106 We developed an ecologically scaled Individual Based Model - IBM, called BioDIM  
107 (*Biologically scaled Dispersal Model*), with the main objective to investigate the independent  
108 and interacting effects of habitat amount, quality, and aggregation on species' movements  
109 and persistence. We programmed a fully continuous model (in space and response patterns)  
110 that simulated bird movements for species with different profiles, considering edge  
111 sensitivity, habitat requirements (home-range sizes, Wang and Grimm, 2007), varying  
112 performances of gap-crossing, and sensitivity to habitat quality. Mortality and dispersal rate,  
113 movement cost and movement variability were analyzed as response variables summarized at  
114 landscape scale. BioDIM allows us to better understand what influences individual  
115 movements within fragmented landscapes which will contribute to better support  
116 conservation decisions.

117

## 118 **2. Methods**

119 Information on species responses to habitat amount, aggregation, and quality is still  
120 sparse and is mostly restricted to a few well-studied species from temperate regions. For the

121 vast majority of species, especially tropical ones, little or no information is available.  
122 Moreover, researchers, given experimental constraints, have mostly focussed on one aspect,  
123 such as mortality, movement patterns, dispersal aspects, reproduction, gap crossing, edge  
124 effects, home range, habitat amount, patch size, patch-scale or landscape-scale connectivity;  
125 to analyse all these aspects together is still a difficult task.

126 We combined available information from field studies focussing on the understorey  
127 bird community of the Atlantic Forest, a highly deforested and fragmented biome (12% of the  
128 original forest remains; Ribeiro et al., 2009), and one of the biodiversity hotspots in the world  
129 (Myers et al. 2000; Tabarelli et al., 2010). We believe that since we selected a vast range of  
130 plausible response patterns (i.e. birds with different characteristics), we have encompassed  
131 the behaviour of a larger set of species from other regions and groups, especially tropical  
132 ones. Figure 1 shows a schematic representation of how species with different perceptions (or  
133 profiles) can access habitat patches on a subset of sample landscapes. We consider the  
134 amount of habitat accessible for a species as a functional habitat patch, or simply a functional  
135 patch (Dyck and Baguette, 2005; Martensen et al., 2008; Metzger et al., 2009).

### 136 *2.1. Simulated landscapes*

137 We generated a set of 10 000 simulated landscapes using the QRULE program  
138 (Gardner and Urban, 2007). The landscapes combine information for habitat amount,  
139 aggregation, and quality. All factors were simulated as continuous variables. The amount of  
140 habitat varied from 5% to 70%, and aggregation varied from 0.1 (i.e., ~random) to 1.0 (i.e.,  
141 clumped). We also implemented an algorithm in R 2.9 (R Development Core Team 2009) to  
142 attribute habitat quality at a sub-patch scale. Therefore, different parts of patches (i.e., sub-  
143 patches) received different habitat-quality attributes, ranging from 0.1 to 1.0 to reflect within-  
144 patch spatial heterogeneity. To assure that all habitat or matrix quality was equally distributed  
145 between simulations and within landscapes, we used an uniform distribution to set these  
146 values. For the context of our study patches with quality <0.4 could be classified as matrix,  
147 and quality >0.4 are habitat patches. We arbitrarily considered that qualities <0.4 consisted of  
148 farmland, grazing land, tree plantations, and rural and urban buildings, as well as early stages  
149 of vegetation succession (from grazing land with shrubs up to sparse vegetation <2 m tall,  
150 which is very common in Atlantic Forest landscapes given the high rates of forest  
151 regeneration; Teixeira et al., 2009). Qualities between 0.4 and 0.7 included forest structures  
152 in the initial and intermediate stages of succession (from 5 to 40 years old), with many trees  
153 with diameter at breast height < 20 cm, and a closed understory (Viana and Tabanez, 1996;  
154 Viana et al., 1997; Teixeira et al., 2009). Habitat quality >0.7 consisted mainly of mature

155 forest and old stages of succession (>40 years), with many large trees, and with a sparser  
156 understory than the other ages of regeneration (Teixeira et al., 2009).

157 We derived a set of secondary maps from each landscape, including maps of: (a)  
158 distance in relation to habitat edge pixels (independent of the species profile), where  
159 “negative distances” refers to a location inside a patch, and “positive distances” refers to the  
160 matrix, producing a continuous representation of the habitat features of the landscapes; (b)  
161 functional patch identity, which is dependent on the connectivity rules employed (see Figure  
162 1); (c) amount of functionally connected habitat; and (d) effective amount of functional  
163 habitat (amount of functional habitat weighted by habitat quality). Maps (b) to (d) were  
164 generated for each of our five species profiles, so we had a total of 15 auxiliary maps for each  
165 simulated landscape (see Table S1 for complementary information).

## 166 2.2. Explanatory variables

167 We quantified four variables for each landscape: amount of habitat (considering all  
168 habitat patches have the same quality, i.e. 1.0), landscape quality (considering the quality of  
169 both matrix and habitat patches), habitat quality (considering only habitat patches for  
170 estimating the quality), and habitat aggregation. Figure 2 shows a scatter plot for these  
171 variables. Only the amount of habitat and landscape quality are highly correlated (Pearson  
172 correlation  $r=0.9$ ,  $p<0.01$ ). All other variables are poorly correlated (Pearson correlation  
173  $|r|\leq 0.2$ ;  $p>0.05$ ).

## 174 2.3. Response variables

175 The outputs of the simulations include four response variables: (a) dispersal rate,  
176 which is a ratio between the number of individuals that are dispersing in time step  $i$  and the  
177 total number of individuals alive in the same time step; (b) mortality rate, which is the  
178 proportion of individuals that died during each simulation, and is measured at the end of the  
179 simulation process; (c) movement variability, which is a ratio between the effective  
180 displacement (Euclidian distance between the initial and ending positions of all individuals)  
181 and the cumulative distance of all movements made by all individuals during the simulations;  
182 (d) movement cost, which is the sum of all individual movement costs, in all time steps, and  
183 includes both the safeness of the positions according to the distance to habitat edge in all time  
184 steps (inside habitat patches is safer and the cost is lower, outside is more dangerous for  
185 individuals and the cost is higher and increase with distance to the habitat edge) and habitat  
186 quality within patches.

## 187 2.4. Individual Based Model Description

188 To describe BioDIM we adopted the ODD (Overview, Design concepts, and Details)  
189 protocol proposed by Grimm et al. (2006). These authors suggested structuring the model  
190 description in steps, organised in three main blocks of information: A. Overview [Purpose;  
191 State variables and scales; Process overview and scheduling]; B. Design concepts; and C.  
192 Details [Initialisation; Input; Submodels]. The first two blocks (A. Overview and B. Design  
193 concepts) and part of the third block (initialisation and input in C. Details) are presented  
194 below. Submodels and tables with parameters are available in the supporting online material.  
195 A flowchart for BioDIM is shown in Figure 3. Hereafter, “individual” and “bird” are used as  
196 synonyms.

#### 197 *A.1. Overview - Purpose*

198 The purpose of this model is to allow the user to assess how habitat amount,  
199 aggregation, and quality influence ecological processes and species responses (mortality rate,  
200 dispersal rate, movement variability, and movement cost) which determine species  
201 persistence at the landscape scale. Simulated species can have different home-range sizes  
202 (amount of habitat required for an individual), different dispersal capabilities (usage or not of  
203 corridor, and different gap-crossing capabilities), and different preferences for locations in  
204 relation to the habitat edge (some species prefer to remain in core locations, whereas others  
205 can explore near-edge locations; some others can either cross small distances through the  
206 matrix or longer ones, which again produces a continuous response to parameters usually  
207 considered as categorical variables). The model also provides an option for the user to  
208 consider habitat quality when estimating carrying capacity at the patch and landscape scales.  
209 All information (including response variables) is stored for each landscape or simulation, for  
210 each time step, for each species profile and for each individual. Landscape maps are stored in  
211 GRASS GIS 6.4, and Python 2.5 was used as the programming language.

#### 212 *A.2. Overview - State variables and scales*

213 BioDIM model is composed of five components: species profiles; state values,  
214 functional habitat patch, population, and landscape.

215 For this paper, only one species profile will be used for illustration purpose, but in  
216 total, five species profiles are already implemented (Figure 1): (a) edge-sensitive,  
217 representing species that prefer to remain in the interior of patches (>90 m from any edge;  
218 Hansbauer et al., 2008a, 2009); (b) edge-tolerant, for species that can move through the  
219 whole patch, including edges, but do not use corridors <60 m wide; (c) edge- and corridor-  
220 tolerant, for species that can access all habitats that are structurally connected by corridors  
221 (sensu Martensen et al., in prep); two generalist profile, with (d) low (< 60 m) and (e)

222 medium (< 120 m) gap-crossing capabilities in routine movements, which are able to use all  
223 forested areas, and respectively cross up to 60 m or 120 m of open habitat between forest  
224 patches (Awade and Metzger, 2008; Boscolo et al., 2008; Martensen et al., 2008).

225 Individual state values include: individual identity, starting location (X-Y  
226 coordinates), current location (X-Y coordinates), dispersing (yes or no), alive (yes or no),  
227 cumulative cost of movement, cumulative distance of movements, species profile, and age. In  
228 the current version of BioDIM, aging has no effect in mortality, besides a higher propensity  
229 for exploratory movements of younger individuals (Dyck and Baguette, 2005).

230 Functional habitat patches are inputted from the landscape map set, and depend on the  
231 selected species profile. In the context of this IBM, a population is a set of individuals that  
232 share the same functional habitat patches. The carrying capacity of a functional habitat patch  
233 depends on functional patch size, habitat quality, and home-range size (Wang and Grimm,  
234 2007).

235 The landscape component includes all maps related to each landscape (see *Simulated*  
236 *landscapes* section for detail). All the model components, with their state variables, starting  
237 parameters, distributional functions, explanations of formulae, and supporting literature are  
238 summarised in Table S1 (See Figure 3 for the flowchart of the model).

### 239 A.3. Overview - Process overview and scheduling

240 The first step of the simulation is to randomly select a landscape from the map  
241 database (see *Simulated landscapes* section for details). After that, the amount of habitat is  
242 estimated, and the starting population size is defined as a ratio between the total amount of  
243 habitat and the home-range size (Wang and Grimm, 2007) required per individual. Each bird  
244 is positioned in a random habitat location. The time step is the user's choice, and could be  
245 minutes, hours, days, weeks, years, etc. This adds flexibility to BioDIM, allowing the user to  
246 parameterise the model for different taxonomic groups and regions. Here, for simplicity  
247 matters, we opted to set the time step for days. In the simulations, individuals can move once  
248 a day (within-day movements are not explicitly considered), following a uniform distribution  
249 between zero and the maximum routine or explorative distance (in m). The functional habitat  
250 patch is a set of one or more habitat patches that can be accessed by individuals in routine  
251 movement. The accessibility of habitat patches that will compose a functional habitat patch  
252 depends on the species profile (Figure 1). If the number of home ranges in a functional  
253 habitat patch is higher than the carrying capacity, younger birds are forced to disperse to find  
254 a new available functional habitat patch. The cost of movement is calculated cumulatively for  
255 each individual and for each time step, and depends on the bird's location in terms of habitat

256 quality at each time step. We use the distance from the edge as an indication of how safe a  
257 position is for individuals within a given habitat patch (Figure S1). This information is used  
258 in combination with habitat quality to estimate movement costs. We assume that when  
259 individuals are dispersing or crossing the matrix, the mortality rate increases (Dyck and  
260 Baguette, 2005; Munkemuller and Johst, 2006), following an exponential function (Figure  
261 S2). Therefore, the distance from edges (inside and outside of habitat patches) influences  
262 both the chance of mortality and the movement cost. The reproduction rate was established  
263 by calibration, using simulations for landscapes with >60% of habitat, so that reproduction  
264 compensates for mortality after 500 time steps. This calibration was obtained for edge-  
265 sensitive, edge-tolerant, and edge- and corridor-tolerant species. We acknowledged that  
266 landscapes with more than 60% of habitat were above the percolation threshold (Stauffer,  
267 1985; Metzger and Décamps, 1997), so in theory these landscapes could provide a quite  
268 stable condition for population maintenance compared to landscapes with smaller amounts of  
269 habitat.

#### 270 *B. Design concepts*

271 The population dynamics over short time scales (days, months, years) is important  
272 because it can influence species persistence and community structure through time.  
273 Population density is a function of habitat quality (Munkemuller and Johst, 2006), species'  
274 capability to access functional habitats, and species' habitat requirements. Crowding  
275 stimulates exceeding individuals to disperse. When moving (dispersing or not), individuals  
276 consume energy, and we consider that there is a cost of movement depending on the location  
277 of the birds. Patterns of movement variability, mortality, dispersal rate, and movement costs  
278 are expected to emerge as a function of landscape properties (amount, quality, and  
279 aggregation of habitat) and species profiles.

280 Individuals respond to the amount of habitat available in each functional patch, and  
281 also to the crowding of individuals within that patch. They perceive their position in relation  
282 to the edge (Dyck and Baguette, 2005) and are sensitive mainly to edge proximity and matrix  
283 costs. Habitat quality is also perceived by birds, and the quality influences both the density of  
284 individuals and a bird's decision to disperse or not. Because BioDIM is a density-dependent  
285 model, we used a combination of habitat quality and patch size to estimate the number of  
286 home ranges (which gives a clue to the carrying capacity per habitat patch; Munkemuller and  
287 Johst, 2006).

288 Overcrowding depends on the functional habitat patch (Dyck and Baguette, 2005).  
289 When there is an excess of individuals in a functional patch, they disperse and attempt to

290 establish home ranges in new patches. For example, edge-sensitive species, when not  
291 dispersing and when their location is  $< 90$  m from an edge, will attempt to move to a safer  
292 location (i.e., move to a core location, following a correlated random walk).

293 Individual success varies according to the species profile, landscape properties, and  
294 number of home ranges available in a functional habitat patch. An individual in the matrix,  
295 i.e., in a location with lower habitat quality, is more prone to die than an individual in a  
296 habitat with higher quality, i.e. in a safer location, as for example inside a habitat patch.

297 BioDIM records information at four hierarchical data structures for each simulation,  
298 which is defined by a randomly selected landscape, and a given species profile, simulated  
299 with a defined time step:

- 300 i. for each species and simulation;
- 301 ii. for each species and simulation, but also by each time step;
- 302 iii. for each individual;
- 303 iv. for each individual, by each time step.

304 For the purpose of general species responses and for simplicity reasons, only the  
305 results for species profiles (items i and ii) are presented here.

### 306 *C. Details - Initialisation*

307 A new landscape is selected randomly for each simulation. The following parameters  
308 were defined at the beginning of the simulation:

- 309 (a) species profiles, selected from a list of available options;
- 310 (b) number of time steps (in minutes, hours, days, months; integer, in this case “days” was  
311 chosen);
- 312 (c) home-range size (in ha; float);
- 313 (d) maximum routine movement distance (meters; float; uniform distribution);
- 314 (e) maximum explorative movement distance (meters; float; uniform distribution);
- 315 (f) inclusion of habitat quality in the modeling process (yes/no);
- 316 (g) inclusion of mortality in the modelling process (yes/no);
- 317 (h) number of runs (i.e., number of simulations; if  $> 1$ , in each simulation a new landscape is  
318 picked up, and a new starting population size is calculated). Rather than having the starting  
319 population size be calculated as a function of habitat amount and home-range size, the user  
320 can also set a desired population size.

321 To explore the feasibility, the user can change the current landscape selection process  
322 (randomly selected) to any other one, as well as inspect a set of auxiliary landscape-derived  
323 maps on the screen (see *Simulated landscapes* section for the list of available landscape

324 maps). The user can also enable or disable the observation of the animation of an individual's  
325 movements when simulating.

326

### 327 **3. Experimental design and model simulation**

328 We ran an experiment to evaluate the relative contributions of habitat amount, habitat  
329 quality, and degree of aggregation to explain the response variables. Because the main  
330 objective of this paper is to present the model description and methodological approach  
331 adopted to develop BioDIM, we decided to run the experiment only for edge- and corridor-  
332 tolerant species. We consider this species profile as a good starting point because it allows us  
333 to explore how structurally connected habitat patches can influence species movements in  
334 fragmented landscapes, and how these structural patches influence the response patterns. We  
335 set a maximum routine movement of 30 m and a maximum explorative distance of 150 m  
336 (Boscolo et al., 2008). All simulations of the current experiment used 500 time steps. Home-  
337 range size was defined as 10 ha. This home-range size is similar to values obtained for  
338 Atlantic Forest understory bird species (e.g., Hansbauer et al., 2008b) and seems to be similar  
339 for other bird, such as those in the Brazilian Amazon (Develey and Stouffer, 2001) and  
340 French Guiana (Jullien and Thiollay, 1998). The total number of replications is 10 000. A  
341 new landscape was randomly selected on each simulation.

342

### 343 **4. Data analysis**

344 We used generalised additive models (GAM; Bolker et al., 2009) to assess the relative  
345 contribution of habitat amount, habitat quality, and aggregation, and their consequent  
346 interactions to explain the response variables, The analysed response variables were  
347 summarised at the landscape scale, and we adopted the model selection approach (Burnham  
348 and Anderson, 2002) and Akaike's Information Criterion (AIC) to compare concurrent  
349 models. We considered that differences of AIC values smaller than 2 ( $\Delta AIC < 2$ ) were equally  
350 plausible to explain the observed patterns.

351 Mortality and dispersal rates were modelled based on a Binomial distribution of their  
352 residuals, and movement cost and movement variability were analysed as a Gamma  
353 distribution. Because mortality and dispersal rates follow the Binomial distribution, we  
354 weighted the model by the starting population size of each simulation. Although landscape  
355 quality is highly correlated to the amount of habitat, we kept this variable constant in the  
356 model, because we have a special interest in the variability of landscape quality for larger

357 amounts of habitat. We split the analysis into two sets of models. The first set was composed  
 358 only by univariate models. The second set of concurrent models included combinations of  
 359 two or three variables, and also included their interacting terms. When analysing the second  
 360 group of models, we included all univariate models in the selection process. A null model  
 361 was also included in the model selection process. The following sets of concurrent models  
 362 were compared:

363 Univariate models:

364  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \epsilon_i$

365  $Y = \alpha + \beta_1 * f_1(\text{AGGREG}) + \epsilon_i$

366  $Y = \alpha + \beta_1 * f_1(\text{HABQUAL}) + \epsilon_i$

367  $Y = \alpha + \beta_1 * f_1(\text{LANDQUAL}) + \epsilon_i$

368 Compound models:

369  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{AGGREG}) + \epsilon_i$

370  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{AGGREG}) + \beta_3 * (\text{AMOUNT:AGGREG}) + \epsilon_i$

371  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{HABQUAL}) + \epsilon_i$

372  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{HABQUAL}) + \beta_3 * (\text{AMOUNT: HABQUAL}) + \epsilon_i$

373  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{LANDQUAL}) + \epsilon_i$

374  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{LANDQUAL}) + \beta_3 * (\text{AMOUNT: LANDQUAL}) + \epsilon_i$

375  $Y = \alpha + \beta_1 * f_1(\text{AGGREG}) + \beta_2 * f_2(\text{HABQUAL}) + \epsilon_i$

376  $Y = \alpha + \beta_1 * f_1(\text{AGGREG}) + \beta_2 * f_2(\text{HABQUAL}) + \beta_3 * (\text{AGGREG: HABQUAL}) + \epsilon_i$

377  $Y = \alpha + \beta_1 * f_1(\text{AGGREG}) + \beta_2 * f_2(\text{LANDQUAL}) + \epsilon_i$

378  $Y = \alpha + \beta_1 * f_1(\text{AGGREG}) + \beta_2 * f_2(\text{LANDQUAL}) + \beta_3 * (\text{AGGREG: LANDQUAL}) + \epsilon_i$

379  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{AGGREG}) + \beta_3 * f_3(\text{HABQUAL}) + \epsilon_i$

380  $Y = \alpha + \beta_1 * f_1(\text{AMOUNT}) + \beta_2 * f_2(\text{AGGREG}) + \beta_3 * f_3(\text{LANDQUAL}) + \epsilon_i$

381  $Y = \alpha + \beta_1 * f_1(\text{AGGREG}) + \beta_2 * f_2(\text{HABQUAL}) + \beta_3 * f_3(\text{LANDQUAL}) + \epsilon_i$

382

383 where: Y is the response variable; AMOUNT= habitat amount ; AGGREG=degree of  
 384 aggregation; HABQUAL= habitat quality ; LANDQUAL= landscape quality;  $\alpha$ ,  $\beta_1$ ,  $\beta_2$ , and  
 385  $\beta_3$  are estimates for parameters,  $f_1$ ,  $f_2$ , and  $f_3$  are smoothing functions for GAM, and  $\epsilon_i$  is the  
 386 error term, which is  $\sim N(0, \sigma^2)$ . The “:” character in the models indicates interactions between  
 387 factors. The linking function for the mortality and dispersal rates is logit, while for movement  
 388 cost and movement variability the linking function is log with a Gamma distribution. Quality  
 389 of habitat considers only the weighted quality of the habitat patches (those with quality >  
 390 0.4), while landscape quality also includes the quality of the matrix. We included a null  
 391 model to assure that the explained patterns were always better than a neutral model. All

392 models were fitted using the *mgcv* package available in the R language 2.9 (R Development  
393 Core Team 2009). Piece-wise regression and quantile regression were applied to thresholds  
394 identification on trend and variability of response variables as function of explanatory ones.

395

## 396 **5. Results**

397 The correlation between response variables was highest for movement cost and  
398 dispersal rate (Pearson correlation  $r=0.7$ ,  $p<0.01$ ), but slightly lower ( $r=0.5$ ,  $p<0.05$ ) between  
399 dispersal rate and mortality. Although movement cost and dispersal rate showed a correlation  
400 of 0.7, we did not consider these variables as redundant, and we therefore analysed them  
401 independently. All other response variables were poorly correlated ( $r\leq 0.4$ ).

402 In analysing the univariate models, we found that habitat amount was the best model  
403 to explain dispersal rate and movement cost (Table 1), while aggregation best explained  
404 movement variability and mortality rate. The compound models (which also included  
405 univariate models) suggested that the model including habitat amount, aggregation, and their  
406 interaction (amount:aggregation) best explained movement variability, mortality rate, and  
407 movement cost (Table 1). For dispersal rate, the best models also included habitat amount  
408 and aggregation, but habitat quality was included in the model. No other models are shown  
409 on Table 1 because only one model have  $\Delta AIC < 2$  per response variable and per set of  
410 analysis (univariate and compound models).

411 We observed non-linear relationships between some response and explanatory  
412 variables. Dispersal rate (Figure 4A) presented a threshold for habitat amount  $\sim 29\%$ , showing  
413 more variability and higher dispersal rates below this threshold. Dispersal rate also showed a  
414 threshold at the aggregation level of 0.51, with more variability for lower aggregation levels.  
415 Mortality rate suggested a less clear but significant (quantile regression;  $p=0.042$ ) threshold  
416 at habitat amount  $\sim 16\%$  for response variability (Figure 4B, left panel). Mortality also  
417 showed a threshold for the aggregation level of 0.57 (piece-wise regression;  $p<0.001$ ), below  
418 which the trend was almost constant, with a decaying mortality response just after this break-  
419 point (Figure 4B, central panel). Movement cost suggested a threshold for habitat amount of  
420 13% (piece-wise regression;  $p<0.001$ ), with a higher cost in lower habitat amounts (Figure  
421 4C, left panel).

422 Although we used model selection to analyze univariate and compound models, we  
423 also observed that three out of four response variables were visually well explained by the  
424 individual explanatory variables. The best explained patterns were observed for movement

425 cost ~ habitat amount (Figure 4C, left panel). A second clear pattern was observed between  
426 mortality rate ~ aggregation (Figure 4B, central panel). Dispersal rate (Figure 4A, left panel)  
427 also showed a clear pattern as a function of habitat amount, but in this case both the trend and  
428 the variability appeared to be well delineated, with a higher dispersal rate and higher  
429 variability for lower habitat amounts.

430

## 431 **6. Discussion**

### 432 *6.1. Relative contribution of amount, aggregation, and quality of habitat*

433 Habitat amount and aggregation (or configuration) are the two most important factors  
434 that influence species response at the landscape scale (Fahrig, 2003; Riitters et al., 2009), but  
435 few studies have evaluated which aspects of species' movement and survival might be most  
436 influenced by these factors. Our results agree with previous studies (Fahrig, 2003; Riitters et  
437 al., 2009), because habitat amount and aggregation were present in all the best compound  
438 models selected to explain response variables (Table 1). However, habitat quality was also an  
439 important factor, especially for movement cost. Our results highlighted also that the best  
440 habitat predictors change with ecological process consider. Particularly, we observed that  
441 movement variability, mortality and movement cost were best explained by habitat amount,  
442 aggregation, and their interactions, whereas dispersal rate was best explained by the model  
443 that included habitat amount, aggregation, and quality.

444 Empirical data highlight the important contribution of habitat quality to species  
445 persistence, biodiversity maintenance, and movement pattern at the landscape scale  
446 (Castellón and Sieving, 2005; Uezu et al., 2008; Hansbauer et al., 2009). Although these  
447 studies have provided important information for the understanding of how habitat quality  
448 influences the response patterns, it is difficult to obtain data that will allow us to explore this  
449 contribution across the full range of amounts of habitat and the degree of habitat aggregation.  
450 Simulated landscapes (Riitters et al., 2009), in combination with IBMs, are very powerful  
451 tools to aid in this task. Our results suggest that, depending on the response variable of  
452 interest, the importance of habitat quality increases or decreases. This was observed for  
453 dispersal rate, where habitat quality was included in the best compound model, in  
454 combination with the amount and aggregation of habitat (Table 1). Recently, Shanahan and  
455 Possingham (2009) evaluated the contribution of different landscape parameters in patch  
456 occupancy estimation for birds in fragmented landscapes, and found that vegetation quality  
457 was the best variable to explain the patch occupancy, when compared to isolation and patch  
458 shape. Shanahan and Possingham (2009) observed that in some cases, vegetation quality and

459 percentage of suitable habitat in the landscape overcome the contribution of habitat amount  
460 and patch size to explain patch occupancy. This empirical result agrees with the findings  
461 from the simulations carried out with BioDIM. Additionally, several studies that analysed  
462 how bird species respond to landscape structure and quality of habitat have emphasised that  
463 habitat quality is a very important explanatory variable (Castellón and Sieving, 2005; Uezu et  
464 al., 2008; Hansbauer et al., 2009). Why was only one of our response variables (dispersal  
465 rate) partially influenced by habitat quality? Several factors could have influenced this result.  
466 Firstly, habitat quality influences mainly the carrying capacity of habitat patches (or the  
467 number of individuals or home-ranges that a functional habitat patch can support), but no  
468 constraints were imposed forcing individuals to choose positions with higher levels of habitat  
469 quality. Secondly, the studies that explore the relationship between response patterns and  
470 habitat quality are carried out, in general, at the patch scale. Although BioDIM allows us to  
471 analyse information at functional habitat patch scale, the current experiment considered only  
472 the summary at landscape scale. Future analysis using information at individual and patch  
473 scale could provide fine tuned information regarding the importance of habitat quality on  
474 explain the response patterns of species.

475         Tischendorf and Fahrig (2000) developed a similar approach to that used in BioDIM  
476 and the current experimental analysis. The authors also considered the quality of habitat in  
477 their model, but they emphasised the quality of matrix, whereas our emphasis was on the  
478 quality of habitat. Another difference is that all the parameters that we used to generate the  
479 landscapes (habitat amount, aggregation, and quality of habitat) are fully continuous, while  
480 Tischendorf and Fahrig (2000) used landscapes with three cover classes (habitat, hospitable  
481 matrix, and inhospitable matrix) in their analysis (see also Rayfield et al., 2010). Another  
482 similarity between BioDIM and the models developed by Tischendorf and Fahrig (2000) is  
483 the species' sensitivities to habitat disturbance. The model of these authors includes four  
484 species profiles (extreme specialist, moderate specialist, moderate generalist, and extreme  
485 generalist). Similarly, BioDIM also considers different levels of species' sensitivity, but our  
486 model is calibrated to respond to core and edge conditions as some species are capable of  
487 using habitat corridors, and others are not. We also considered species with two possible  
488 levels of gap crossing of an open matrix (60 and 120 m). One difference between BioDIM vs.  
489 Tischendorf and Fahrig's model is that our model uses a set of equations and functions to  
490 define how individuals will move during simulations (Figures S1 and S2), instead of using of  
491 discrete transition rules.

492

## 493 6.2. *Advantages of BioDIM*

494 To model the full complexity of an ecological system is challenging, if not  
495 impossible. Models are approximations of our understanding about how patterns and  
496 processes interact or emerge in nature. When comparing outcomes from models, we are,  
497 overall, testing whether our model understanding and assumptions make sense. BioDIM is an  
498 ecologically scaled IBM that focuses on simulating bird movement for species with different  
499 responses to edge proximity and habitat quality, and for species with different capabilities to  
500 cross an inhospitable matrix. Although the model was developed to determine how sensitive  
501 bird species are to landscape structure and habitat quality in the Brazilian Atlantic Forest, it is  
502 very easy to set up BioDIM for species that responds to other environments or scales, as well  
503 as to the interaction between other characteristics of the landscapes (such as proximity to  
504 water, roads, urban areas). The model is also easily adaptable to species in regions other than  
505 the tropical Atlantic Forest.

506 The number of possible sensitivity analyses for an IBM is infinite. Some of them  
507 could be experimentally tested to check the model's sensitivity to input parameters, or in  
508 some cases to effectively run a testable hypothesis of interest. It was not our intention here to  
509 explore the full spectrum of sensitivity of the model, but rather to assess how the amount and  
510 quality of habitat and the degree of its aggregation influence the response patterns of edge-  
511 and corridor-tolerant species (see *Future developments and new experimental tests*).

512 Our IBM has several advantages over previous ones (With and Crist, 1995;  
513 Tischendorf and Fahrig 2000; Hilker et al., 2006). First, the model respond to continuous  
514 functions (not to discrete rules), including the birds' locations (which can assume subpixel  
515 locations, with other individuals sharing the same space); the home-range size can be set at  
516 any area value  $> 0$ , and can accept decimal precision; and the home-range size can vary  
517 following uniform, normal, Gamma, or Poisson distributions. The maximum distances  
518 (routine and explorative) can also either be fixed, or can follow a uniform or normal  
519 distribution. The second advantage is that the IBM has the capability to consider functional  
520 connectivity while individuals are moving, and the movement restrictions are set up using  
521 species profiles and not through a set of categorical or discrete conditions or constraints. The  
522 third, and innovative, characteristic is that BioDIM incorporates the perception of habitat  
523 quality, which can influence the cost of movement, and also the number of home ranges that  
524 can be supported within a functional habitat patch. Birds are able to respond to overcrowding,  
525 and excess individuals are forced to disperse. Finally, each bird can perceive its location in  
526 relation to the edge of a functional patch at any time, and can perceive how safe that location

527 is; the probability of mortality is not defined as classes of distance, because it follows  
528 asymptotic or exponential decay functions depending on the user's preference. New functions  
529 are easily included in the model by sub-model coding when parameterisation is possible.

### 530 *6.3. Future developments and new experimental tests*

531 We consider our IBM as an on-going process, mainly because we feel that in the  
532 course of its development, new features could be implemented as new information for the  
533 Atlantic Forest bird species becomes available. An in-depth set of tests of the degree that  
534 habitat amount, habitat quality, and aggregation influence the responses (general trends of  
535 responses and outcome variances) should be the main target to pursue. In this case,  
536 simulating species for the full spectrum of sensitivity to their location in relation to the patch  
537 edge, different home-range sizes, and varying degrees of maximum routine and dispersive  
538 movement distances could be very important to understand species dynamics and species  
539 persistence in fragmented landscapes. Species interactions (prey-predation, sympatric  
540 relationship) and incorporating complete life cycles are also important features to be  
541 improved. Finally, considering that in fragmented landscapes, connectivity is very important  
542 for the movement of individuals (Martensen et al., 2008), and that species dispersal  
543 influences gene flow/variability (Dixo et al., 2009), incorporating genetic information into  
544 future versions of BioDIM will allow us to simulate experiments using a landscape genetics  
545 approach (Manel et al., 2003).

546

## 547 **7. How do IBMs contribute to conservation biology and landscape planning?**

548 Although BioDIM was developed for Atlantic Forest bird species, it can be adjusted  
549 and applied to other regions, as well as to other taxonomic groups that respond to the amount,  
550 the degree of aggregation, and the quality of habitat. BioDIM can also be helpful in  
551 addressing issues related to species dynamics and persistence through time, to develop  
552 conservation and restoration plans, and to simulate how landscape structure and natural  
553 barriers can influence gene flow on different temporal and spatial scales. The greatest value  
554 of our contribution is the inclusion of habitat quality at the patch and landscape scales.  
555 Habitat quality has been historically analysed mainly at the stand or patch scale. We advocate  
556 that habitat quality should be included in all scales of analysis, from patch-level to macro-  
557 regional scale. Although habitat amount, patch size, and spatial arrangement are very  
558 important features to maintain high biodiversity at the landscape scale, we observed that  
559 habitat quality cannot be neglected. Because all these landscape features interact with each  
560 other, we observed that depending on the amount of habitat, the strength of importance of

561 other variables shifts from low to high. Considering that biological information is very costly  
562 to obtain, and that the number of species of interest involved in conservation and restoration  
563 planning is also large, the simulation of potential response patterns considering landscape  
564 features (habitat amount, habitat quality, and aggregation) and species profiles is a very  
565 promising first step to run prior to the collection of new field-level information, and to  
566 establish programs for biodiversity maintenance.

567

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574

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- 719

720 Figure captions

721

722 Figure 1: Schematic representation of how species with different "species' profiles" perceive  
723 functional habitat patches in sample landscapes, where each color represents a different  
724 structural or functional patch. For the context of this study each pixel represents 30x30 m.  
725 (A) original binary map (gray is habitat; white is matrix); (B) edge-sensitive species, avoiding  
726 one pixel of edge zone; (C) edge-tolerant species that do not use corridors less than 2 pixels  
727 wide; (D) edge- and corridor-tolerant species; (E) generalists, with low (< 60 m) gap-crossing  
728 ability; (F) generalists, with medium (<120 m) gap-crossing ability. Dashed line in E and F  
729 delimitates the boundaries for patches that belongs to each functional habitat patches.

730

731 Figure 2: Scatter plots of explanatory variables (n=10 000). The diagonal panel shows the  
732 histogram distribution for each variable. Pearson correlations are shown on the upper  
733 triangular panels, where the label sizes are proportional to the correlation values. Each point  
734 on lower triangular panels represent one simulation, for a different landscape.

735

736 Figure 3: Flowchart for the Individual Based Model BioDIM 1.0 calibrated for bird  
737 movements in fragmented landscapes of the Brazilian Atlantic Forest. HR=home-range size.  
738 See Table S1 for complementary information.

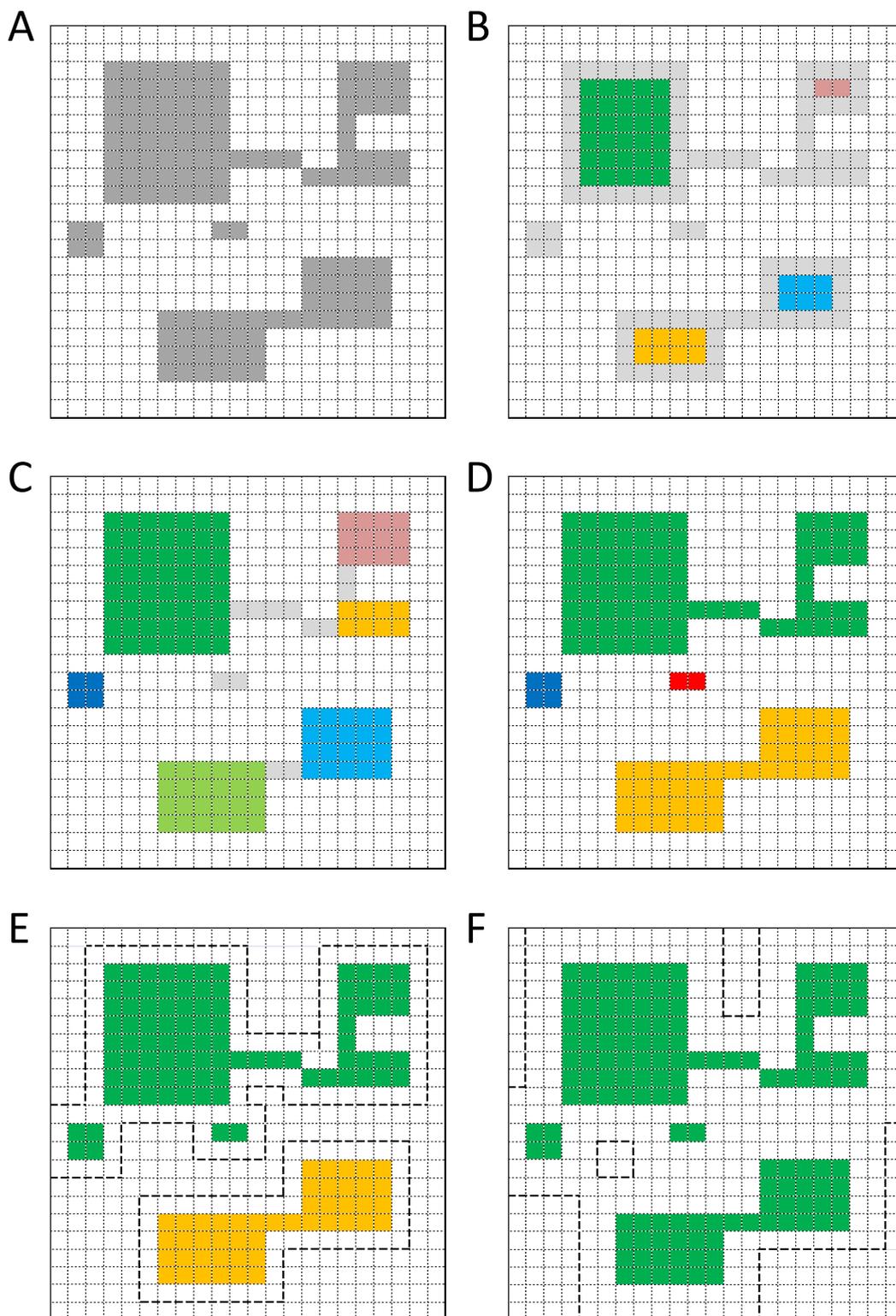
739

740 Figure 4: Response variables across habitat amount and aggregation, for edge- and corridor-  
741 tolerant species, home-range size 10 ha, routine maximum distance 30 m, and maximum  
742 explorative distance 150 m. Panel (A) mortality rate; (B) movement cost. Black dots are  
743 simulated values, and the line shows the estimated response trend.

744

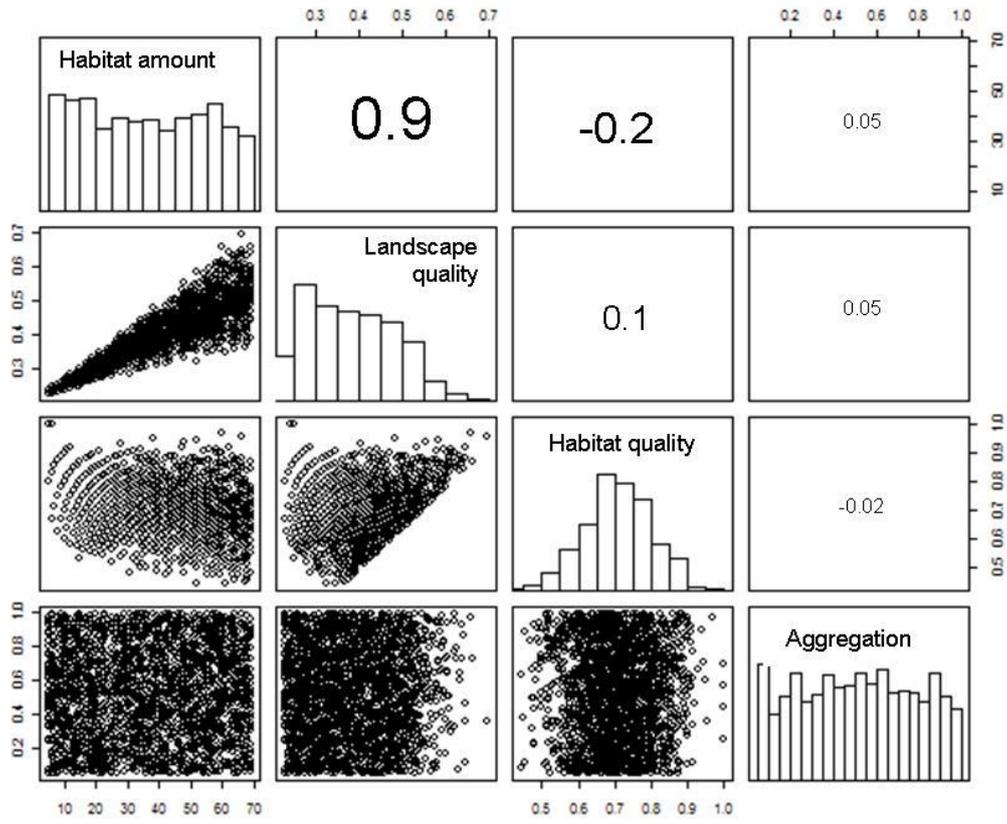
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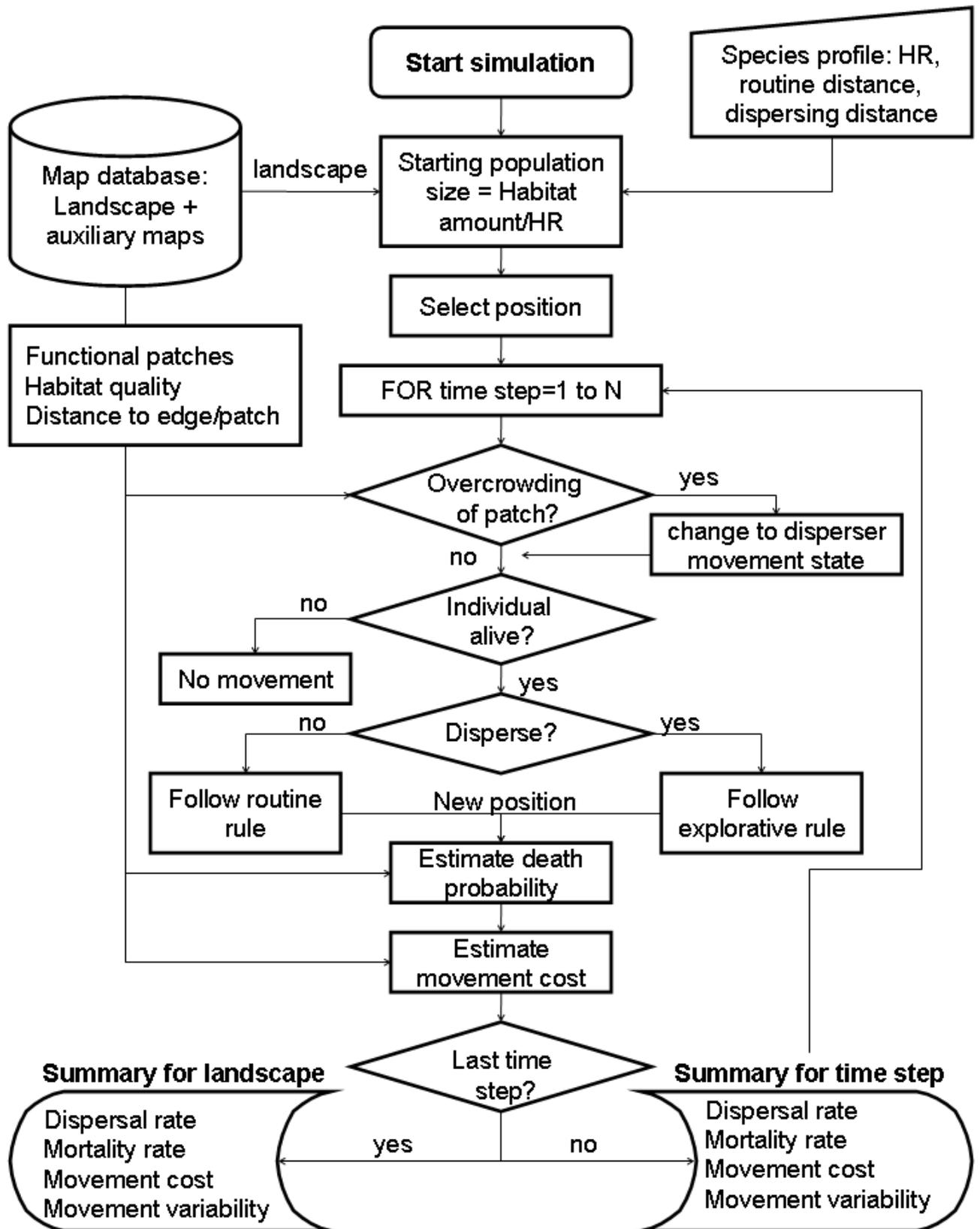
748 Figure 1



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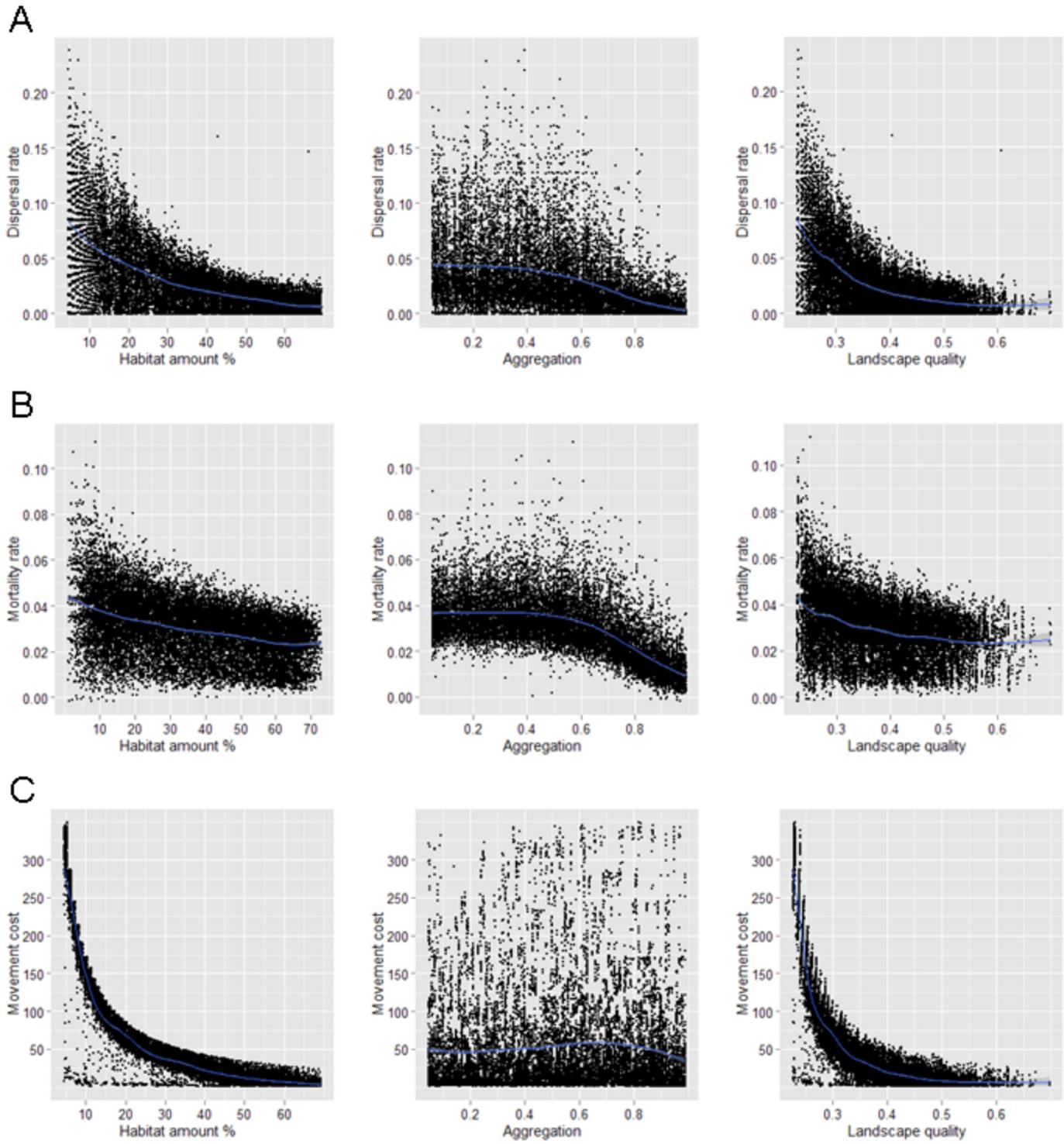
750 Figure 2

751



752  
753

Figure 3



754  
755 Figure 4

756 Table 1: The best set of models to explain the dispersal rate, mortality rate, movement  
 757 variability, and movement cost estimated from Individual Based Model simulations. Only  
 758 one model is shown per response variable or set of analyzes (univariate and compound  
 759 models) because no other model presented  $\Delta AIC \leq 2$ . The weight of Akaike's information  
 760 criterion is indicated by wAIC. See *Data analysis* section for details of the models.

Response variable	Best models	wAIC
<i>Univariate models</i>		
Movement variability	AGGREG	0.77
Dispersal rate	AMOUNT	0.83
Mortality rate	AGGREG	0.89
Movement cost	AMOUNT	0.90
<i>Compound models</i>		
Movement variability	AMOUNT+AGGREG+AMOUNT: AGGREG	0.79
Dispersal rate	AMOUNT+AGGREG+HABQUAL	0.89
Mortality rate	AMOUNT+AGGREG+AMOUNT: AGGREG	0.84
Movement cost	AMOUNT+AGGREG+AMOUNT: AGGREG	0.92

761

762 Support Online Material

763 *A1. Submodels*

764 *A1.1. Survival*

765 In time step=1, all birds are set as “alive” status = “Yes”. If during the simulation the  
766 individual die, the “alive” status changes to “No”, and all subsequent submodels are ignored.

767 *A1.2. Home-range size and population size*

768 Home-range size is an important part of the model, because it defines the starting  
769 population size. Also, if a functional habitat patch is overcrowded, some birds will be forced  
770 to change the “dispersing” status from “No” to “Yes”. We consider the number of home-  
771 ranges in a functional habitat patch as a surrogate for carrying capacity. When an individual  
772 is dispersing, it will experience matrix conditions that increase its chance of mortality, as well  
773 as influence the cost of movement, and may also change the movement variability. The larger  
774 the home-range size required for one individual, the smaller the allowed population density  
775 per functional habitat patch.

776 *A1.3. Perceptual range*

777 Each individual is capable of "perceiving" the population density in the same  
778 functional habitat patch. If a patch is overcrowded, non-dispersing birds have equal chance to  
779 change its status of “dispersing” to “Yes”. Individuals perceive their location in relation to  
780 the habitat edge, and can change their movement pattern to find a safe location (toward the  
781 core location for edge sensitive species). They can also avoid the matrix (except for the two  
782 generalist species), and can perceive the quality of the habitat at any location.

783 *A1.4. Routine movement*

784 A bird which is in its routine movement (i.e., dispersing=“No”) can move to any  
785 location around the current functional habitat patch. A set of possible new locations is  
786 randomly defined, considering a uniform distribution between 0 and maximum routine  
787 movement distance (m) around the current location. Locations not allowed by the species  
788 profiles (such as a location < 90 m from the edge for edge sensitive species, or a matrix  
789 location for edge and corridor tolerant) are discarded. If a species profile is edge sensitive,  
790 and the current location is <90 m, only those locations in the direction of the core will be  
791 chosen. If by chance no location satisfies the requirements of the species profile, one of the  
792 available locations is randomly selected.

793 *A1.5. Dispersal*

794 If the “dispersing” status is “Yes”, the maximum distance defined for dispersing birds is  
795 considered, and a correlated random-walk pattern is followed (Dyck and Baguette, 2005). A  
796 general dispersal direction is chosen, and individuals have a 50% chance of moving in the  
797 direction of dispersal, and 50% of changing in a random direction. The amplitude range for  
798 the directional dispersing pattern is 45°. If an individual reaches a new functional habitat  
799 patch that is not overcrowded, the “dispersing” status changes to “No”, and the individual  
800 follows the routine movement rules.

#### 801 *A1.6. Movement cost*

802 The cost for each movement is calculated as a function of habitat quality at the  
803 location of an individual, and how "safe" that location is for the individual. Each species can  
804 perceive differently how safe its location is, and this "safety" is in relation to the edge (Figure  
805 2). Habitat quality is acquired from the landscape map. The degree of safety of a bird is  
806 estimated from a negative asymptotic-shaped response curve defined for each species profile.  
807 The farther inside a habitat patch, the safer is that location for a bird. Individuals in the matrix  
808 have a low degree of safety. Figure 2 illustrates the safety response curves for all species  
809 profiles. These curves were defined arbitrarily, but following a logical sequence of species  
810 sensitivity to habitat disturbance. The total cost of movement for each individual and for all  
811 time steps is calculated by the equation: movement cost =  $\sum 1 / (\text{habitat quality} * \text{safety})$ .

#### 812 *A1.7. Mortality*

813 Mortality follows an exponential decaying probabilistic response to the location of  
814 birds in relation to the edge zone, and varies for species profiles. A location inside the habitat  
815 patches has a probability of lower mortality compared to a matrix location. The farther inside  
816 the habitat patch, the lower is the mortality rate. The more sensitive a species is, the higher is  
817 the probability of mortality for the same location. Figure 3 shows mortality probability curves  
818 for simulated species profiles. As for the movement cost, we again defined these curves  
819 arbitrarily, but following a logical sequence of species sensitivity to habitat disturbance.

#### 820 *A1.8. Reproduction*

821 The reproduction submodel is of secondary importance in the present model. The  
822 reproduction rate was generated by calibration after several simulations for landscapes with  
823 larger amounts of habitat (>60%). We consider that landscapes with a large habitat amount  
824 must show equilibrium between mortality and reproduction. Simulations for different species  
825 profiles and for different home-range sizes suggest that, for landscapes with a habitat amount  
826 >60%, the mortality rate is almost constant, independently of the time steps. We also selected  
827 this range of habitat amounts because according to the percolation threshold (Stauffer, 1985;

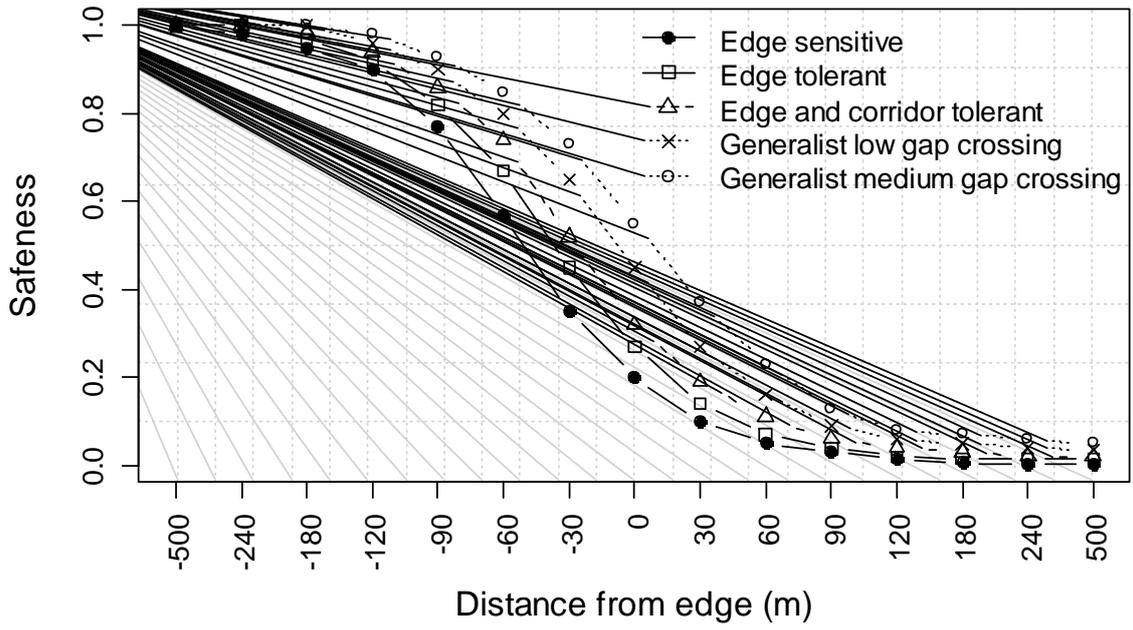
828 Metzger and Décamps, 1997), landscapes with more than 60% habitat have a high chance  
829 that the patches will remain interconnected, facilitating movement and increasing  
830 accessibility to all patches within landscape. To compensate for the mortality, a fixed  
831 reproduction rate of 0.61 (per 1 000 time steps/individual) was used for each time step.  
832

833 Figure captions for supplementary online material

834 Figure S1: Asymptotic safety response curve as a function of distance from edge (m) and for  
835 each species profile. Negative distances refer to locations within habitat patches, zero is the  
836 edge zone, and positive values refer to the matrix. See *Individual Based Model Description*  
837 section for species profile.

838

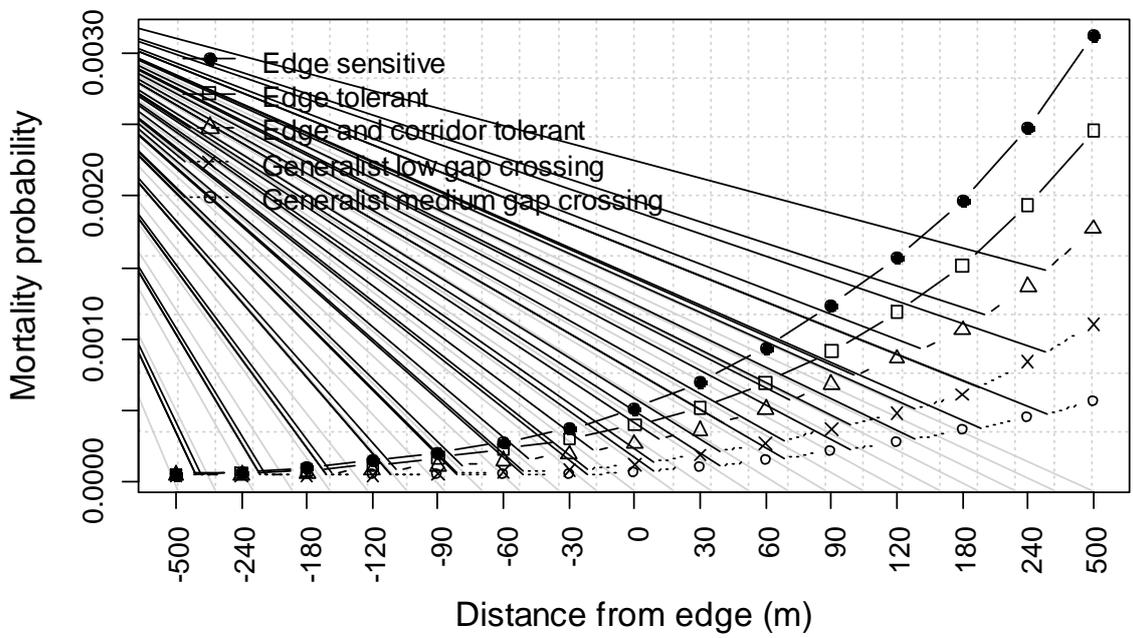
839 Figure S2: Exponential response curve for probability of mortality as a function of distance  
840 from edge (m) and for each species profile. Negative distances refer to locations within  
841 habitat patches, zero is the edge zone, and positive values refer to the matrix. See *Individual*  
842 *Based Model Description* section for species profile.



843

844 Figure S1

845



846

847 Figure S2

Table S1 - Overview of processes, parameters, functions, and default values of parameters for the Individual Based Models to describe bird dispersal in fragmented landscapes of the Atlantic Forest, Brazil.

Parameter	Unit	Values, ranges, and functions	Description	References and additional information
<u>General Settings</u>				
Output files	Text		A prefix for output filenames. User can choose four levels of hierarchical information to be stored.	
Number of simulations	Integer value	>0	Number of successive repetitions per experimental session.	
Time step	Integer value	>1	Defines the number of steps for each simulation, is unit-free, and can assume minutes, hours, days, weeks, months, years, depending on the user's interest and focal species aspects.	
Starting population size	Integer	>0	User can set a fixed starting population size; if this is not done, the IBM will estimate the starting population size as a ratio between total habitat amount in the landscape (in ha) and home-range size (in ha); ratios are rounded to have positive integer values.	
Reproduction rate	Float	0.061 per 100 time steps/individual	Obtained by calibration from simulations considering different home-range sizes, and for 500 time steps. Only landscapes with > 60% of habitat were used for this calibration.	
<u>Species characteristics</u>				

Species profile	Choice list	<p>Options:</p> <ol style="list-style-type: none"> <li>0. Random walk</li> <li>1. Edge sensitive</li> <li>2. Edge tolerant</li> <li>3. Edge and corridor tolerant</li> <li>4. Generalist with low gap crossing</li> <li>5. Generalist with medium gap crossing</li> </ol>	<p>Six species profiles define how a functional habitat will be formed, and affect routine individual movement, perception of overcrowding, and stimulate individuals to change their movement pattern from routine to dispersive movement. For the current implementation, edge sensitive individuals attempt to avoid locations &lt; 90 m from the edge; edge tolerant are individuals that use indiscriminately any location in the habitat patch, but avoid using corridors &lt; 60 m; edge and corridor tolerant are species that use any structurally connected habitat patch (including corridors); generalist species with low mobility can cross non-habitat up to 60 m; generalist species with medium mobility can access areas up to 120 m.</p>	<p>For edge avoidance we used Hansbauer et al. (2008a);</p> <p>Edge tolerant and edge and corridor tolerant species profiles used the findings of Martensen et al. (2008) and Martensen et al. (in prep.); Banks-Leite et al., 2009; Hansbauer et al., 2009 .</p> <p>Gap-crossing capability information came from Awade and Metzger (2008) and Boscolo et al. (2008).</p> <p>See text for additional information.</p>
Home range (HR) size	Positive float; Area (ha)	<p>Option 1: any positive fixed value;</p> <p>Options 2-5: following probabilistic distributions</p>	<p>Home-range size defines the amount of functional habitat required for each individual. This variable directly influences the starting population size (see below). User can choose between six options to set the home-range size:</p> <p>Option 1: the user-provided value</p>	<p>For experimental simulations, and for Atlantic Forest birds, we referred to Hansbauer et al. (2008b) for home-range size ranges.</p>

will be used for all simulations;  
 Option 2: a set of HRs will be defined following a normal distribution - user must provide  $\mu$  and  $\sigma$  parameters;  
 Option 3: a set of HRs will be defined following a uniform distribution - user must provide minimum and maximum HRs;  
 Option 4: a set of HRs will be defined following a Poisson distribution - user must provide  $\mu$  parameter;  
 Option 5: a set of HRs will be defined following a Gamma distribution - user must provide  $\mu$  and  $\kappa$  parameters; useful for inverted J and other complex shapes.

Routine maximum distance	Positive float; Area (m)	$\geq 0$	Refers to the maximum distance for each time step; follows a uniform distribution between 0 and the value provided; other distributions (normal, Poisson, or Gamma) are easily adjusted;	We used, partly, Boscolo et al. (2008) to calibrate our experimental simulations.
maximum explorative distance	Positive float; Area (m)	$\geq 0$ ; generally greater than routine maximum distance	Maximum distance to be traveled for each time step when the individual is forced to disperse; follows a uniform distribution between 0 and the value provided; other distributions (normal, Poisson or Gamma) are easily adjusted.	Boscolo <i>et al.</i> (2008) and Hansbauer <i>et al.</i> (2008a) partially support current experimental simulations.

## Individuals

Individual identity	Integer	1 – N	Sequential number, where N is the total number of individuals per landscape/simulation.	
Initial location	Float, list [X, Y]	-	Any valid X,Y location in the landscape; important to estimate movement variability.	
Current location	Float, list [X,Y]	-	Any valid X,Y location in the landscape.	
Age	Integer; in time units	>0	Any positive integer value; when the number of individuals in a functional habitat patch is greater than the supported population size, excess younger individuals are forced to disperse. At the end of the simulation, the age is used to estimate the mean movement cost for the life history of each individual.	The current version of the model does not yet consider the full life cycle, so age information is only partially included.
Alive	Binary	0=dead; 1=alive	When the individual dies, it stops moving, there is no increase in movement cost, and it is not included in the population size estimate.	
Dispersing	Binary	0=No 1=Yes	If dispersing status = "No", individuals follow a routine movement pattern. Otherwise change the movement pattern to a correlated random walk, with a general direction of dispersal. Maximum distance for each time-step movement is influenced by this	

Total movement length	Float; (m)	>0	variable. Cumulative movements for all time steps.	
Distance from edge	Float; (m)	- inf to inf	Negative values refer to interior of patch; positive values refer to matrix.	
In which functional patch	Integer	NULL or >0	Identity of functional habitat patch in which non-dispersing individuals are located; otherwise is NULL.	
Total movement cost	Float	>0; Each movement cost is calculated by the function : $1 / (\text{habitat quality} * \text{safety})$	Cumulative cost to each individual for movement during the simulation. The cost for each movement depends on the habitat quality at the individual's location and the safety that the location offers to the individual.	We partially used the information available for preference for interior of patch (Hansbauer et al., 2008a), and avoidance of long distance from the patch when an individual is dispersing in the matrix (Awade and Metzger, 2008; Boscolo et al., 2008).
<u>Populations</u>				
Population identity	Integer	>0	Identity of all populations	
Functional habitat patch identity	Integer	>0	Each population occupies a different functional habitat patch	
Individual identity	List	-	List of all individuals that occupy the same functional habitat patch; Only individuals with [is dispersing] = "No" are considered as belonging to a population.	
<u>Functional habitat patches</u>				
Functional habitat patch identity	Integer	>0	A functional habitat patch is a list of all patches that an individual can	

			access when following a routine movement pattern. Information on species characteristics (such as use or not of corridors; gap-crossing capability) defines whether a habitat patch belongs - or not - to a functional habitat patch.	
Functional area	Float; (ha)	>0	Sum of all functional areas available for a population.	
Functional area including habitat quality	Float; (ha)	>0	Sum of all functional areas weighted by the habitat quality available to a population.	
<u>Landscapes</u>				
Landscape identity	Integer	1-10 000	A sequential identity for the landscapes.	Initial landscapes were generated using the QRule program (Gardner and Urban; 2007).
Dimensions	Integer; list[row,col]	[512, 512]	Total number of rows and columns for the simulated landscapes; however, BioDIM itself can be run for any dimension.	
Pixel resolution	Float; list[Res X,ResY]; (m)	[30,30]	The current map dataset was generated with imposed resolution of 30x30 m; however, the BioDIM is easily adaptable for any resolution.	
Percentage of habitat		5-70%	The percentage of habitat was defined a priori, following a uniform distribution.	
Amount of habitat	Float; in ha	>0	Quantification of the total amount of habitat.	
Aggregation	Float	0-1	The aggregation followed a	

Habitat quality	Float	0.1 - 1.0	<p>uniform distribution; habitat aggregation = 0 is completely random; aggregation = 1 is clumped.</p> <p>A structural patch may be composed of several sub-patches, and those sub-patches can have different habitat qualities; smaller values (0.1-0.4) were set for low quality (i.e., matrix); values &gt;0.4-1.0 were set as quality of sub-patches of habitats, so a habitat patch is composed of sub-patches with different levels of quality.</p>
Effective amount of habitat	Float	>0 and ≤ amount of habitat	<p>Sum of all habitats patches area weighted by habitat quality of sub-patches.</p>

# CAPÍTULO V

*Untangling the effects of landscape structure,  
habitat quality, and species traits on ecological  
processes*

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Untangling the effects of landscape spatial structure, habitat quality, and species traits on  
ecological processes

Running title (50 characters including spaces)

*Species traits and landscape structure effects*

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## **Abstract**

Habitat amount, aggregation, quality, and species traits influence population persistence in fragmented landscapes, but few studies have evaluated them jointly in order to untangle their relative contribution. Using an individual-based model calibrated for birds species of the Brazilian Atlantic Forest, we simulated species movements within simulated landscapes that varied greatly in habitat amount, aggregation and quality. Using sensitivity analysis, we assessed the influences of species traits, landscape structure, and habitat quality on five ecological processes: dispersal rate, mortality, movement cost, movement detour, and encounter rate. Species traits and landscape structure strongly influenced the ecological processes, but habitat quality was not an important factor. Species sensitivity, habitat amount, habitat aggregation and home-range were the most important variables, but the strength of influence varied according to the ecological processes in focus and the species profile. Our results stress the importance of landscape-based management, and that they should take in to consideration the focal species traits when planning conservation and restoration actions as well as highlight the effects of habitat aggregation independently of habitat amount.

*Key-words:* habitat fragmentation, confounding factors, sensitivity analysis, individual-based model, species movement, species traits, Brazilian Atlantic Forest, BioDIM.

## 1. Introduction

Habitat amount, aggregation, and quality affect population persistence (With 1994), and ultimately species conservation (Fischer & Lindenmayer 2007; Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010). These variables are inherently “confounding factors” (*sensu* Ewers & Didham 2006), which makes it difficult to separate their influences on species responses. Moreover, their effects vary widely between species, adding more complexity to ecological problems (Fahrig 2003; Ewers & Didham 2006; Oliver et al. 2010). The acquisition of empirical biological data from species with different biological traits, across a wide variety of conditions of amount, spatial arrangement, and degrees of habitat quality is costly in time and money, and in most cases is impossible to carry out. Simulations using individual-based models (IBMs) have emerged as an option to address these complex questions, where multi-scale influences are important (Railsback 2001; DeAngelis & Mooij 2005; Grimm et al. 2006), and ecological processes (e.g., dispersal, biomass production, mortality, and gene flow) are affected differently by each of these factors.

IBMs have been widely used to investigate landscape-structure influences on species responses (With & Crist 1995; Neel et al. 2004; Riitters et al. 2009), to analyze top-down (landscape influencing species) and bottom-up influences (variability of responses measured at the individual level influencing landscape-scale processes), and also, to identify emerging properties across scales (DeAngelis & Mooij 2005; Bridle et al. 2010). However, most of these IBMs are calibrated for North American or European ecosystems, and very few have attempted to understand the strength of influence of these interacting factors in more complex regions such as the tropic (Drinnan 2005). Such use of IBMs in tropical regions requires a balance between model simplification and

complexity in order to make them more realistic and hence useful (Ewers & Didham 2006; Moore et al. 2008; Clobert et al. 2009; Boyle & Smith 2010; Webb et al. 2010). Therefore more realistic knowledge about how species with different traits and how different ecological processes are influenced by confounding factors is important to allow better landscape management in degraded tropical areas.

In this study, we used an IBM to disentangle the effects of landscape structure, habitat quality, and species traits on ecological processes related to species movement and maintenance in fragmented landscapes. We simulated species movements using BioDIM (*Biologically scaled Dispersal Model*), an individual-based model calibrated for tropical bird species of the Atlantic Forest (Ribeiro et al., in review). We analyzed five important ecological processes for biodiversity conservation in fragmented landscapes: dispersal rate, mortality, movement cost, encounter and movement detour. BioDIM simulates individual movements (i.e., bottom level); however, all simulations were summarized at the landscape scale. Sensitivity analyses were used to measure the strength of influence of variables of interest: amount and aggregation of habitat, habitat quality on the patch and landscape scale, routine and explorative dispersal capacities, species sensitivity, and home-range size. Our sensitivity analysis is a multifactorial experimental design combining continuous variation of all these factors. Our findings reinforce the importance of considering landscape-based strategies for conservation and restoration planning. We also observed that, as expected by theory, species traits were particularly important; however, ecological processes were influenced in different ways by the analyzed factors, and for different species. Although the literature stresses the importance of habitat aggregation only below some threshold of habitat amount (Fahrig 2003), our results suggest that habitat aggregation was important, independently of cover. Yet, for

particular ecological processes, such as dispersal rate and mortality, aggregation overwhelm habitat amount.

## **2. Methods**

### *2.1. Simulated landscapes*

We focused on tropical forest ecosystems, since there is an urgent need for information to support landscape management, which could prevent the extinction of many threatened species (Myers et al. 2000; Fischer & Lindenmayer 2007; Secretariat of the Convention on Biological Diversity 2010), and thus avoiding to paid the huge “extinction debt” of those complex and endangered systems (Tilman et al. 1994; Ford et al. 2009; Metzger et al. 2009 ). QRULE (Gardner & Urban 2007) was used to generate a mapset of 10 000 landscapes with forest amount varying continuously from 5% to 70%, and habitat aggregation ranging from 0.1 (~random) to 1.0 (clumped). Then, habitat quality was randomly assigned at the sub-patch scale, when values <0.4 were considered as matrix (for example, farmlands, pastures, exotic-tree plantations, rural and urban buildings, as well as early stages of native vegetation succession); values ranging from 0.4 to 0.7 were considered as forests in the initial or intermediate stages of succession (5 to 40 years old; *sensu* Viana et al. 1997; Teixeira et al. 2009); and values >0.7 were considered as mature forest or in advanced successional stages (>40 years), with many large trees, and with a sparser understory (Teixeira et al. 2009).

### *2.2. The Individual-based Model and Species traits*

BioDIM 1.1 is an individual-based model that allows the simulation of species movement considering different species traits calibrated with extensive literature data: (a) sensitive to habitat spatial structure (Martensen et al. 2008); (b) varied home-range size (Hansbauer et al. 2008); (c) diverse maximum routine (i.e., daily movement, Hansbauer

et al. 2008) and (d) explorative distances (i.e., dispersal movement, Awade & Metzger 2008; Boscolo et al. 2008). Five species profiles (i.e., sensitivity) were modeled in BioDIM to cover a broad range of species sensitivity response to landscape heterogeneity (Fig.1): (1) edge-sensitive (ES), representing species that prefer core habitat position, avoiding habitats close ( $\leq 90$  m) to edges; (2) edge-tolerant (ET), for species that can move through the whole patch, including edges, but not using corridors  $\leq 60$  m in width; (3) edge- and corridor-tolerant (ECT), for species that can access all habitats that are structurally connected by corridors; and two generalist species, with (4) low ( $< 60$  m; GC60m) and (5) medium ( $< 120$  m; GC120m) gap-crossing capabilities in routine movements, able to use surrounding patches (Martensen et al. 2008). Home-range size (in ha) was used to estimate the starting population size, and to define the carrying capacity of a functional habitat patch (Munkemuller & Johst 2006; Wang & Grimm 2007; Börger et al. 2008). Because we were interested in species local responses, we modelled two general movement rules: routine and explorative movements (Dyck & Baguette 2005). Routine movements occur mainly within a functionally connected habitat patch, over short distances and in a nearly random pattern (Dyck & Baguette 2005). Explorative (i.e., dispersal) movements are longer than routine distances, with a more directional pattern, and where individuals choose a dispersal route, following a correlated-random-walk-like pattern (Morales et al. 2004; Dyck & Baguette 2005). For the purpose of this study, we considered that each individual will move once a day, and the routine or explorative distances are in meters. Overcrowding within functional habitat patches forces surplus individuals to change their movement pattern from routine to explorative. A complete description of BioDIM is provided in Ribeiro et al. (in review), and Fig. S1 presents its flowchart.

### *2.3. Response variables as ecological processes*

Five response variables were measured for any given landscape and any given species profile (i.e. sensitivity), and summarized at the landscape scale: (a) dispersal rate as the proportion of individuals that are dispersing at the end of the simulation; (b) mortality rate as the proportion of individuals that died during the simulation; (c) movement cost, which consider both the safeness of locations where individuals passed (low costs for the interior of habitat patches; high costs for the matrix) and the habitat quality in the pixel scale; (d) encounter rate quantified as the encounter events between males and females, and is a clue for potential gene flow across space and time; (e) movement detour as the ratio between the Euclidean distance among the initial and final positions and the cumulative distance, estimated at the end of the simulation. We consider these five response variables as surrogates for different ecological processes of interest in the management of fragmented landscapes.

### *2.4. Experimental design*

Using Monte Carlo Markov Chain (MCMC), 10 000 replicated simulations (~ 6 million individuals and ~ 3 billion movements) were performed combining information for three groups of factors of interest (Table 1): (a) landscape spatial structure, (b) habitat quality, and (c) species traits. Each simulation starts with a different landscape, which is selected randomly from the mapset. The number of time steps was 500 per simulation, which in our case was considered in days. The perceptual range for quantifying the encounters rate was set as 50 m.

## 2.5. Data analysis

### *Sensitivity analysis*

To quantify how systematic changes in model parameters influence the emerging patterns, we performed a sensitivity analysis (Saltelli et al. 2008). We built a global model including all nine explanatory variables (Table 1) and ran a multiple regression analysis for each response variables. Standardized regression coefficient (*src*) from sensitivity analysis (Saltelli et al. 2008) was used to estimate the strength of influence of explanatory variables. We estimated the mean and standard errors for each of the *src* values (*sensitivity* package available in R; Pujol 2008), which vary between  $-1$  and  $+1$ . Estimated *src* were classified as strong, intermediate, low, or null effect (Table S1) in order to facilitate interpretation and summarization of results. To answer the main question, we calculated the mean *src*, summarizing the effects of response variables, independently of ecological processes. We also conducted a sensitivity analysis within the species profiles, to identify the relative contributions of the other eight variables (Table 1) in explaining the ecological processes. The consistency of each explanatory variable between different processes (i.e., response variables) is summarized and discussed.

## **3. Results**

Species traits and landscape structure were the most important factors influencing the ecological processes, whereas habitat quality did not presented strong influence (Fig. 2). Species sensitivity (mean *src*=0.38) and habitat amount (mean *src*=0.36) showed the highest strength of influence, but habitat aggregation (mean *src*=0.28) and home-range size (mean *src*=0.24) were also of high explanation capacity.

### 3.1. *Dispersal rate and mortality*

Dispersal and mortality processes showed comparable behaviour, where the strongest effects was species sensitivity (Fig. 3A-B). Habitat aggregation was the second most important factor in explaining both dispersal and mortality ( $src=-0.34\pm 0.01$  and  $src=-0.42\pm 0.01$ ), followed by habitat amount ( $src=-0.22\pm 0.04$  and  $src=-0.29\pm 0.04$ ).

Considering each species sensitivity profile, habitat aggregation showed strong negative effects on dispersal and mortality in the three most sensitive species (ES, ET, and ECT; Table 2; Figs. S2-S3). The effect ranged from strongly negative to low positive influence, with decreasing species sensitivity. In general, habitat amount had an intermediate negative effect, while routine distance had an intermediate positive effect on dispersal rate for the three most sensitive species (ES, ET, ECT; Table 2; Figs. S2-S3), but was not important for mortality. Although amount of habitat was always present as an important factor for dispersal rate, no trend was observed across species sensitivity; the same occurred for mortality.

### 3.2. *Movement cost*

Habitat amount was the strongest variable influencing movement cost, with a negative influence ( $src=-0.63\pm 0.03$ ; Fig. 3C). Home-range size and species sensitivity were classified as intermediate positive effects ( $src=0.34\pm 0.01$  and  $src=0.28\pm 0.01$ , respectively; Fig. 3C).

Within species sensitivity, the strong negative effect of habitat amount was reinforced, independently of the species group (Table 2; Fig. S4). Similarly, home-range size was also influential on movement cost for all species (Table 2; Fig. S4). No trend was observed across species sensitivity for the effects of habitat amount and home-range size (Table 2).

### 3.3. Encounter rate

Home-range size had a strong negative influence on encounter rate ( $src = -0.65 \pm 0.01$ ; Fig. 3D). Species sensitivity had an intermediate positive effect ( $src = 0.35 \pm 0.01$ ), while habitat amount and aggregation positively influenced the encounter rate, but to a lesser extent ( $src = 0.22 \pm 0.03$  and  $src = 0.22 \pm 0.01$ ; Fig. 3D).

Home-range size was always influential, independently of species sensitivity, but the effects of habitat amount and aggregation varied between species (Table 2; Fig. S5). Habitat amount was more important for the most sensitive species, and habitat aggregation influenced less sensitive ones (Table 2; Fig. S5). No trend was observed between species sensitivity and the magnitude of the influence of these variables on encounter rate (Table 2).

### 3.4. Movement detour

We did not obtain a clear pattern for movement detour, which was the least well explained process, with  $src$  values always  $< 0.15$  (i.e., low effect; Fig. 3E). Species sensitivity did not appear to influence movement detour (Table 2; Fig. S6), and no trend was detected between species and the magnitude of influence of the explanatory variables on movement detour (Table 2).

## 4. Discussion

Our results revealed that ecological processes are strongly affected by species traits and landscape structure, but not by habitat quality. Landscape structure is relevant for most of the species and ecological processes, especially for mortality, dispersal rate and movement cost, and the importance of habitat amount and aggregation varies predominantly in relation of the analyzed ecological processes than according to the species profile. From another side, home range size, which is a surrogate for species

habitat requirement, is the species characteristics that most influence the ecological processes. Habitat quality was not relevant in explaining any of the ecological processes at landscape scale, especially for forest-dependent species.

We analyzed these aspects in a fully continuous framework varying over a wide gradient of habitat amount, aggregation, quality and several species traits variables. We consider that all plausible attribute combinations that may occur in real-world landscapes are encompassed within our simulated landscapes, which made possible an in-depth analysis for a range of variation for which empirical studies are not viable. More than that, we gathered data on the landscape scale, originated by processes occurring on the individual and patch levels, which makes our work a fully landscape-level study. Besides the importance of a good understanding of landscape-scale patterns for supporting conservation-management decision-making, this type of information is particularly costly to gather, and the employment of IBMs helped us to understand the influences of landscape scale aspects as well as species sensitivity on ecological processes.

Tropical regions, where biological complexity is impressively high, makes environmental patterns particularly variable, making it difficult to extract generalizations about the ecological processes that generate them (Secretariat of the Convention on Biological Diversity 2010). We provided strong evidences that ecological processes, particularly those related to individual movements and thus to connectivity, respond differently to landscape aspects, such as habitat amount and aggregation. The literature is replete of examples exploring the effects of habitat amount and aggregation on biodiversity in general (Radford et al. 2005; Martensen et al. 2008; Metzger et al. 2009, Zuckerberg & Porter 2010). Here we demonstrated that their influences may differ according to the ecological processes analyzed, which makes it even more complicated to disentangle their influences. Astonishingly, we observed that aggregation was chiefly in

explaining two of the processes independently of the amount of habitat and species profile; and particularly for mortality and dispersal rate (Fig. 3A-B). This is the opposite of what has been suggested in the literature, where habitat aggregation has been proposed to be particularly influential below a certain threshold region (reviewed in Fahrig 2003, Radford et al. 2005; Zuckerberg & Porter 2010), and not independently of the amount of habitat as we observed, at least between 5 and 70%.

Another unexpected result was the absence of habitat quality influences on the ecological processes. This could be given by the fact that quality effects occur at the patch scale (Vögeli et al. 2010), and have less influence at the higher hierarchical scales. However, we analyzed the influence of habitat quality on the patch and landscape scale, and in none of the cases it was important. Habitat quality has been proposed as a key variable influencing species composition in different regions (Castellón & Sieving 2005; Hansbauer et al. 2010), as well as for different species groups (Munkemuller & Johst 2006; Oliver et al. 2010; Vögeli et al. 2010). Moreover, it has been shown by empirical studies that a higher habitat quality in the matrix could facilitate species movement between patches (Antongiovanni & Metzger 2005; Umetsu et al. 2008; Pardini et al. 2009). Species occurrence is usually based on some particular habitat characteristics, especially tropical species, which are well known to be influenced by low habitat quality (Moore et al. 2008; Vögeli et al. 2010). We agree that patches with higher habitat quality contain more species; however, we observed that this is a patch-scale effect with low influence on the landscape scale for any given amount and aggregation of habitat. This suggests that conservation management to guarantee benefits to regional biodiversity will be more effective if applied at the landscape rather than the patch scale, which is the opposite of what have been proposed by some patch-scale observational studies (Vögeli et al. 2010). However, we acknowledge the fact that there are also some emergent

properties across scales (for example, the mortality of individuals could be summarized at patch scale, and the mortalities within several patches influence the mortality rate at landscape scale), which are particularly influential and need to be taken into consideration when considering ecological processes in general, especially at landscape scale, but this was not observed for the habitat quality aspects.

For some ecological processes, such as mortality and dispersal rate, ecological processes are influenced by species sensitivity; whereas for others, species sensitivity is of secondary importance. This makes essential to clearly define for landscape management purposes the target species, as much as to understand their characteristics, in order to properly comprehend the influences of landscape and environmental features on species occurrence, and thus to accurately manage for this focal species.

Clues for the improvement of these simulations can involve their validation in real-world landscapes, as well as the calibration of the species sensitivity with new field data. However, as species traits are not possible to be managed, our study reinforces the importance of considering habitat amount and aggregation for biodiversity conservation planning, and that aggregation should be considered independently of forest cover.

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Table 1: Description of variables analyzed for three groups of confounding factors:

landscape structure, habitat quality, and species traits.

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*Landscape structure:*

- PLAND: Amount of habitat, or percentage of habitat cover within landscape, varying continuously between 5% to 70%;
- AGGREG: Aggregation of habitat, varying from random (~0.1) to clumped (1.0).

*Habitat quality:*

- HQBIN: binary response to include, or not, habitat quality in current simulation;
- HQLAND: estimate of landscape quality considering the quality for habitat patches, and for the matrix;
- HQFRAG: estimate of average habitat quality, considering only habitat patches;

*Species traits:*

- SPECSENSIT: Species sensitivity to habitat disturbance or species profile, where more sensitivity species prefer core position, and less sensitivity species can access forest habitat up to 120 m apart;
  - HORANG: home-range size, varying continuously from 5 to 30 ha, and following a uniform distribution; we referred to Hansbauer et al. (2008) to set this range of values;
  - ROUTDIST: maximum routine distance was set varying continuously from 30 to 90 m (Boscolo et al. 2008), and this variable followed a uniform distribution;
  - EXPLDIST: maximum explorative distance was set to vary between 1.0 and 3.0 times the ROUTDIST, so the maximum explorative distance varied continuously between 90 and 270 m (Hansbauer et al. 2008). This variable followed a uniform distribution.
-

Table 2: Summary for the strength of influence for the group of factors (landscape structure, habitat quality and species traits), and for each ecological process response, considering the standardized regression coefficient obtained from the sensitivity analysis. Species traits were included only in the global model that considers all species. Gray highlights the strongest effects, and light gray is for intermediate effects. See Table 1 for descriptions of explanatory variables.

Response variables	Explanatory variables	All species	Edge-sensitive	Edge-tolerant	Edge- and corridor-tolerant	Low gap-crossing	Medium gap-crossing	Behaviour summary
Dispersal rate	SPECSENSIT	+++						
	PLAND	--	--	--	-	--	--	always present
	AGGREG	--	---	---	---	-	+	strong/trend/always present
	HQBIN	0	0	0	0	0	+	
	HQLAND	0	0	+	-	0	--	Partial
	HQFRAG	0	0	-	0	0	+	
	HORANG	0	-	-	0	+	+	trend/partial
	ROUTDIST	+	++	++	++	+	0	trend/partial
	EXPLDIST	0	0	0	-	-	-	Partial
Mortality	SPECSENSIT	+++						
	PLAND	--	--	---	--	--	--	strong/always present
	AGGREG	--	---	---	---	---	--	strong/always present
	HQBIN	0	0	+	+	0	0	
	HQLAND	-	-	0	--	-	0	Partial
	HQFRAG	+	+	0	+	+	0	Partial
	HORANG	0	0	0	0	0	0	
	ROUTDIST	+	+	+	+	0	+	Partial
	EXPLDIST	0	0	0	0	0	0	
Movement Cost	SPECSENSIT	++						
	PLAND	---	---	---	---	---	---	strong/always present
	AGGREG	0	-	-	-	+	+	trend/always present
	HQBIN	+	+	0	0	+	+	Partial
	HQLAND	-	-	0	-	-	--	Partial
	HQFRAG	+	+	+	0	+	++	Partial
	HORANG	++	++	++	++	++	++	always present
	ROUTDIST	0	0	0	0	0	0	
	EXPLDIST	-	0	-	-	-	-	Partial

+++/- = strongest positive/negative effect; ++/- = intermediate positive/negative effect; +/- = low positive/negative effect; 0 = null effect

Table 2: continued

Response variables	Explanatory variables	All species	Edge sensitive	Edge tolerant	Edge and corridor tolerant	Low gap crossing	Medium gap crossing	Behaviour summary
Encounter rate	SPECSENSIT	++						
	PLAND	++	++	++	+	++	+	always present
	AGGREG	++	0	++	++	++	++	Partial
	HQBIN	0	0	-	0	0	0	
	HQLAND	0	0	0	+	0	0	
	HQFRAG	0	0	-	-	0	0	
	HORANG	---	---	---	---	---	---	strong/always present
	ROUTDIST	0	+	0	0	0	0	
	EXPLDIST	0	0	0	0	0	0	
Movement detour	SPECSENSIT	0						
	PLAND	+	-	++	0	0	++	Partial
	AGGREG	+	0	0	+	+	+	Partial
	HQBIN	-	-	-	-	-	0	Partial
	HQLAND	+	++	0	0	0	0	
	HQFRAG	-	-	-	-	-	0	Partial
	HORANG	0	-	-	0	0	0	
	ROUTDIST	0	-	0	-	0	-	Partial
	EXPLDIST	+	++	++	+	+	0	trend/partial

+++/- = strongest positive/negative effect; ++/-- =intermediate positive/negative effect; +/- =low positive/negative effect; 0=null effect

Table 3: Mean of standardized regression coefficients for each explanatory variable and for each species profile, considering all ecological processes<sup>(1)</sup>. See Table 1 for descriptions of factors.

Explanatory variable	All species	Edge sensitive	Edge tolerant	Edge and	Low gap	Medium gap
				corridor tolerant	crossing	crossing
SPECSENSIT	0.38	n.a.	n.a.	n.a.	n.a.	n.a.
PLAND	0.30	0.37	0.42	0.34	0.40	0.31
AGGREG	0.22	0.30	0.33	0.31	0.25	0.25
HQBIN	0.03	0.03	0.07	0.05	0.05	0.04
HQLAND	0.07	0.11	0.07	0.15	0.10	0.16
HQFRAG	0.06	0.08	0.09	0.10	0.08	0.09
HORANG	0.21	0.27	0.27	0.22	0.22	0.22
ROUTDIST	0.06	0.12	0.11	0.08	0.03	0.04
EXPLDIST	0.04	0.09	0.06	0.08	0.04	0.05

<sup>(1)</sup> The analyzed ecological process responses were: dispersal rate, mortality, movement cost, encounter rate, and movement detour. n.a.= not available

## Figure captions

Figure 1: Schematic representation of how species with different degrees of sensitivity perceive functional habitat patches within sample landscapes (each color represents a different structural or functional patch). For the context of this study, each pixel represents 30×30 m. (A) original binary map (gray is habitat; white is matrix); (B) edge-sensitive species, avoiding one pixel of edge zone; (C) edge-tolerant species, which do not use corridors less than 2 pixels wide; (D) edge- and corridor-tolerant species; (E) generalists, with low (< 60 m) gap-crossing ability; (F) generalists, with medium (<120 m) gap-crossing ability. Adapted from Ribeiro et al. (in review).

Figure 2: Standardized regression coefficients (*src*) obtained from sensitivity analysis for five ecological process responses recorded from bird movement simulations using BioDIM (an individual-based model calibrated for Atlantic Forest bird species). The explanatory variables represent three major groups of factors: landscape structure, quality of habitat, and species traits. Values of *src* are ranked within response variables. Gray bar represents positive *src* values, and white bars negative ones. One standard error bars estimated using bootstrap (n=1 000) are included.

Figure 3: Mean of standardized regression coefficients (*src*) obtained from sensitivity analysis, summarizing all ecological process (n=5) recorded from bird movement simulations using BioDIM (an individual-based model calibrated for Atlantic Forest bird species). The explanatory variables represent three major groups of factors: landscape structure, quality of habitat, and species traits.

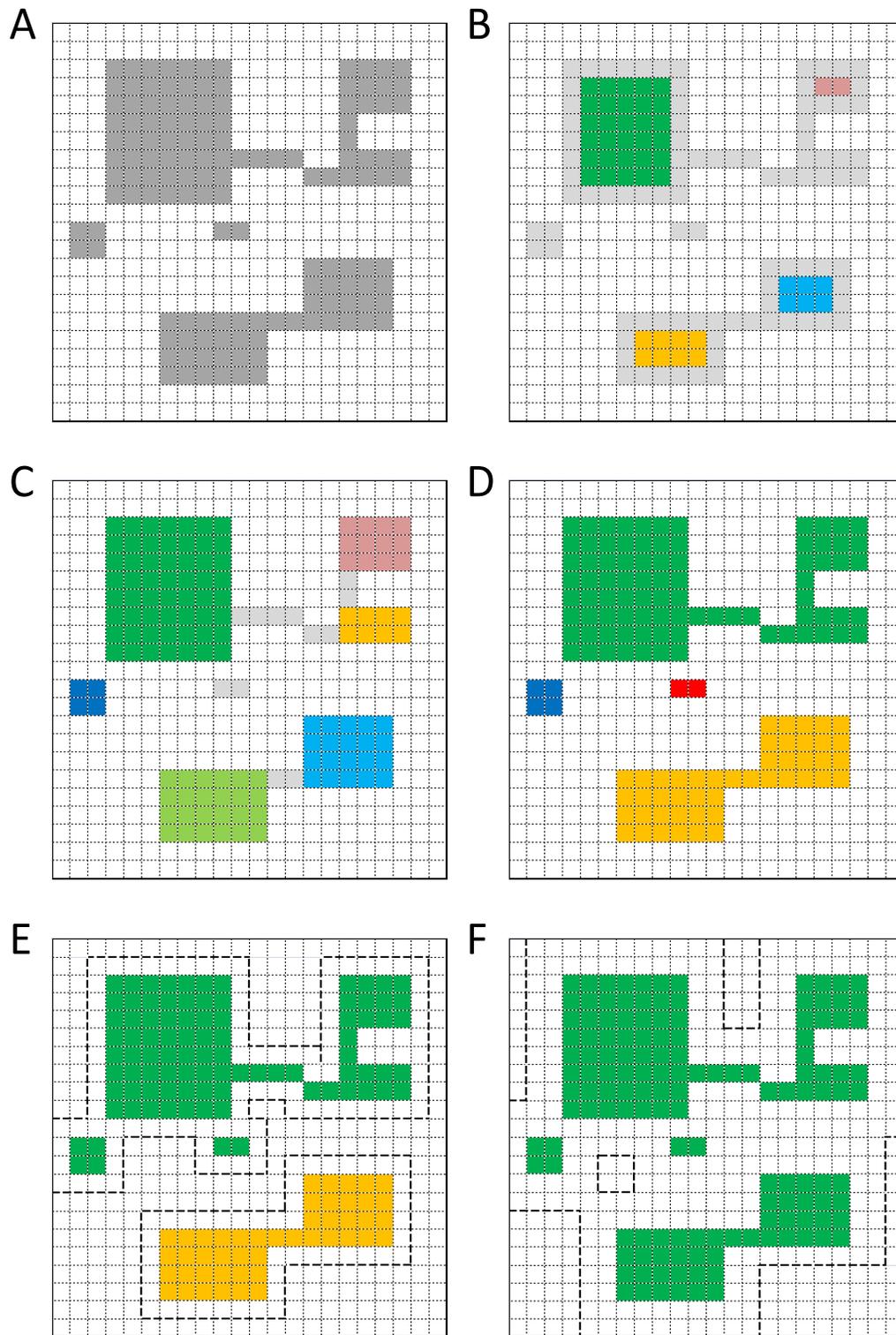


Figure 1

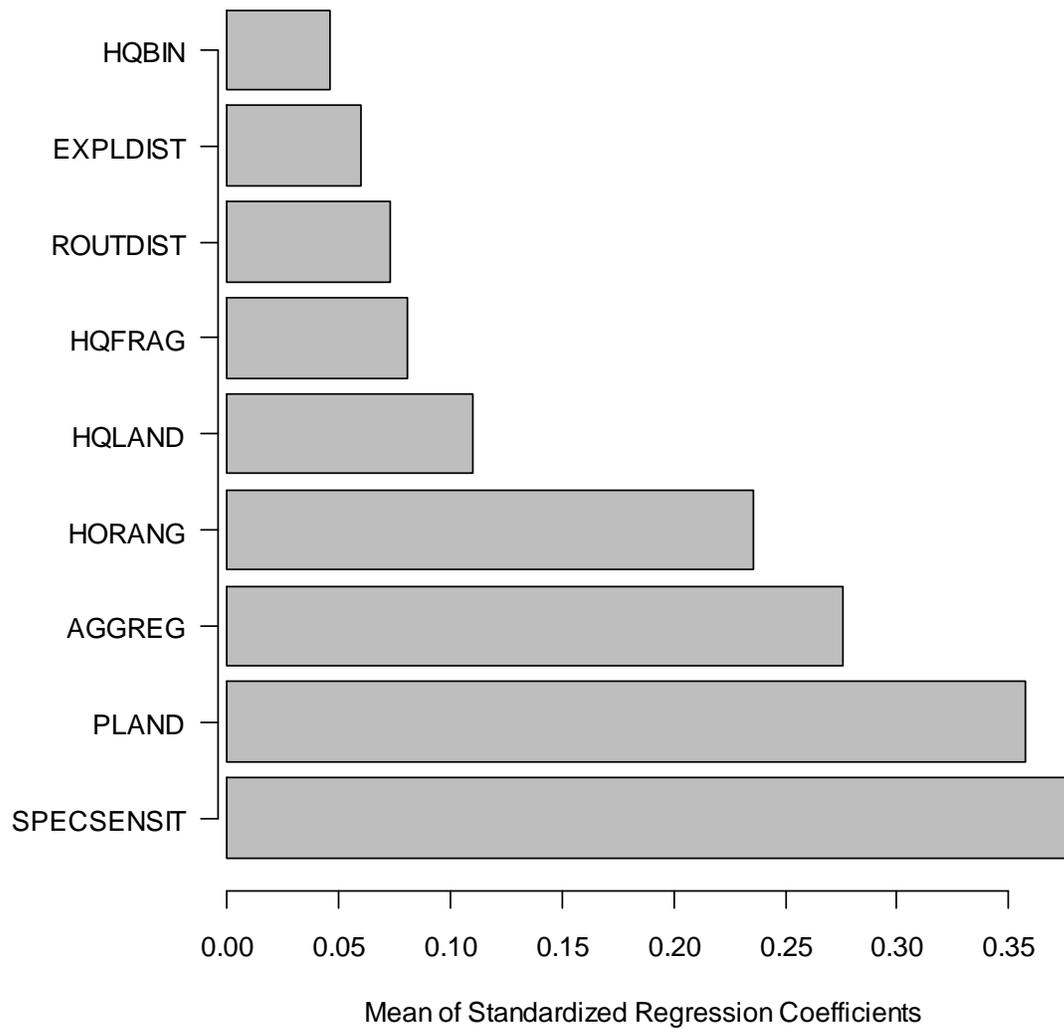


Figure 2

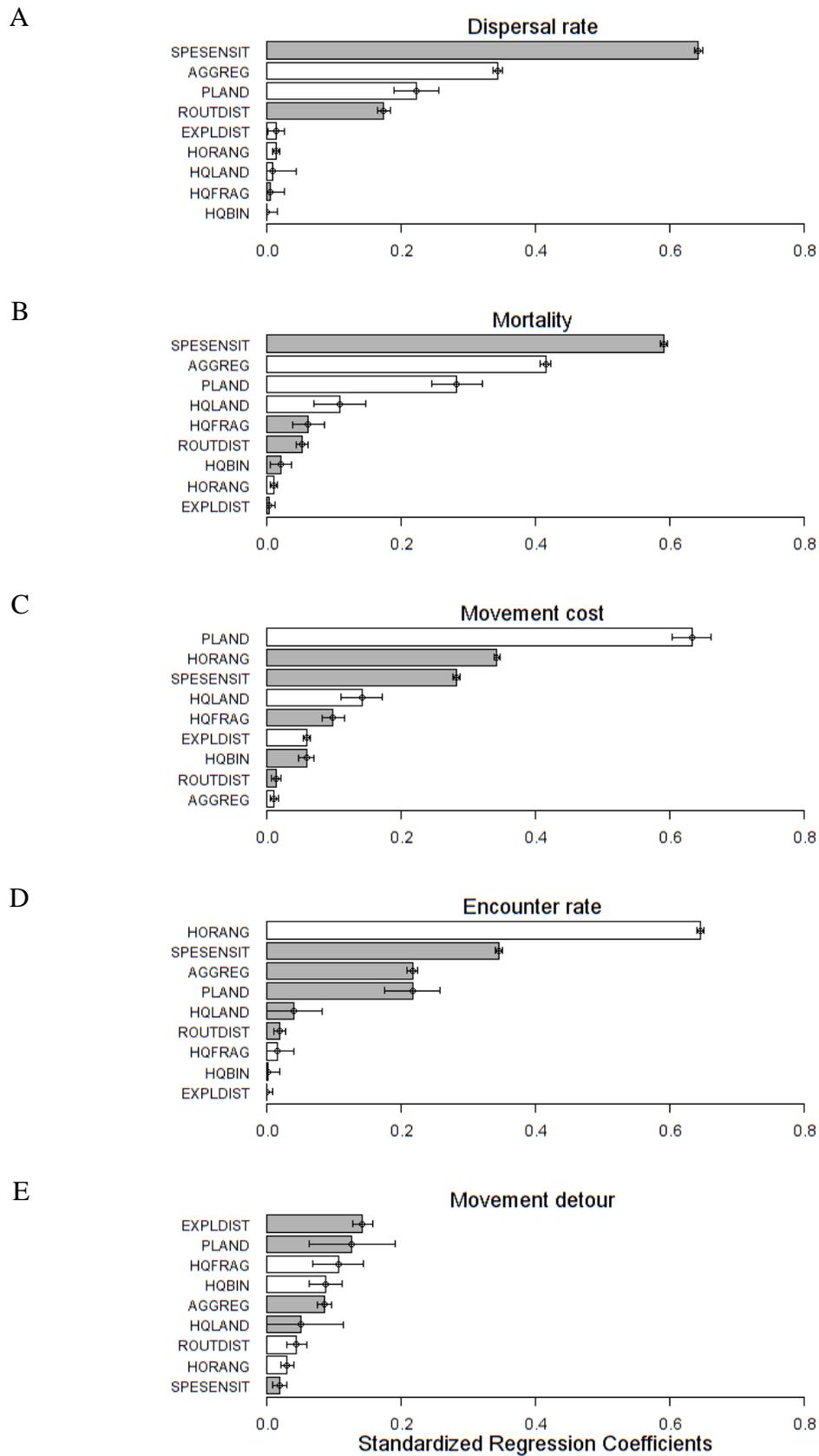


Figure 3

Table S1 – Categorization of standardized regression coefficients (*src*) values obtained from sensitivity analysis.

<i>src</i> classification	<i>src</i> description
'+++'	Strong positive effect, when the mean <i>src</i> value are $\geq 0.5$
'++'	Intermediate positive effect, when mean <i>src</i> value are $\geq 0.2$ and $<0.5$ , and its standard error not includes the zero
'+'	Low positive effect, when mean <i>src</i> value are $\geq 0.05$ and $<0.2$ , and its standard error not includes the zero
'0'	Null effect, when the standard error of <i>src</i> includes the zero, independently of mean <i>src</i> be positive or negative
'-'	Low negative effect, when mean <i>src</i> value are $\leq -0.05$ and $> -0.2$ , and its standard error not includes the zero
'--'	Intermediate negative effect, when mean <i>src</i> value are $\leq -0.2$ and $>-0.5$ , and its standard error not includes the zero
'---'	Strong negative effect, when the mean <i>src</i> value are $\leq -0.5$

## Figure legends for supporting information

Figure S1: Flowchart for the individual-based model BioDIM calibrated for bird movements in fragmented landscapes of the Brazilian Atlantic Forest. HR=Home-range size in ha. Adapted from Ribeiro et al. (in review).

Figure S2: Standardized regression coefficients (*src*) estimated for dispersal rates, where different explanatory variables are ranked within each species sensitivity profiles: A-Edge sensitive; B-Edge tolerant; C-Edge and corridor tolerant; D-Low gap crossing; E-Medium gap crossing. Gray bar represents positive *src* values, and white bars negative ones. One standard error bars estimated using bootstrap (n=1 000) are included.

Figure S3: Standardized regression coefficients (*src*) estimated for mortality, where different explanatory variables are ranked within each species sensitivity profiles: A-Edge sensitive; B-Edge tolerant; C-Edge and corridor tolerant; D-Low gap crossing; E-Medium gap crossing. Gray bar represents positive *src* values, and white bars negative ones. One standard error bars estimated using bootstrap (n=1 000) are included.

Figure S4: Standardized regression coefficients (*src*) estimated for movement cost, where different explanatory variables are ranked within each species sensitivity profiles: A-Edge sensitive; B-Edge tolerant; C-Edge and corridor tolerant; D-Low gap crossing; E-Medium gap crossing. Gray bar represents positive *src* values, and white bars negative ones. One standard error bars estimated using bootstrap (n=1 000) are included.

Figure S5: Standardized regression coefficients (*src*) estimated for encounter rates, where different explanatory variables are ranked within each species sensitivity profiles: A-Edge sensitive; B-Edge tolerant; C-Edge and corridor tolerant; D-Low gap crossing; E-Medium gap crossing. Gray bar represents positive *src* values, and white bars negative ones. One standard error bars estimated using bootstrap (n=1 000) are included.

Figure S6: Standardized regression coefficients (*src*) estimated for movement detour, where different explanatory variables are ranked within each species sensitivity profiles: A-Edge sensitive; B-Edge tolerant; C-Edge and corridor tolerant; D-Low gap crossing; E-

Medium gap crossing. Gray bar represents positive *src* values, and white bars negative ones. One standard error bars estimated using bootstrap (n=1 000) are included.

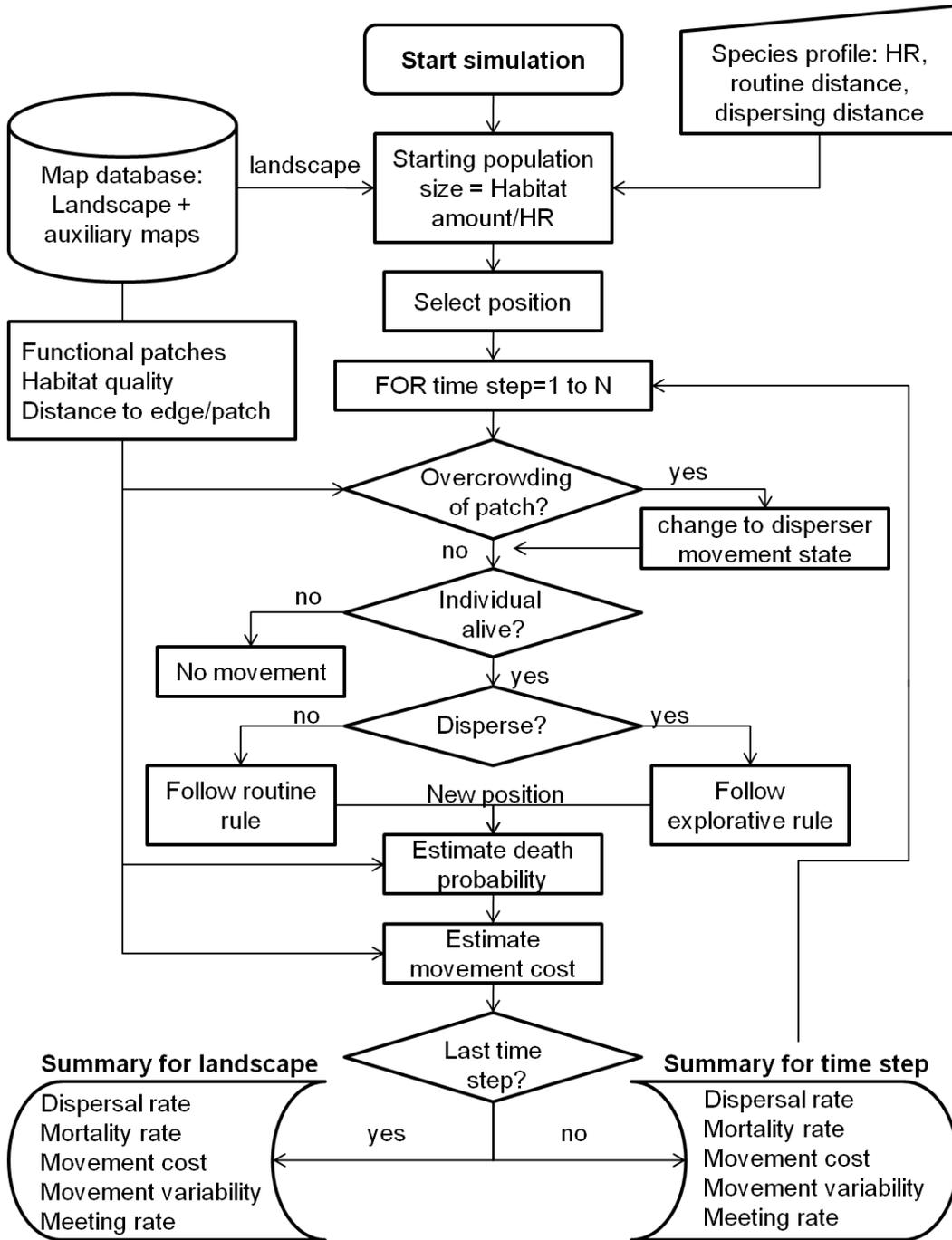


Figure S1

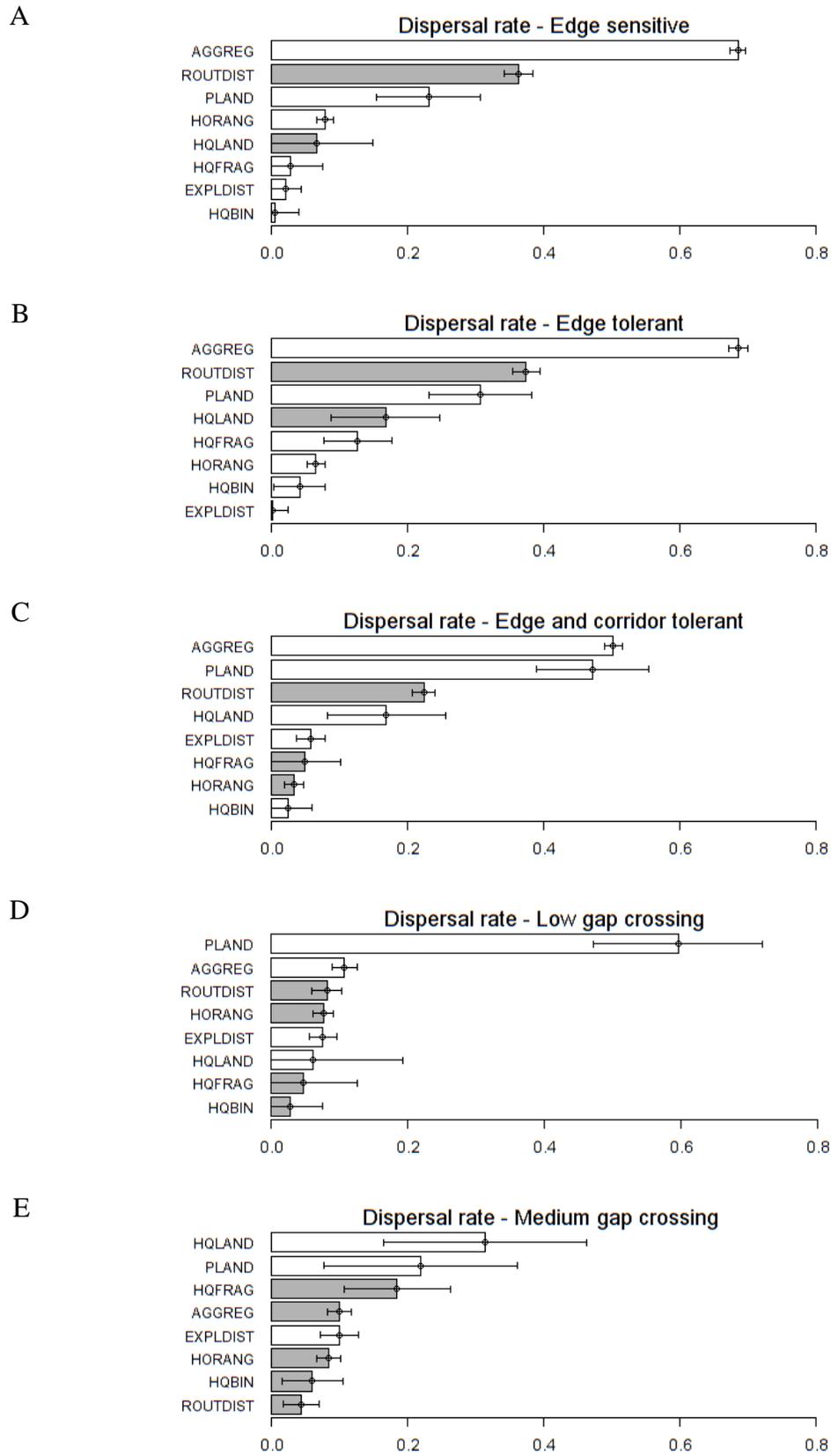
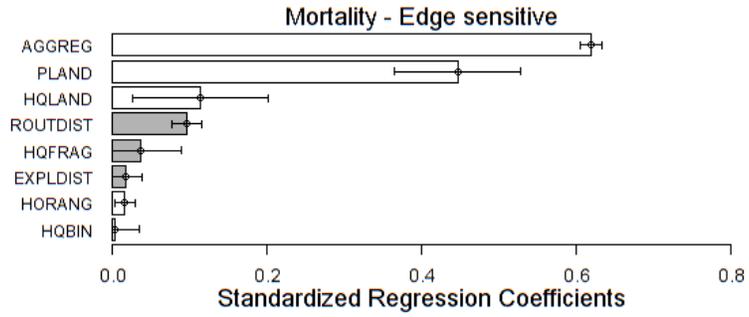
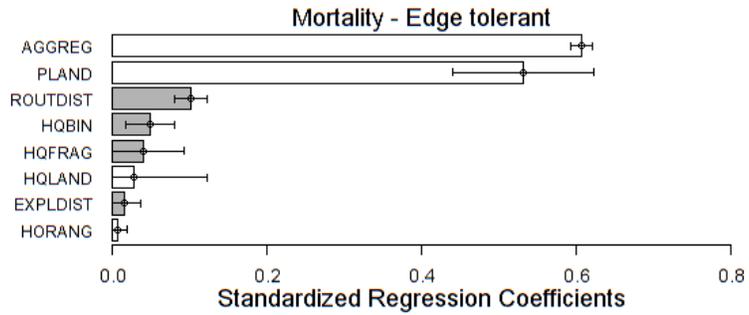


Figure S2

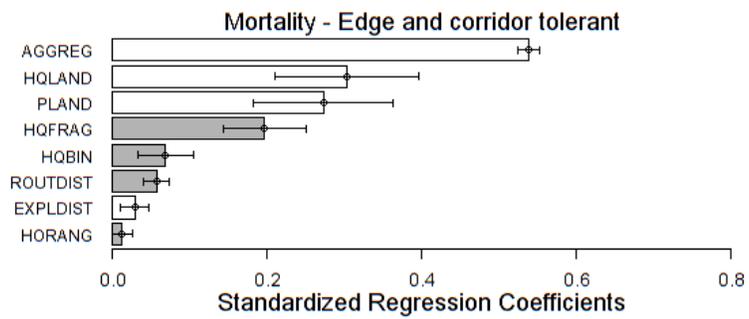
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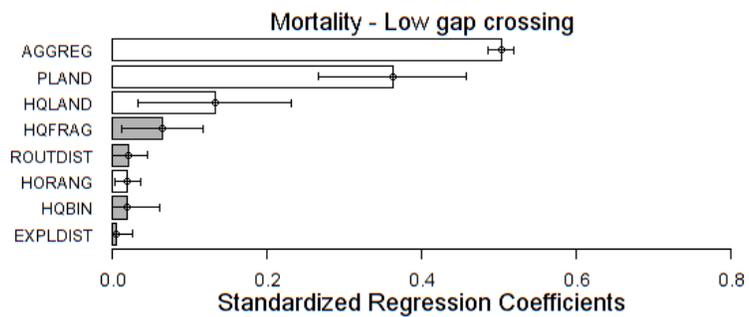
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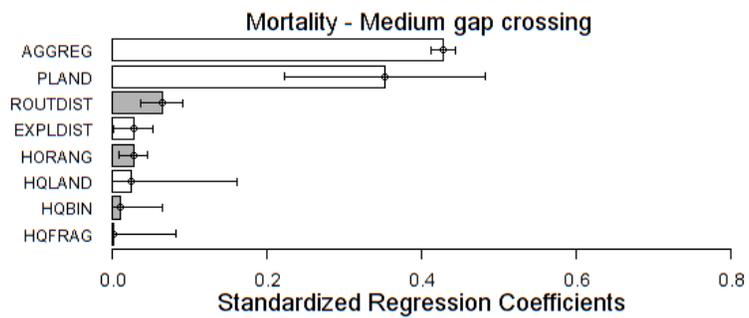
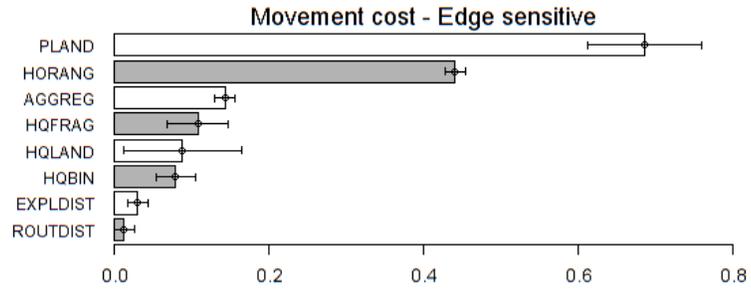
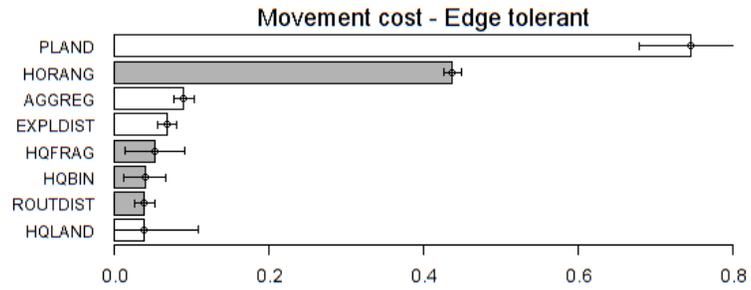


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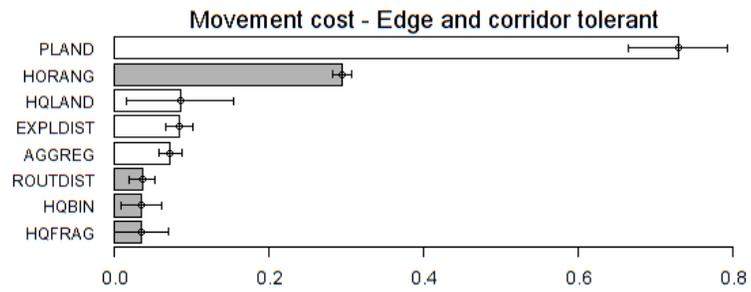
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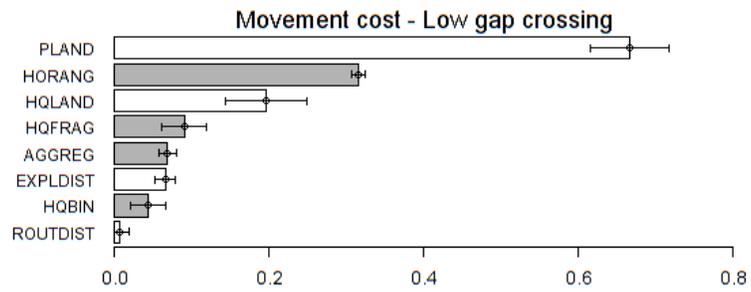
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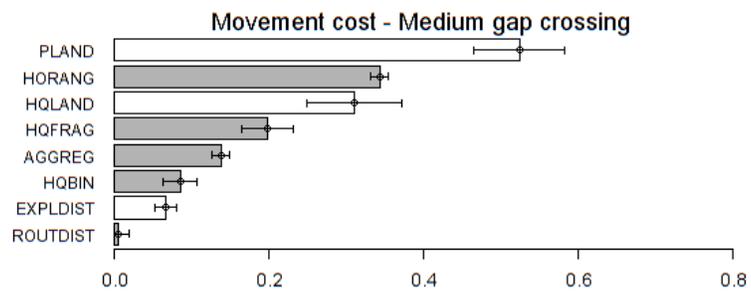
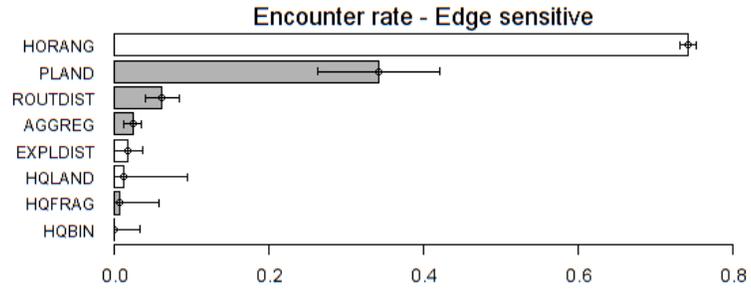
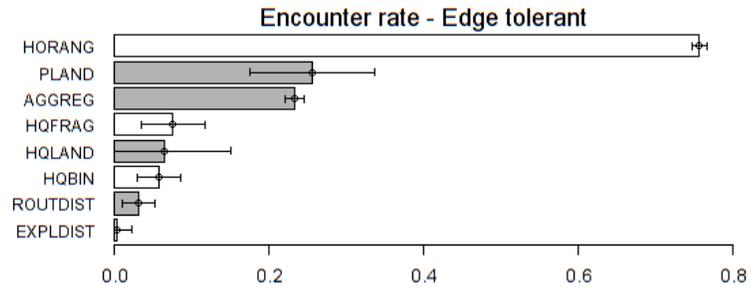


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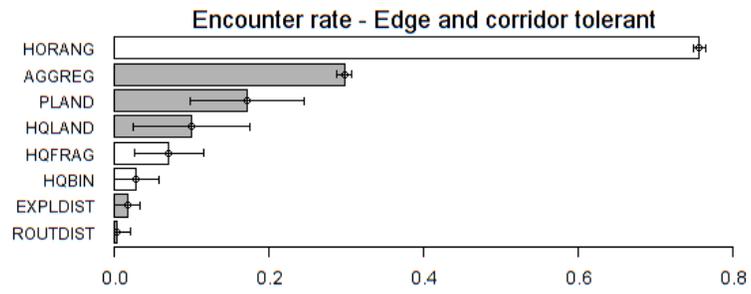
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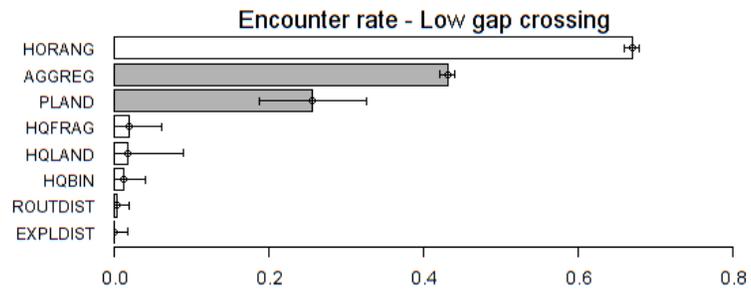
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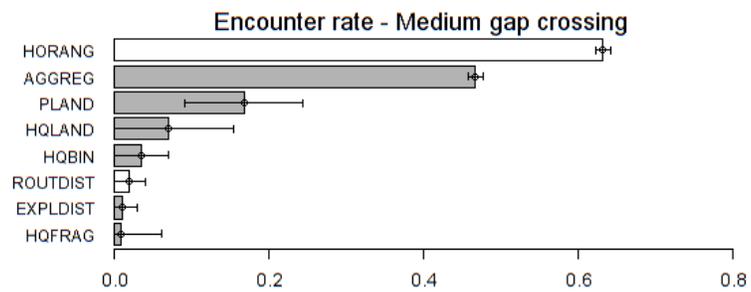
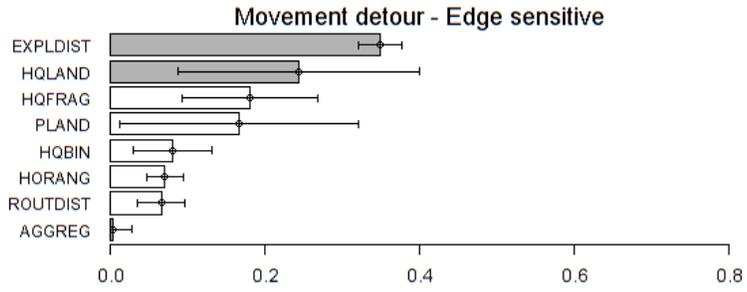
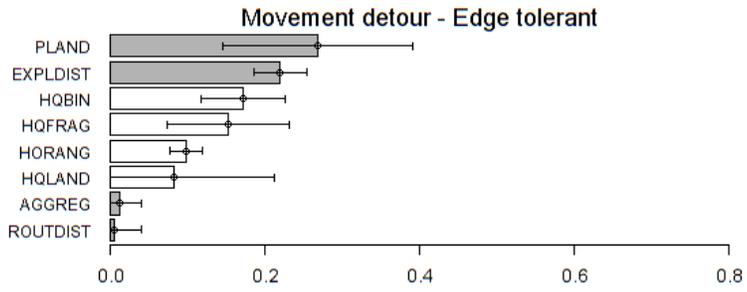


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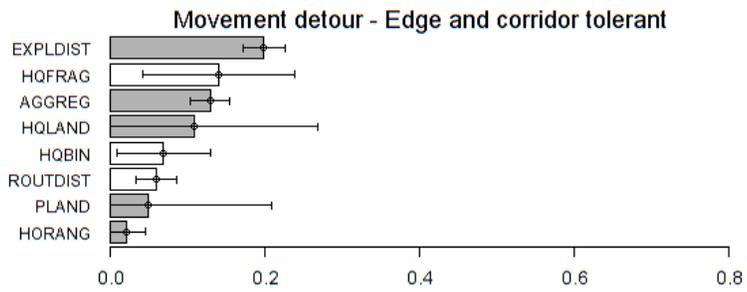
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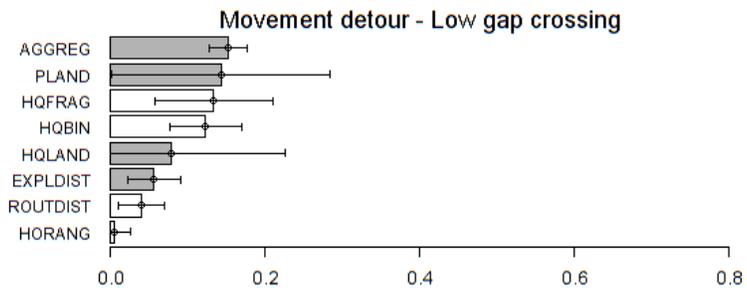
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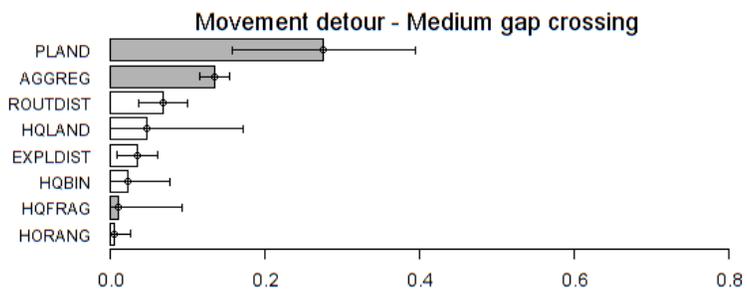


Figure S6



# CAPÍTULO VI

*Discussão geral*

&

*Conclusão*

# CAPÍTULO VI

## 6.1 Discussão geral

Esta tese gerou informações inéditas e atualizadas sobre a quantidade e a distribuição de florestas nativas nas paisagens da Mata Atlântica Brasileira. Permitiu também avaliar a relação entre a cobertura florestal e as posições no relevo, a altitude e a orientação da vertente, o que nos forneceu importantes informações sobre os padrões espaciais dos remanescentes de Mata Atlântica. Também foi proposta uma nova divisão, utilizando informações bioclimáticas e altitudinais, que resultou em 55 novas sub-regiões. Desta maneira, tentou-se contribuir com o entendimento espacial dos remanescentes de forma a subsidiar ações voltadas à conservação biológica, particularmente na seleção de áreas prioritárias para a conservação ou restauração, mas também no manejo integrado da paisagem.

Ademais, no âmbito desta tese foi desenvolvido o BioDIM (*Biologically scaled dispersal model*), que é um programa computacional calibrado para simular movimentação de aves florestais considerando dados empíricos disponíveis na literatura. Por fim, utilizou-se o BioDIM para se avaliar o efeito relativo da estrutura da paisagem, da qualidade do habitat e dos atributos das espécies na modelagem dos processos ecológicos de grande interesse para a conservação. Apresentamos aqui algumas considerações sobre cada capítulo, e ao final concluímos apresentando alguns dos principais resultados da tese e sugestões para novos estudos que possam aumentar o entendimento das questões relacionadas aos padrões espaciais dos remanescentes de Mata Atlântica, ou mesmo a processos ecológicos associados à movimentação de espécies em paisagens fragmentadas.

## ***6.2. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation***

Neste capítulo sugerimos ações urgentes que devem ser tomadas para a conservação das espécies da Mata Atlântica, especialmente as relacionadas à restauração florestal e à priorização dos locais para manejo, de forma a promover a efetiva preservação da biota desta que é um das florestas mais ricas do mundo, mas também uma das mais ameaçadas pelas atividades humanas. Um dos principais pontos deste artigo é a sua abrangência, já que foi considerada toda a extensão da Mata Atlântica. É a maior área já abordada através de uma análise estrutural de paisagens, com este grau de detalhamento (escala refinada de mapeamento), que se tem notícia para todo o planeta. Ao suprir um sério déficit de informação, o trabalho revelou um cenário bastante difícil para a conservação das espécies da Mata Atlântica:

- Mais de 80% dos fragmentos remanescentes são menores que 50 hectares, tamanho extremamente reduzido e incapaz de preservar a maioria das espécies florestais;
- Quase a metade da floresta existente está a menos de 100 m de ambientes antropizados, como áreas agrícolas, pastagens ou mesmo áreas urbanas, o que compromete amplamente a conservação de espécies florestais. Além disso, as áreas mais distantes da borda ficam a aproximadamente 12 km destes ambientes antropizados, o que significa que em nenhum local se consegue ficar mais do que 12 km no interior da mata;
- A distância média entre os remanescentes de mata é muito grande (média de 1.440 m), o que torna difícil - senão impossível - que espécies florestais cruzem de um fragmento para outro de floresta;
- As unidades de conservação de proteção integral, como parques nacionais e estaduais, estações ecológicas entre outros, preservam aproximadamente 1% da Mata Atlântica original, bem abaixo dos 10% sugeridos internacionalmente como sendo o mínimo para a manutenção de espécies.

Apesar do alerta quanto à delicada situação da Mata Atlântica, o artigo traz algumas boas notícias, como no tocante à proporção de floresta remanescente (entre 11.4 a 16%), que é superior ao estimado previamente pela SOS Mata Atlântica/INPE (7 a 8%). Contudo, esta diferença se deu especialmente pela contagem de remanescentes de tamanho bastante reduzido e de florestas em estágio inicial de regeneração, que caracterizam áreas florestais mais degradadas.

Cabe ressaltar que as taxas de remanescentes freqüentemente divulgadas pelos órgãos oficiais, pesquisadores e ONGs não contabilizavam, por exemplo, remanescentes inferiores a 100 hectares, uma vez que estas áreas eram consideradas como de reduzido potencial para a conservação das espécies. No entanto, dados recentes, que consideram a conectividade em mosaicos de fragmentos, mostram que pequenos fragmentos (< 100 ha) têm também papel fundamental na redução do isolamento entre fragmentos grandes, e são assim essenciais para a conservação da diversidade biológica.

O artigo aponta ainda importantes alternativas para a conservação, ao sugerir remanescentes importantes a serem convertidos em unidades de conservação, além de assinalar regiões para formação de mosaicos ecológicos, estimular o uso do solo de formas menos agressivas e ao mesmo tempo menos contrastantes com as florestas, além de indicar onde a restauração de corredores florestais é urgente para a conservação da biodiversidade. O artigo traz também informações detalhadas para as sub-regiões biogeográficas e zonas de transição propostas por Silva e Casteleti (2003), informações estas que têm servido como base para demais estudos que vêm sendo desenvolvidos em escalas regionais (Muchailh et al., 2010; Silva, 2010).

### ***6.3. The Brazilian Atlantic Forest: a shrinking biodiversity hotspot***

Por fazer parte de um de livro sobre *Hotspots* de biodiversidade do mundo, o capítulo III traz uma detalhada revisão de literatura sobre os principais aspectos relacionados à conservação da biota da Mata Atlântica, acrescenta importantes informações originais sobre a distribuição da floresta em função do relevo, contribuindo assim para o melhor entendimento, planejamento e conservação deste Domínio Fitogeográfico. Utilizamos a teoria de nicho ecológico, dados bioclimáticos e de altimetria, organizados para 2.650 sub-bacias de 5ª ordem, o que permitiu particionar as regiões biogeográficas propostas por Silva e Casteleti (2003) em 55 novas sub-regiões. Esta nova sub-divisão possibilita melhores condições de análises de estrutura da paisagem e outros aspectos importantes para o planejamento em escalas mais locais. Ao sobrepor os remanescentes florestais e a altimetria foi possível observar que a faixa entre 1200-1600 m mantém 20% da cobertura original, enquanto as altitudes >1600 mantém 40%. Já para a faixa de altitude 400-800 m, somente 10% da floresta ainda é mantida. Ao se considerar as posições de relevo (áreas de várzea e próximas à rios, terrenos planos, encostas e cristas), observou-se que

61% da distribuição original da Mata Atlântica encontrava-se em áreas com declividade superior à 12%, sendo que atualmente 88.020 km<sup>2</sup> de florestas (o que representa mais de 50% dos remanescentes) estão nesta condição de relevo. Somente 7,6% das florestas remanescentes encontram-se nas proximidades de rios, enquanto 10,6% permanece nas terras mais planas, e 33% nas áreas mais acidentadas. Em relação ao aspecto do terreno (i.e. orientação das vertentes), a distribuição original da Mata Atlântica não apresentou diferenças entre as oito orientações analisadas, mas, em contraste, ao se comparar a cobertura florestal original e atual, observou-se que a vertente sul apresentou 20% menos desmatamento ou mais regeneração quando comparado à média observada para a Mata Atlântica. Este resultado é influenciado principalmente pelo maciço da Serra do Mar, que acumula mais de 1 milhão de ha da floresta remanescente. Além disto, este resultado reforça a preferência pelas demais orientações de vertentes para os diversos tipos de uso da terra, onde as áreas voltadas ao sul são menos preferidas (Mello 2009) por receberem menores intensidades luminosas, o que as tornam menos favoráveis para agricultura (Silva et al. 2007).

#### ***6.4. Assessing simulated bird species responses to habitat amount, aggregation, and quality: a spatially explicit model***

O entendimento dos fatores que influenciam a relação entre os padrões espaciais dos remanescentes e os processos ecológicos é essencial para a definição adequada de ações de manejo da paisagem voltadas à conservação biológica em paisagens fragmentadas. Processos ecológicos associados à movimentação de indivíduos podem ser utilizados como *surrogates* para o embasamento de tais ações. Entretanto, a dificuldade de se obter informações detalhadas para diferentes tipos de paisagens, em condições diversas de cobertura e configuração, e para múltiplas espécies dificulta largamente o entendimento destes fatores, e por conseqüente torna a tomada de decisão das ações de manejo mais complexas. O uso de modelos baseados em indivíduos (IBMs) é uma alternativa interessante, especialmente se bem calibrados com dados empíricos específicos das regiões de interesse. Estudos anteriores desenvolveram IBM para florestas temperadas (With e Crist, 1995; Tischendorf et al., 2003), porém para regiões tropicais as informações básicas ainda são escassas, o que dificulta o uso destes modelos. De acordo com nosso conhecimento, este é o primeiro IBM calibrado para simular movimentação de aves

florestais da Mata Atlântica. O ambiente computacional é de fácil parametrização, podendo inclusive ser utilizado para outras espécies tropicais (p.ex., insetos, mamíferos de pequeno, médio e grande porte). Embora este IBM tenha sido elaborado para avaliar a contribuição relativa da estrutura da paisagem (cobertura e agregação de habitat), da qualidade de habitat e das características das espécies em processos emergentes da movimentação de aves de sub-bosque, outros estudos podem ser realizados. Por exemplo, o modelo desenvolvido pode auxiliar: na comparação do efeito de diferentes protocolos de levantamentos (pontos fixos ou transectos; amostragens aleatórias, sistemáticas ou em bloco; diferentes esforços amostrais); no entendimento dos efeitos de corredores; na comparação de diferentes cenários de manejo sobre processos associados à movimentação de indivíduos, entre outros. Um potencial importante, já implementado na versão corrente do BioDIM, é a incorporação de informação sobre a troca de genes entre indivíduos que se encontram, o que permite avaliar efeitos da estrutura da paisagem na diversidade genética ao longo do espaço e do tempo. Este potencial vem de encontro à demanda de estudos de *landscape genetics* (Manel et al., 2003), campo novo que vem sendo explorado por ecólogos da paisagem e geneticistas, e que tem despontado com promissor para o entendimento dos aspectos da genética da conservação (Vernesi e Bruford, 2009).

### ***6.5 Untangling the effects of landscape structure, habitat quality, and species traits on ecological processes***

Utilizou-se o BioDIM para simular movimentação de aves para gradientes de quantidade, agregação e qualidade de habitat. Foram utilizadas espécies com diferentes níveis de sensibilidades (de espécies com preferência pelo interior dos fragmentos até espécies com capacidade de cruzar até 120 m de áreas abertas), com capacidades distintas de movimentação diária (30 a 90 m) e de dispersão (30 a 270 m), além considerar área de vida (no caso, requerimento de habitat por indivíduo) como um indicador da capacidade de suporte dos fragmentos. Os atributos das espécies e a estrutura da paisagem são os fatores mais importantes para explicar os processos ecológicos, sendo que a qualidade de habitat não apresentou grande contribuição. Em uma análise mais aprofundada observou-se que alguns processos ecológicos (mortalidade e taxa de dispersão) apontam a sensibilidade das espécies como fator principal para explicar os padrões emergentes, sendo a estrutura da paisagem um efeito secundário, porém

extremamente forte. Outro processo (custo de movimentação) sugere que o fator mais importante para explicar o padrão observado é a quantidade de habitat. Por outro lado, área de vida foi o fator fundamental para explicar taxa de encontro entre indivíduos. No caso análises por perfil de espécies obteve-se que para mortalidade e taxa de dispersão, a agregação de habitat foi mais importante que a quantidade de habitat, demonstrando que alguns processos são mais afetados pela distribuição espacial do habitat do que pela quantidade em si. Dos cinco processos avaliados somente um (*movement detour*) não apresentou um fator principal para explicá-lo. Uma surpresa foi observar que agregação de habitat foi à principal variável explicativa para a maioria dos processos, independente da quantidade de habitat. Isto é o oposto do que tem sido sugerido na literatura, onde a agregação de habitat é considerada importante apenas abaixo de certos limiares de cobertura (Fahrig 2003; Radford et al. 2005; Zuckerberg e Porter, 2010, contudo ver Martensen, 2008), e não independentemente da quantidade de habitat (como observamos neste estudo para quantidades de hábitat variando ente 5 e 70%). Acredita-se que todas as combinações plausíveis de serem observadas em paisagens reais foram contempladas nas paisagens simuladas, permitindo assim explorar de forma extensa os efeitos conjuntos e independentes dos diferentes fatores, o que não seria possível ou viável em estudos empíricos.

## 6.6 Sínteses dos resultados

### Sobre a Mata Atlântica

- A Mata Atlântica apresenta-se extremamente fragmentada, porém a cobertura atual está entre 12-16%, estimativa situada entre os 7-8% ou 22-23% reportados anteriormente;
- Mais de 80% dos fragmentos são menores do que 50 hectares, mais da metade das florestas está a menos de 100 m da borda, e a maior distância de áreas antrópicas é de 12 km;
- O grau de isolamento entre fragmentos é bastante elevado (média de 1.440 m), o que dificulta a movimentação de indivíduos para manutenção das espécies ao longo do espaço e tempo;
- Apenas 1% da cobertura original é protegida por Unidades de Conservação de proteção integral;
- As faixas de altimetria 1200-1600 m e > 1600 m mantêm 20% e 40%, respectivamente, da cobertura original, enquanto a faixa de altitude predominante (400-800 m) mantém apenas 10% da cobertura original.

### Sobre os modelos de simulação

- Características das espécies e estrutura da paisagem são fatores mais importantes do que qualidade de habitat para manutenção de processos ecológicos associados à movimentação de aves de Mata Atlântica em paisagens fragmentadas;
- Dependendo do processo ecológico analisado, características das espécies e estrutura da paisagem se alternam como efeito principal, porém em nenhuma situação a qualidade de habitat apresenta-se como fator mais influente;
- A sensibilidade da espécie e a quantidade de habitat são igualmente importantes, independente do processo ecológico, sendo a agregação de habitat e a área de vida variáveis de efeito secundário;

#### Analisando-se os processos ecológicos dentro dos perfis de espécie

- A contribuição relativa da quantidade e agregação de habitat variou de acordo com o processo ecológico e a sensibilidade da espécie;

- O custo de movimentação foi explicado principalmente pela quantidade de habitat, enquanto a área de vida e a sensibilidade da espécie são fatores secundários;
- Agregação superou a quantidade de habitat para os processos ecológicos de taxa de dispersão e mortalidade, sugerindo que a agregação é um fator importante, independente da quantidade de habitat;
- A taxa de encontros ("surrogate" para fluxo de indivíduos e diversidade genética) é influenciada principalmente pela área de vida; a sensibilidade da espécie apresenta efeito secundário, enquanto quantidade e agregação de habitat, embora menos influentes, são também importantes;
- O uso de modelos de simulação, combinados com paisagens simuladas, apresentaram padrões de respostas consistentes com os padrões esperados, confirmando alguns aspectos teóricos correntes na literatura científica. Adicionalmente, permitiram estimar a magnitude dos efeitos de cada grupo de fator e variáveis exploratórias, o que não seria possível com dados de campo em função do custo e complexidade de se desenvolver estudos contemplando todos os aspectos abordados;
- Considerando que as características das espécies não são passíveis de manejo, esta tese indica a importância de se estabelecer estratégias de manejo de paisagem considerando a quantidade e agregação de habitat como "surrogates" de biodiversidade. Este resultado vem de encontro à necessidade de seleção de áreas para conservação e restauração, cada vez mais frequentes nas mais variadas escalas, dando suporte para o uso da estrutura de paisagem como alternativa eficaz de se promover o planejamento para a manutenção da biodiversidade em paisagens fragmentadas.

### ***6.7 Estudos futuros***

Face ao elevado grau de degradação da Mata Atlântica, torna-se fundamental o estabelecimento de um protocolo que permita identificar as ações mais adequadas para promoção da conservação e restauração das paisagens, preferencialmente em escala regional (p.ex. para cada uma das novas 55 sub-regiões propostas). Embora esta tese tenha abordado a relação entre cobertura remanescente e posições do relevo, consideramos essencial o aprofundamento deste tipo de análise, avaliando-se, por exemplo, a relação entre cobertura, declividade e aptidão para uso do solo. Considerando que cada região da Mata Atlântica possuiu suas peculiaridades de uso e

ocupação do solo, além de diferentes potenciais de restauração e aspectos socioambientais, seria interessante fazer-se um zoneamento, com o objetivo, por exemplo, de identificar as áreas mais propícias para projetos de serviços ambientais. Ademais, uma refinada quantificação e avaliação da adequação da cobertura atual, face à legislação vigente, daria mais subsídio para se avaliar temas de alta relevância para conservação, como a eficiência do Código Florestal Brasileiro e os impactos de seu cumprimento, ou mesmo auxiliando na formulação das diretrizes do Pacto para a Restauração da Mata Atlântica. Por fim, consideramos ser de elevada importância que a SOS Mata Atlântica, o INPE e o Ministério do Meio Ambiente mantenham o trabalho de mapeamento do domínio, possivelmente dando maior ênfase: (a) no mapeamento de remanescentes em escalas mais detalhadas, utilizando-se, por exemplo, produtos de sensoriamento remoto com maior resolução (i.e. < 20 m); (b) na tipologia de vegetação, detalhando-se pelo menos três estádios sucessionais; (c) na identificação de áreas de campos na região de Santa Catarina; (d) no mapeamento dos diferentes tipos de uso predominante em cada região (agricultura, pastagem, silvicultura, área urbana e mineração); (e) na atualização de mapeamentos antigos (85-90 e 90-95, p.ex.), de forma que estes se tornem compatíveis com os mapeamentos atuais, permitindo assim, estudos de dinâmica de paisagem, trazendo informações essenciais para o entendimento das mudanças dos ambientes florestais e antrópicos. Ademais, com base nesta atualização de mapeamentos históricos, estudos envolvendo a dinâmica das paisagens da Mata Atlântica, combinados a modelos de mudanças climáticas, poderiam trazer novos subsídios para a seleção de áreas, e indicação de ações adequadas para mitigar impactos e promover a conservação e restauração da biodiversidade.

Em relação aos desenvolvimentos futuros dos estudos com o BioDIM, consideramos que uma das principais aplicações seria utilizá-lo em paisagens reais, permitindo assim identificar o comportamento destes padrões, dentro do gradiente de combinação de cobertura e configuração das paisagens simuladas. Outro ponto interessante seria aplicar o BioDIM a séries temporais de paisagens, analisando o desenvolvimento histórico dos processos de movimentação e seus potenciais impactos nos padrões atuais de distribuição da biodiversidade. Nestes casos, a dinâmica das paisagens poderia ser detalhadamente estudada, considerando inclusive diferentes cenários futuros, o que permitiria testar hipóteses sobre possibilidades distintas de ações de manejo.

Partindo da premissa de que os padrões de movimentação das espécies são influenciados pela capacidade dos indivíduos movimentarem-se, orientados por sua capacidade de detectar os fragmentos antes de decidir a rota de migração (ou movimentação), incorporar a informação de visibilidade derivada de modelos de terreno poderia expandir os horizontes de aplicação do BioDIM.

Simulações semelhantes às realizadas no Capítulo V podem trazer também nova luz sobre estudos de limiares, em especial por permitirem avaliar limiares de variabilidade das respostas observadas, o que pode sugerir a influência de outras variáveis atuando concomitantemente em um determinado processo ecológico. Por fim, pretende-se ainda realizar novos experimentos incorporando atributos genéticos aos indivíduos, simulando movimentação e reprodução de espécies. Acredita-se que padrões emergentes de estabilidade e diversidade genética obtidas com o BioDIM podem trazer conhecimentos de elevada importância para os estudos de genética na escala da paisagem e, em decorrência, para a conservação de espécies em paisagens fragmentadas.

## ***6.8 Conclusões gerais***

Face ao elevado grau de degradação das florestas tropicais, e em especial da Mata Atlântica, a adoção de medidas adequadas de conservação e restauração da biodiversidade é primordial. Entretanto, considerando a elevada complexidade dessas regiões, e a variabilidade dos padrões ambientais, torna-se difícil extrair generalizações sobre processos ecológicos associados a eles. Assim sendo, para promover a manutenção da biodiversidade ao longo do espaço e tempo, é necessário o estabelecimento de critérios adequados, ecologicamente bem embasados, e realistas do ponto de vista de execução. Embora muitos estudos reforcem a importância de se utilizar dados biológicos para dar suporte a tais critérios, esse tipo de informação não é de fácil obtenção, seja por conta dos custos, ou pela complexidade de levantamentos extensivos. Ademais, muitos processos são espécie-específicos, acrescentando ainda mais complexidade e custos nas análises. A estrutura da paisagem tem sido sugerida como uma alternativa interessante para se representar a biodiversidade, porém a forma com que a paisagem pode ser utilizada em processos de seleção de áreas carece de melhor entendimento, e de informações cada vez mais confiáveis e representativas. Modelos de simulação, como o desenvolvido nesta tese, são uma alternativa

interessante para avaliar-se o efeito da estrutura de paisagens. Ademais, a movimentação de indivíduos, que é uma função da acessibilidade das manchas de habitat, é um aspecto primordial para manutenção do fluxo gênico e da biodiversidade. Logo, o entendimento de como a estrutura da paisagem influencia processos associados à movimentação de indivíduos é de elevada importância. A literatura científica apresenta a cobertura de habitat como a propriedade mais importante influenciando a presença e distribuição de espécies e, desta maneira, para a manutenção da biodiversidade. Sugere ainda que a configuração (i.e. agregação de habitat) só passa a ser importante abaixo de certos limiares de cobertura. Entretanto, nossos resultados apresentam a configuração com um fator importante, independente da cobertura, além do fato de que, para certos processos ecológicos (p.ex. taxa de dispersão e mortalidade), o arranjo espacial é mais influente do que a quantidade de habitat em si. A qualidade de habitat, embora seja sugerido com um fator importante em alguns estudos, apresentou menor influência do que características das espécies e estrutura da paisagem.

Os resultados obtidos nesta tese apresentam contribuição efetiva para o entendimento e conservação da Mata Atlântica, pelo fato de ter gerado informações atualizadas sobre seu real status de conservação, pela análise refinada da relação entre sua distribuição original e atual com o relevo, e pela nova proposta de partição do espaço, que permite análises regionais com maior eficiência. Ademais, desenvolveu-se uma poderosa ferramenta de simulação da movimentação de indivíduos em paisagens fragmentadas, que pode então ser utilizadas para identificação de áreas para conservação, identificação de regiões com maior potencial para formação de corredores ecológicos, ou para estabelecimento de zonas de restauração, considerando a percepção das espécies nas análises. Esta ferramenta de simulação permite comparar a efetividade de diferentes cenários e estratégias de conservação/restauração, incorporando a percepção das espécies da Mata Atlântica, e assim aumentando as chances de sucesso de atividades de manejo.

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# ANEXO 1

## **The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation**

Milton Cezar Ribeiro, Jean Paul Metzger, Alexandre Camargo Martensen, Flavio Jorge Ponzoni,  
Márcia Makiko Hirota

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## The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation

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### ABSTRACT

The neotropical Atlantic Forest supports one of the highest degrees of species richness and rates of endemism on the planet, but has also undergone a huge forest loss. However, there exists no broad-scale information about the spatial distribution of its remnants that could guide conservation actions, especially when systematic biodiversity data are not available. In this context, our objectives were to quantify how much of the forest still remains, and analyze its spatial distribution. We considered the entire Brazilian Atlantic Forest, and eight sub-regions, defined according to species distribution. The results revealed a serious situation: more than 80% of the fragments are <50 ha, almost half the remaining forest is <100 m from its edges, the average distance between fragments is large (1440 m), and nature reserves protect only 9% of the remaining forest and 1% of the original forest. On the other hand, our estimates of existing Atlantic Forest cover were higher than previous ones (7–8%), ranging from 11.4% to 16%. The differences among estimates are mainly related to our inclusion of intermediate secondary forests and small fragments (<100 ha), which correspond to approximately 32–40% of what remains. We suggest some guidelines for conservation: (i) large mature forest fragments should be a conservation priority; (ii) smaller fragments can be managed in order to maintain functionally linked mosaics; (iii) the matrix surrounding fragments should be managed so as to minimize edge effects and improve connectivity; and (iv) restoration actions should be taken, particularly in certain key areas. The clear differences in the amount remaining and its spatial distribution within each sub-region must be considered when planning for biodiversity conservation.

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### 1. Introduction

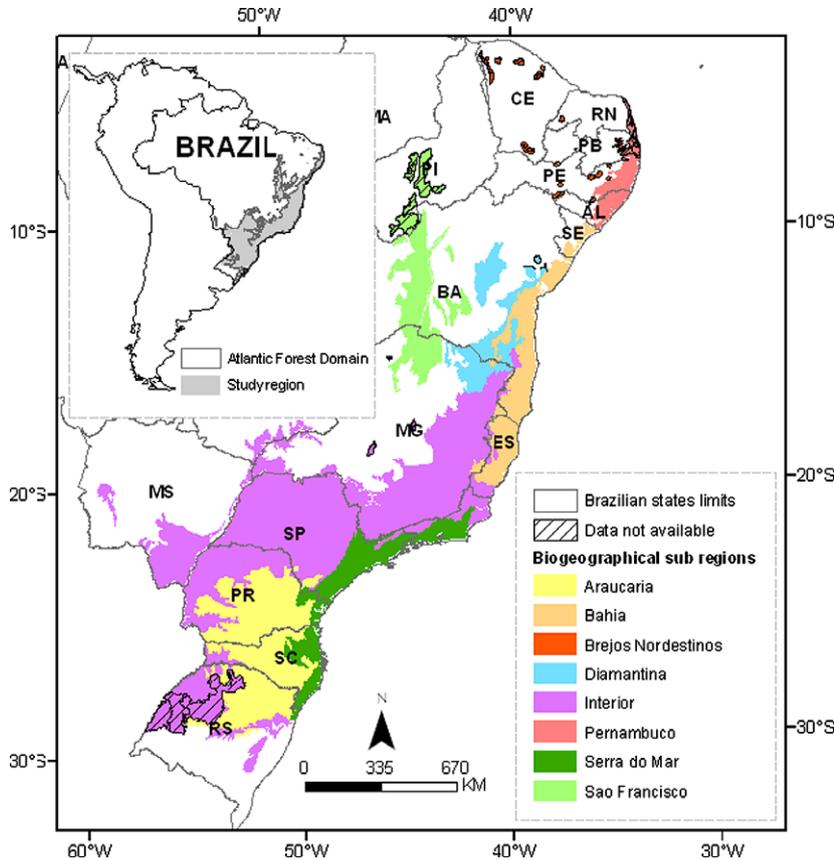
Landscape structure parameters have been recognized as useful biodiversity surrogates, and are used in different steps of conservation planning (Williams et al., 2002; Lindenmayer et al., 2008). Some rules of thumb are employed within a landscape perspective, such as the conservation of large fragments with high structural connectivity, whether provided by corridors, stepping stones, or high permeability of the surrounding matrix (Umetsu and Pardini, 2007; Umetsu et al., 2008; Uezu et al., 2008; Fonseca et al., 2009; Pardini et al., 2009; Vieira et al., 2009); as well as targeting the preservation of as much as possible of all natural landscape heterogeneity (Forman and Collinge, 1997; Haila, 2002; Fischer et al., 2006; Lindenmayer et al., 2006; Metzger, 2006). Although they have some limitations, such as not considering how different species perceive features of the landscape (e.g., functional

connectivity), landscape structure parameters can be particularly useful to establish general guidelines for conservation planning where broad-scale species inventories and biodiversity distribution patterns are still unavailable (Fairbanks et al., 2001; see Uehara-Prado et al., 2009 for an example of ecological indicators), which is the case for most tropical areas.

The Atlantic Forest was one of the largest rainforests of the Americas, originally covering around 150 million ha (Fig. 1), in highly heterogeneous environmental conditions. Its latitudinal range is around 29°, extending into tropical and subtropical regions. The wide longitudinal range is also important in producing differences in forest composition, because of the decreased rainfall away from the coasts. Coastal areas receive large amounts of rain year-round, reaching more than 4000 mm, while inland forests receive around 1000 mm/year (Câmara, 2003). These geographical characteristics, combined with the large altitudinal range, have favored high diversity and endemism, including more than 20,000 species of plants, 261 species of mammals, 688 species of birds, 200 species of reptiles, 280 species of amphibians, and many more

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**Fig. 1.** Biogeographical sub-regions (BSRs) based on the main areas of endemism of birds, butterflies and primates as proposed by Silva and Casteleti (2003). Abbreviations for Brazilian states names are: AL = Alagoas, BA = Bahia, CE = Ceará, ES = Espírito Santo, GO = Goiás, MA = Maranhão, MG = Minas Gerais, MS = Mato Grosso do Sul, PE = Pernambuco, PB = Paraíba, PI = Piauí, PR = Paraná, RN = Rio Grande do Norte, RS = Rio Grande do Sul, SC = Santa Catarina, SE = Sergipe, SP = São Paulo, TO = Tocantins.

species that still require scientific description (Goerck, 1997; Mittermeier et al., 1999; Silva and Casteleti, 2003). The Atlantic Forest flora and fauna may include 1–8% of the world's total species (Silva and Casteleti, 2003).

Most of the remaining Atlantic Forest exists in small fragments (<100 ha; Ranta et al., 1998) that are isolated from each other and are composed by second-growth forests in early to medium stages of succession (Viana et al., 1997; Metzger, 2000; Metzger et al., 2009). The few large fragments survived in locations where the steep terrain made human occupation particularly difficult (Silva et al., 2007). This present-day fragmentation has led to a large proportion of the forest's vast biodiversity being threatened to extinction; for example more than 70% of the 199 endemic bird species are threatened or endangered (Parker et al., 1996; Stotz et al., 1996; Goerck, 1997).

In these heterogeneous and highly diverse forests, which still hold many still-unknown species (Lewinsohn and Prado, 2005), biodiversity inventories are complex, expensive and time-consuming (Gardner et al., 2008; but see Uehara-Prado et al., 2009). Despite the large amount of biological data generated in the Atlantic Forest region in recent decades (Silva et al., 2004; Silva and Casteleti, 2003), the lack of standardized inventory protocols and sampling efforts with poor spatial distribution have resulted in significant geographical data gaps, making it particularly difficult to use this information for conservation planning by the usual methods (see Margules and Pressey, 2000; Groves et al., 2002). At local scales, enough biological data is available for some areas to support conservation plans, but great difficulties arise in planning conservation actions for large regions. Moreover, most of the data are insufficient to properly support conservation planning, and

thus, abiotic surrogates such as landscape structure parameters are in most cases the only alternative (Metzger et al., 2008). In this context, the amount of habitat and fragmentation, which are key factors for biodiversity conservation (Wilcox and Murphy, 1985; Fahrig, 2003), are important variables to be considered in landscape planning and management for biodiversity conservation.

Despite the potential of using landscape structure parameters in conservation planning, information on landscape structure in the Atlantic Forest is only available for small regions (<300,000 ha, Jorge and Garcia, 1997; Viana et al., 1997; Ranta et al., 1998). The only data available for the entire Atlantic Forest region is the percentage of the remaining forest, but even in this case there are huge discrepancies among the different methods employed (e.g., 7–8% of the forest remains according to SOS Mata Atlântica/INPE, 1993, 2000 and Galindo-Leal and Câmara, 2003; 10.6% according to SOS Mata Atlântica/INPE, 2008; and 27% according to IESB et al., 2007; Cruz and Vicens, in press).

We analyzed for the first time the spatial distribution of all the remaining Brazilian Atlantic Forest, in order to provide precise information about how much forest is left and how this forest is spatially arranged. We calculated parameters such as fragment size, amount of edge area, isolation, structural connectivity, and distance to conservation reserves of all existing fragments of the Brazilian Atlantic Forest region (ca. 245,000 fragments). These spatial analyses were performed on a multi-scale approach (Urban, 2005), in order to facilitate the biological interpretation of the landscape indices (within a perspective of *ecologically scaled landscape indices*; following Vos et al., 2001). This approach ensures a variety of biological behaviors, considering for example a wide range of sensitivity to gap-crossing abilities and to edge distance influences.

Additionally, to refine our understanding about the Atlantic Forest spatial structure, considering its different regional contexts, we performed the same analyses dividing the region by biogeographical sub-regions (BSRs). The implications of the observed spatial patterns are discussed with regard to future conservation and restoration priorities for the entire Atlantic Forest in Brazil.

## 2. Methods

### 2.1. Study region and biogeographical sub-regions (BSRs)

The Atlantic Forest originally extended from 3°S to 31°S, and from 35°W to 60°W, covering 148,194,638 ha (Fig. 1), mainly extending along the Brazilian coast (92%), but also reaching into Paraguay (Cartes and Yanosky, 2003; Huang et al., 2007) and Argentina (Giraud, 2003). The forest encompasses 17 Brazilian states, and is narrow in the north and wider in the south. It has complex boundaries with other types of formations such as the pampas in the south and the drier inland formations, such as the Bolivian Chaco and the Pantanal (west–southwest), the Cerrado (South American savanna, west) and the Caatinga (northwest).

We analyzed 139,584,893 ha (~94%) of the original Brazilian Atlantic Forest region, based on the extent defined in Brazilian legislation (Federal Decree No. 750/93 and Atlantic Forest law No. 11 428, of December 22, 2006), and slightly expanded according to the delimitation of BSRs by Silva and Casteleti (2003). The geographical, historical and relief complexities observed in the Atlantic Forest region generate a scenario in which species are not homogeneously distributed, but rather are grouped in different BSRs (Silva et al., 2004; Silva and Casteleti, 2003). In order to properly approach this complexity, we chose to conduct our analyses at two different geographical scales: (i) the entire Atlantic Forest; and (ii) by the BSRs proposed by Silva and Casteleti (2003). These authors defined five centers of endemism (Bahia, Brejos Nordestinos, Pernambuco, Diamantina and Serra do Mar) and three transitional regions (São Francisco, Araucaria and Interior Forests), based on bird, butterfly and primate distributions (Fig. 1). For general descriptions we used all eight BSRs. For structural landscape analyses, the Brejos Nordestinos sub-region (1,251,783 ha) was excluded because of its naturally scattered distribution and relatively small area (<1% of the area studied). A detailed spatial analysis is thus provided for seven different BSRs (Table 1). Within these regions, the Interior is the largest (49%), followed by the Araucaria (17%), and then by the Bahia, Serra do Mar and São Francisco regions with about 8–9% each.

### 2.2. Forest cover

Forest cover analyses were based on an Atlantic Forest vegetation map (reference year 2005; [www.sosma.org.br](http://www.sosma.org.br) and

[www.inpe.br](http://www.inpe.br)) produced by the SOS Mata Atlântica/INPE (2008). The map was projected to the Albers projection and the South America 1969 datum to assure accurate area calculation for large regions such as this one. These institutions have been mapping the Atlantic Forest cover since 1986, at 5-year intervals (SOS Mata Atlântica/INPE, 2000 and 2008). The map used for the analysis was constructed by visual interpretation of TM/Landsat-5 (TM) and CCD/CBERS-2 (CCD) images from 2005 (with a few images from 2004 when cloud cover did not allow image acquisition in 2005), viewed as color compositions on a digital orbital image mosaic with bands TM3 (red region in the blue filter), TM4 (near infrared, NIR, in the red filter) and TM5 (short wavelength infrared, SWIR, in the green filter) for Landsat-5, CCD-2 (green in blue filter), CCD-3 (red in green filter) and CCD-4 (NIR in red filter) for CBERS-2. This map shows three main vegetation classes, grouping several physiognomically and floristically distinct forests: mangroves, “restinga” (lowland forests on sandy soils near the coast) and forests (including coastal forests, *Araucaria* mixed forests, and semi-deciduous forests; Oliveira-Filho and Fontes, 2000). The three classes were included in the forest cover analysis, but mangroves and restingas were not considered in the configuration analyses because of their small spatial extent (~4% of the remaining area) and biological differences. The mapping scale was 1:50,000 in vector format, which was then converted to raster, with a 50 m spatial resolution (60,000 × 48,000 cells), in order to improve metrics computation.

The “forest” class included secondary forests in intermediate to advanced successional stages. The distinction between old growth and secondary forest is particularly difficult for the entire Atlantic Forest region because information about forest age is very scarce and available only at local scales. The old history of disturbances in the region ended in a lack of good age estimation, especially for old forests which regenerated before the 1970', when satellite images started to be available. We are aware that forest definition could originate differences in forest cover and configuration results, and thus we opted to consider as forest areas which have an arboreal structure as seen by TM and CCD orbital images. This definition corresponds to forests >15 years of regeneration, with dense arboreal vegetation and canopy height >10 m (Teixeira et al., 2009).

### 2.3. Map quality

At the end of the visual classification procedure, the preliminary thematic map was reviewed by vegetation experts from each Brazilian state located in the Atlantic Forest region. Fieldwork was also conducted in order to resolve questions of interpretation.

To assess the accuracy of the final map, we superposed the SOS Mata Atlântica map on 10 reference cover maps (Table 1S), which were produced with high spatial accuracy (scales ranging from 1:10,000 to 1:50,000) and extensive field checking. Of these maps,

**Table 1**

Extent of the Atlantic Forest in the biogeographical sub-regions (BSRs, as proposed by Silva and Casteleti, 2003), and area mapped by SOS Mata Atlântica/INPE (2008).

BSR	Abbreviation	Atlantic Forest domain		Mapped by SOS Mata Atlântica/INPE (2008)	
		Area (ha)	Area (ha)	% mapped	% of total mapped <sup>a</sup>
Araucaria	arauc	25,379,316	25,379,316	100	17
Bahia	bahia	12,241,168	12,241,168	100	8
Brejos Nordestinos	brejo	1,251,783	85,249	7	1
Diamantina	diama	8,289,516	8,200,259	99	6
Interior	inter	72,784,790	68,417,731	94	49
Pernambuco	perna	3,893,730	3,132,167	80	3
Serra do Mar	semar	11,413,471	11,413,471	100	8
São Francisco	sfran	12,940,866	10,715,533	83	9
Total		148,194,638	139,584,893	94	100

<sup>a</sup> Percentage of mapped area for each BSR in relation to total mapped area.

eight were available for the state of São Paulo (covering areas from 10,400 to 24,800,000 ha), one for the state of Minas Gerais (143,900 ha), and another for the state of Paraná (748,500 ha). The 10 selected regions have very different reliefs and climates, but were limited to the forest pattern observed in southeast Brazil. As a consequence, our accuracy analysis may be biased towards the patterns that occur in this area. We estimated the Kappa (Landis and Kock, 1977) and the G (percentage of pixels correctly classified) statistics to check map accuracy (Table 1S). The Kappa values ranged from 0.167 to 0.818 (mean = 0.486). The SOS Mata Atlântica map showed low accuracy for only the region of one reference map. For the other nine reference maps the analyzed map was classified as acceptable ( $n = 3$ ), intermediate ( $n = 4$ ), high ( $n = 1$ ) and very high ( $n = 1$ ) accuracy (according to the categories defined by Landis and Kock, 1977). To arrive at an overall statistic, we calculated a Kappa value weighted for the area of the reference maps, and obtained  $K = 0.4$  (i.e., acceptable according Landis and Kock, 1977 classification).

We also estimated the errors of commission and omission, to capture the bias of our map. The commission error ranged from 0.2% to 8% (mean = 3%), with an area weighted mean of 2.9%. The omission error ranged from 3% to 89% (mean = 49%), with an area weighted mean of 37%. These results indicate that the map used for the analysis tends to underestimate the actual remaining vegetation. This underestimation may occur because (1) early successional stages are poorly mapped and (2) it is difficult to correctly map the small fragments (<30 ha). We also noticed that for some regions, the map does not accurately show remnants on slopes, which resulted in some confusion between “forest” and *Eucalyptus* ssp. plantations or early successional vegetation stages. Riparian forests were also poorly mapped, either because of their narrow shape or their overall small area. Despite these errors, the overall accuracy (G) ranged between 76% and 97%, which is an acceptable rate for maps at this large regional scale.

#### 2.4. Forest configuration indices

Forest cover and configuration metrics were computed for the entire study region and for each of the different BSRs using GRASS 6.3 (Neteler and Mitasova, 2008; <http://www.grass-gis.org>), with some procedures done on ArcGis 9.2 (Esri, 2007) and Erdas 9.1 (Leica, 2006). The R language version 2.7.1 (R Development Core Team, 2008) was used for all data processing. We selected five configuration metrics that could be easily employed in conservation planning: fragment size, edge area, connectivity, isolation and distance to nature reserves (Table 2). For edge area (and core area), connectivity and isolation, we performed a multi-scale approach (Urban, 2005) in order to consider different species' perception of landscape structure.

**Table 2**  
Landscape metrics used to analyze the Atlantic Forest configuration.

Index	Explanation	Classes or rules
Fragment size distribution	Number of fragments and percentage of forest cover for different size classes	Fragment size classes (ha): <50, 50–100, 100–250, 250–500, 500–1000, 1000–2500, 2500–5000, 5000–10,000, 10,000–25,000, 25,000–50,000, 50,000–100,000, 100,000–250,000, 250,000–500,000 and 500,000–1200,000
Edge area	Percentage of area submitted to edge effects for different edge widths	Edge widths (m): <50, 50–100, 100–250, 250–500, 500–1000, 1000–2500, 2500–5000 and 5000–12,000
Connectivity	Area of functionally connected fragments considering different distance rules for fragment linkage	Linkage distances (m): 0, 100, 200, 300, 400, 500, 1000 and 1500
Mean isolation	Mean isolation of random points to the nearest forest fragment. To analyze the effect of small fragments in estimating isolation, the smallest fragments were successively removed.	Size of the small fragments removed (ha): 0 (i.e., no fragment removed), <50, <100, <150, <200, <350 and <500
Distance from Nature Reserves	Distance of any given forest pixel to the nearest nature reserve	Distance classes (m): 0 (i.e., inside a Nature Reserve), <200, 200–600, 600–1000, 1000–2000, 2000–5000, 5000–7500, 7500–10,000, 10,000–25,000, 25,000–50,000 and >50,000

Fragment size distributions allowed us to account the forest amount and number of fragments for different classes of size (Table 2). Edge area was computed as the amount and percentage of forest area submitted to edge effects for different edge widths. All forest pixels with distances higher than an edge width level (Table 2) were classified as core area.

Connectivity metrics were computed based on the graph theory (Urban and Keitt, 2001; O'Brien et al., 2006; Minor and Urban, 2007; Fall et al., 2007), which is a method of measuring the functionally connected clump of fragments based on some simple linkage rules (Urban and Keitt, 2001). As linkage rules for our analysis we considered the distance among fragments reflecting different gap-crossing capacities (Martensen et al., 2008; Boscolo et al., 2008; Awade and Metzger, 2008; Table 2). The connectivity index was then calculated as the sum of the areas of clumped fragments, which can be interpreted as the functional available area (Martensen et al., 2008; Metzger et al., 2009). After generating connectivity maps, we computed the expected cluster size as the mean clump size for each functional distance. The highest cluster size was also identified for the entire study region, as well as for each sub-region and for each functional distance.

To estimate mean isolation, we proposed an index adapted from the “Empty Space Function”, which is a spatial point pattern analysis (Baddeley and Turner, 2005; Fortin and Dale, 2005), that represents the mean isolation of a given random pixel from any forested one. We randomized 1,000,000 points over the entire Atlantic Forest region, and a distance map was generated for all fragments. We then successively removed the smaller fragments in several steps (Table 2) and computed the distance to the nearest forest in each step. These values represent the isolation of forest areas, but are particularly useful in providing insights about the importance of the smaller fragments (or the capacity of the species to use these small fragments as stepping stones; Uezu et al., 2008).

To assess the amount of Atlantic Forest protected by the Brazilian Protected Area network, we superposed on the remnants map, a map of Nature Reserves (strictly protected areas classified as “proteção integral”; MMA, 2007), which comprises 249 reserves (2,260,350 ha). The distance from nature reserves was also calculated for each forest pixel (see Table 2 for classes of distance from reserves).

### 3. Results

#### 3.1. Forest cover

Of the total mapped area (139,584,893 ha), 15,719,337 ha of forest (11.26%) and 658,135 ha (0.47%) of restinga and mangrove

**Table 3**

Remaining Atlantic Forest in each biogeographical sub-region (BSR), with its area in ha and percentage. Data were obtained by superposing the map generated by SOS Mata Atlântica/INPE (2008) and the boundaries of BSRs adapted from Silva and Casteleti (2003).

BSR	Remaining forest		Remaining restinga/mangrove		Total remaining Atlantic Forest	
	Area (ha)	% <sup>a</sup>	Area (ha)	% <sup>a</sup>	Area (ha)	% <sup>a</sup>
Araucaria	3,202,134	12.6			3,202,134	12.6
Bahia	2,047,228	16.7	115,059	0.9	2,162,287	17.7
Brejos Nordestinos	13,656	16.0			13,656	16.0
Diamantina	1,109,727	13.5			1,109,727	13.5
Interior	4,807,737	7.0	32,451		4,840,188	7.1
Pernambuco	360,455	11.5	19,363	0.6	379,818	12.1
Serra do Mar	3,678,534	32.2	491,263	4.3	4,169,797	36.5
São Francisco	499,866	4.7			499,866	4.7
Total	15,719,337	11.26	658,135	0.47	16,377,472	11.73

<sup>a</sup> Percentages are in relation to the BSR area.

vegetation (Table 3) still remain. Thus, 88.27% of the original Atlantic Forest has been lost, and only 11.73% of the original vegetation (16,377,472 ha) remains (Fig. 2 and Fig. 1S[a–g]). Considering the estimated commission and omission errors for the map analyzed (Table 1S; see *Map quality* section for details), we consider that the actual remaining vegetation might range from 11.4% to 16.0% in the entire Atlantic Forest region.

The best-preserved BSR is the Serra do Mar, which holds 36.5% of its original vegetation, followed by the Bahia (17.7%) and Brejos Nordestinos (16%) regions. In contrast, the São Francisco region has only 4.7% of forest cover, and the Interior Forest, 7.1% (Table 3). However, in absolute terms, more than half of the remaining forest is located in the Serra do Mar and Interior Forest regions, whereas less than 15% is located in the Diamantina, São Francisco, Brejos Nordestinos and Pernambuco regions (Table 3).

### 3.2. Number of fragments and size distribution

The Atlantic Forest is currently distributed in 245,173 forest fragments. The largest fragment is located in the Serra do Mar, mainly along the coastal mountains of the state of São Paulo, and extends from the state's southern border northwards into the southern part of the state of Rio de Janeiro. This single fragment contains 1,109,546 ha of continuous forests, which represents 7% of what remains (Fig. 2 and Fig. 1S-f). The second- and third-largest fragments are also located in the Serra do Mar, and contain 508,571 ha (coastal zone of Paraná state) and 382,422 ha (coastal zone of Santa Catarina state). Altogether, the three largest fragments account for more than 2 million ha, i.e., more than 13% of the remaining forest. In contrast, 83.4% of the Atlantic Forest fragments (204,469 fragments) are smaller than 50 ha, and together

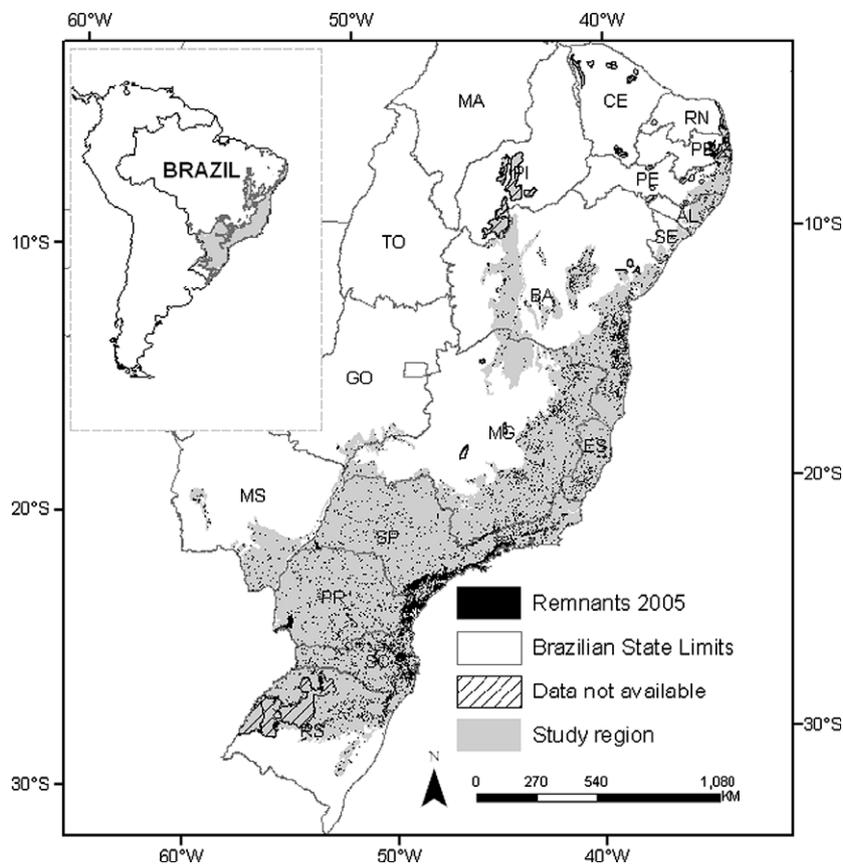
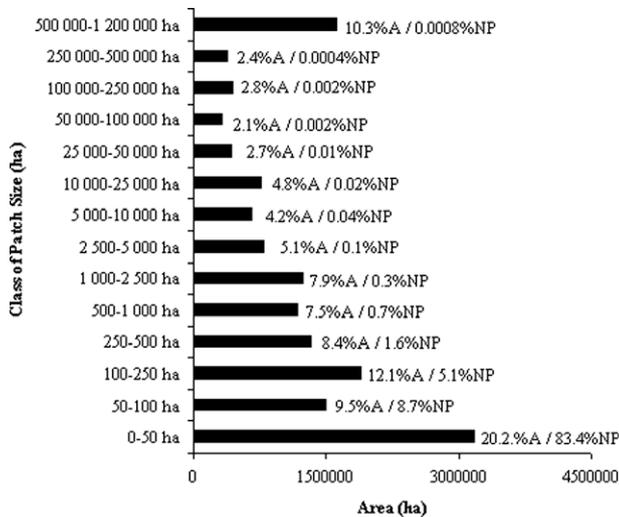


Fig. 2. Remaining forest in the Brazilian Atlantic Forest region (source: SOS Mata Atlântica/INPE, 2008). See Fig. 1 for the abbreviations of Brazilian states names.



**Fig. 3.** Distribution of remaining forest fragment sizes in the full extent of the Atlantic Forest region. %A: percentage of total area; %NP: percentage of number of fragments.

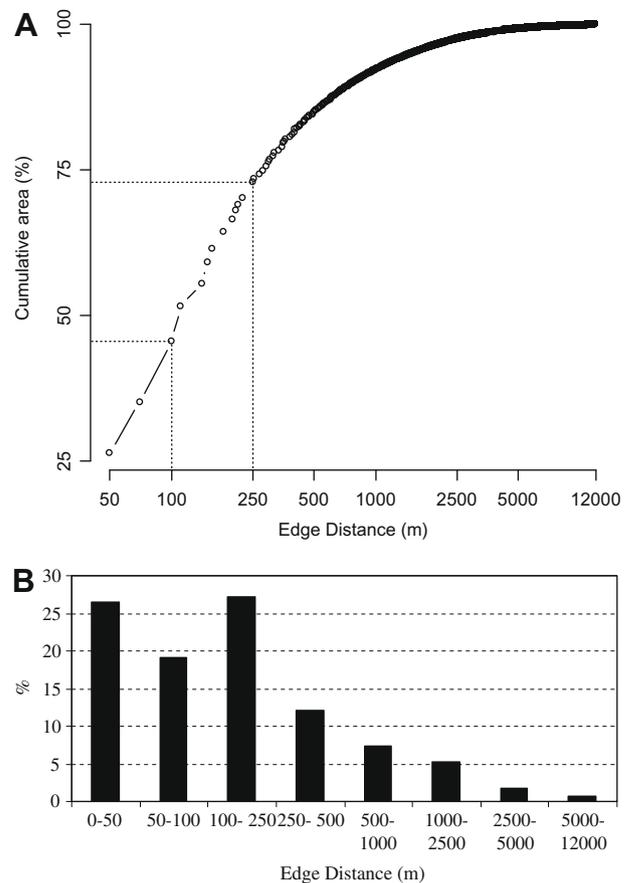
they account for 20.2% of the total forest remnants (ca. 3,178,030 ha; Fig. 3) according to our estimates. Fragments smaller than 250 ha represented more than 97% of the total number, and accounted for almost 42% of the total forest area. In contrast, only 0.03% (77 fragments) are larger than 10,000 ha, and together these include almost 4 million ha.

Small fragments (<50 ha) are, by far, the largest part of the number of remnants in all BSRs. The distribution of fragments according to their size followed an inverted “J” shape (Fig. 2S). However, the Serra do Mar region, in addition to having many small fragments (~79% of the fragments is <50 ha), has much of the forest existing as large fragments (>50,000 ha), which represent more than 50% of the forest cover in the region. This region is the only one with a fragment larger than 1 million ha in size, which is located along the coastal mountains of São Paulo. The other regions do not contain any fragment larger than 250,000 ha, and only the Araucaria Forest ( $n=4$ ) and the Interior Forest ( $n=1$ ) have forest fragments larger than 50,000 ha (Fig. 2S): the inland forests of Santa Catarina, including the São Joaquim National Park, and the Iguaçu National Park, respectively. In the Bahia region, the largest fragment covers approximately 29,000 ha, while in the São Francisco and the Pernambuco regions, none exceeds 10,000 ha (see Fig. 2S[a–g] for detail); and in the Diamantina, none is larger than 25,000 ha.

### 3.3. Core and edge area

Of the total forest area remaining, 73% is located less than 250 m from any non-forest area, and 46% is less than 100 m distant from edge (Fig. 4). Only 7.7% is located farther than 1000 m from any edge, and 12 km is the maximum distance from any non-forested area in the Atlantic Forest region.

A similar pattern was observed for the BSRs, where most of the forest area is less than 250 m from non-forest areas (Fig. 3S). In the Interior and Pernambuco regions, approximately 60% of the forest is less than 100 m from any edge, while São Francisco, Araucaria, Bahia and Diamantina have between 40% and 50% of their forests within 100 m from any edge. Only the Serra do Mar region showed a different pattern, where only 25% of the remaining forest is located less than 100 m from any edge. This is reflected in the highest percentage of core-area forest in this BSR, with 256,040 ha at least 2.5 km from the edges, and 56,993 ha at least 5 km from the edges. In addition to the large fragments of the Serra do Mar



**Fig. 4.** Cumulative (A) and per class (B) area under edge effect at different depths for the remaining Brazilian Atlantic Forest. Edge depths of 100 and 250 m are highlighted in (A).

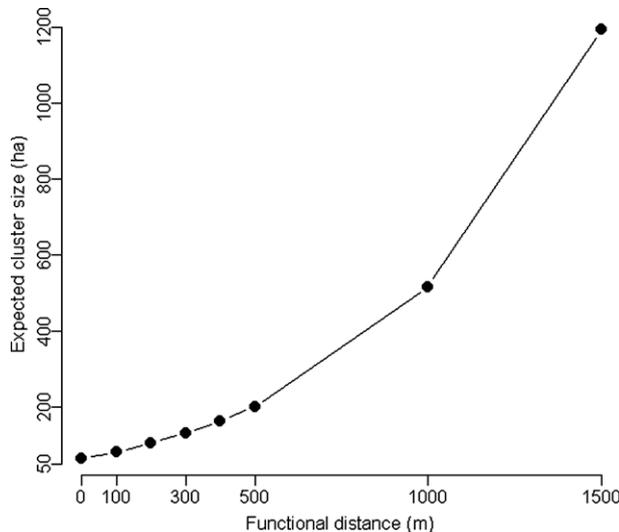
region, the Iguaçu National Park is the only one that also has areas of forest that are 12 km distant from any edge.

### 3.4. Connectivity

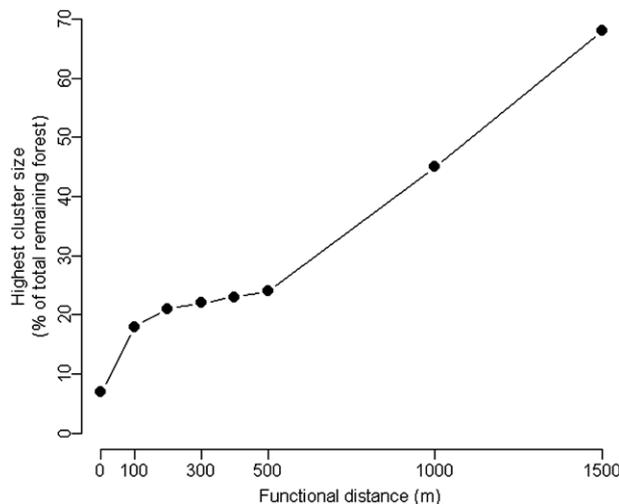
For species that are not able to cross open areas, the average functionally connected area is 64 ha (Fig. 5), while for those that are able to cross 300 m it is 131 ha. The largest functionally connected cluster of fragments for species that are able to cross 100 m, is comprised of the Serra do Mar and the nearby functionally connected fragments, which encompass more than 2,803,000 ha (18% of the remaining forest, Fig. 6) and stretches from the state of Rio de Janeiro all the way south to the state of Rio Grande do Sul. In the Bahia region, species that are able to make short crossings between fragments, such as 100 m, can reach a forest area of more than 50,000 ha (17% of the remaining forest in the region); whereas in Diamantina the gap that needs to be crossed to reach a functionally connected area of this size is 200 m (Fig. 4S-c). Longer distances separate fragments in the other regions, such as 400 m to reach 50,000 ha in the São Francisco (Fig. 4S-g) BSR, and more than 500 m in the Pernambuco to reach the same area (Fig. 4S-e).

### 3.5. Mean isolation

The mean isolation for the entire Atlantic Forest region was 1441 m, with values ranging from a few meters to dozens of kilometers. The small fragments were particularly important in reducing isolation (Fig. 7). When we exclude the fragments <50 ha, the mean isolation increases to 3532 m. If fragments smaller than 200 ha were lost, the mean isolation would reach more than 8000 m.



**Fig. 5.** Expected cluster size (mean functional size; ha) for functionally connected forest fragments estimated across varying functional linkage distances (m), for the Brazilian Atlantic Forest region.

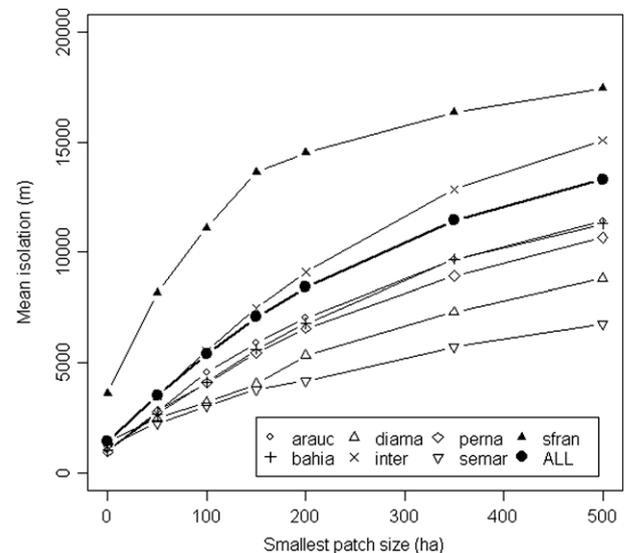


**Fig. 6.** Highest functionally connected forest cluster (% of total remaining forest) estimated across varying functional distances (m), for the Brazilian Atlantic Forest region.

Small fragments were important in reducing isolation in all regions. However, a gradient of importance could be seen, with the Interior and São Francisco BSRs being particularly affected by the exclusion of these small fragments, whereas in the Serra do Mar a relatively low isolation is maintained, since the remaining forest exists as larger pieces (Fig. 7). The isolation in the São Francisco BSR is the most-affected by the exclusion of small fragments, since isolation increases from 3.6 to 14.5 km when excluding fragments smaller than 200 ha. The second most-affected BSR is the Interior, where the mean isolation increases from 1344 m (without fragment removal) to 9112 m if we remove fragments <200 ha. For other regions, exclusion of fragments of this size results in an isolation that ranges from 4182 m (in the Serra do Mar) to 7048 m (in the Araucaria BSR).

### 3.6. Nature reserve cover and proximity

The total protected area within the Atlantic Forest region is approximately 2.26 million ha, or 1.62% of the region (Table 4, Fig. 8). Nature reserves represent 14.4% of the remaining forest



**Fig. 7.** Influence of the smallest fragment size (ha) on the mean isolation (m) between fragments, for the Brazilian Atlantic Forest region, and for its biogeographical sub-regions (BSRs). See Table 1 for BSRs abbreviations. Smallest fragments sizes: 0 ha (all fragments), 50 ha, 100 ha, 150 ha, 200 ha, 350 ha and 500 ha.

cover, but they protect only 9.3% (Table 4) of this remaining forest, since other types of vegetation or land cover also occur within these reserves. All regions have a small percentage (Fig. 5S[a-g]) of their areas covered by nature reserves. However, the Serra do Mar has 25.2% of its remaining forest under protection, followed by the Interior (6.8%) and the Bahia (4.2%). All other regions have less than 4% of their small amount of remaining forest under protection (Table 4; Fig. 5S[a-g]). Given these facts, the Serra do Mar accounts for 63% of the total remaining forest under protection, followed by the Interior BSR (22%). Moreover, only 1.05% of the original forest cover is protected, and in most regions (except Serra do Mar and Bahia) this percentage is <0.5%.

Some reserves are contiguous, and thus we could identify seven large protected regions with areas of about 100,000 ha. Five are in the Serra do Mar region: (1) Serra do Mar State Park and Bocaina National Park; (2) Jacupiranga State Park and Superagui National Park; (3) Paranapiacaba [Petar State Park, Intervalles State Park, Xituê Ecological Station and Carlos Botelho State Park]; (4) Serra do Tabuleiro State Park and (5) Jureia [Banhados de Iguape Ecological Station, Jureia-Itatins Ecological Station, Itinguçu State Park and Prelado State Park]. The other two regions are in the Interior (Iguaçu National Park) and the Diamantina (Chapada da Diamantina State Park) regions. Together they have a total area of 1,212,800 ha, which encompasses 53.6% of the protected areas. Seventeen reserves range in size from 20,000 ha to 60,000 ha (in total 585,120 ha; 26% of the protected areas); six of them are in the Interior, five in the Serra do Mar, three in the Bahia, two in the Araucaria, and one in the São Francisco BSRs.

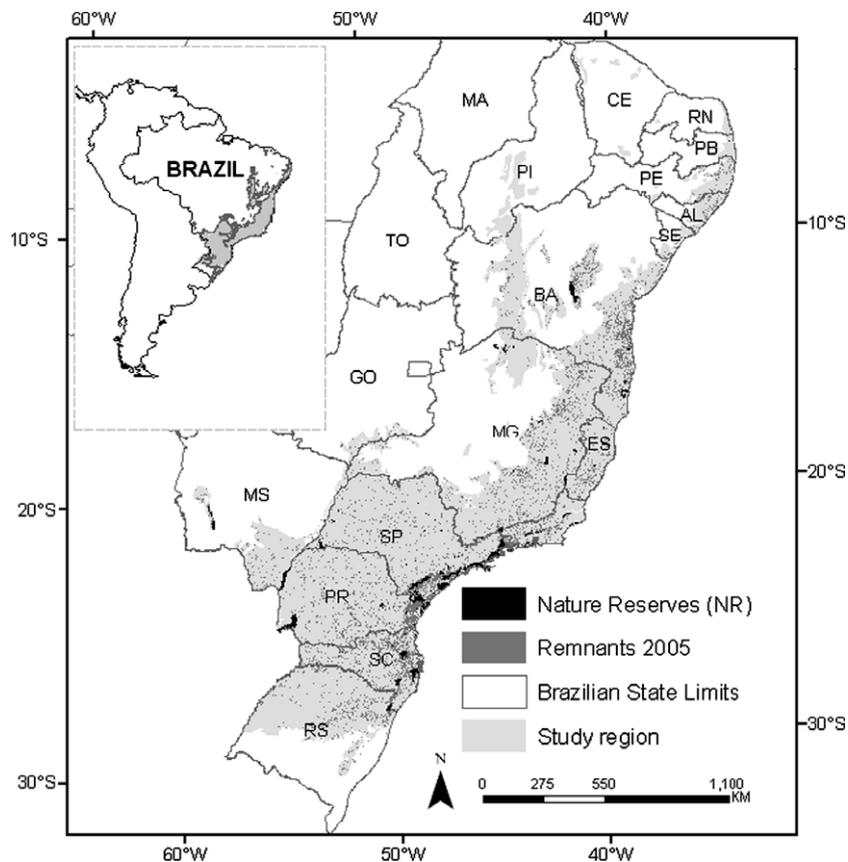
Only 22.6% of the remaining forest is located within 10 km of nature reserves, whereas 61% is farther than 25 km (Fig. 9). Most BSRs have a small amount of forests close (<10 km) to nature reserves, whereas a large amount is more distant (>50 km, Table 4; Fig. 5S[a-g]). A different pattern is encountered in the Serra do Mar, where 59% (2,163,163 ha) of the remaining forest is less than 10 km, and 41% (1,515,371 ha) is farther away.

## 4. Discussion

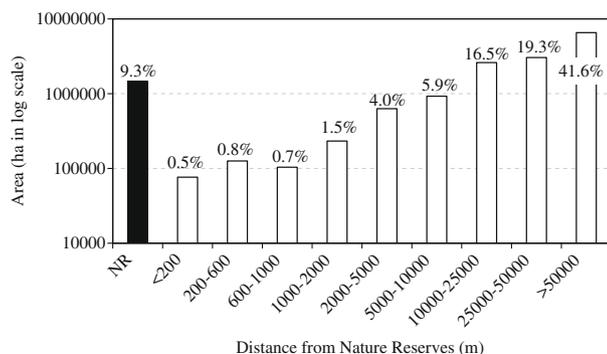
Our results showed that: (i) there is more forest left than previously estimated; (ii) most fragments are very small, less

**Table 4**  
Protected area and forest under protection for the Atlantic Forest domain, and within seven biogeographical sub-regions (all BSRs except “Brejos Nordestinos”) adapted from Silva and Casteleti (2003).

BSR	Area of sub-region (a) (ha)	Protected area		Remaining forest (c) ha	Protected remaining forest (d) ha	Protected forest in relation to remaining forest within sub-regions (d)/(c) %	Protected forest between sub-regions (di)/S(d) %	Protected forest in relation to original forest within sub-regions (d)/(a) %
		(b) (ha)	(b)/(a) %					
Araucaria	25,379,316	164,651	0.65	3,202,134	98,121	3.1	6.7	0.39
Bahia	12,241,168	113,447	0.93	2,047,228	86,053	4.2	5.9	0.70
Diamantina	8,200,259	151,412	1.85	1,109,727	12,451	1.1	0.9	0.15
Interior	68,417,731	561,381	0.82	4,807,737	325,261	6.8	22.2	0.48
Pernambuco	3,132,167	4314	0.14	360,455	3731	1.0	0.3	0.12
Serra do Mar	11,413,471	1,201,848	10.53	3,678,534	926,184	25.2	63.3	8.11
São Francisco	10,715,533	63,297	0.59	499,866	11,823	2.4	0.8	0.11
Total	139,499,644	2,260,350	1.62	15,705,681	1,463,622	9.3	100.0	1.05



**Fig. 8.** Nature reserves in the Brazilian Atlantic Forest region (source: MMA, 2007).



**Fig. 9.** Remaining forest (area and percentage) within nature reserves (NR) and amount of forest per class of distance from nature reserves (m) for the Brazilian Atlantic Forest region.

than 50 ha (ca. 83% of the total number of fragments); (iii) much of the remaining forest is close to forest edges (ca. 45% <100 m of the edges), indicating that matrix influences may have strong effects on many forest ecological processes (Umetsu and Pardini, 2007; Umetsu et al., 2008; Uezu et al., 2008; Fonseca et al., 2009; Pardini et al., 2009; Vieira et al., 2009); (iv) short gap-crossings (<100 m) through the matrix can be highly effective to increase the functionally connected area for forest species (Boscolo et al., 2008; Martensen et al., 2008); (v) small fragments (<200 ha) play a crucial role in reducing fragment isolation among larger fragments, suggesting that they are highly important as stepping stones; and (vi) nature reserves protect a small amount of the remaining forest in all the BSRs (except in the Serra do Mar), and most of the remaining forest is distant (>25 km) from the existing nature reserves (61%; 9,564,900 ha).

#### 4.1. How much forest is left?

Our study exposed the extreme degradation of the Atlantic Forest, where only 11.7% of the original vegetation remains (15,719,337 ha). This proportion might range from 11.4% to 16.0% if we consider errors of commission and omission. This estimated area is larger than the usual total given for the Atlantic Forest (7–8%; SOS Mata Atlântica/INPE, 1993, and 2000; Galindo-Leal and Câmara, 2003), but below the recent estimate of 27% by IESB et al. (2007) and Cruz and Vicens (in press). Differences among these estimates could be caused by several factors, including mapping errors. However, our field survey demonstrated that the map quality is acceptable for regional analyses. Apparently, one of the main factors causing these discrepancies in estimating the Atlantic Forest cover is related to the criteria used to include secondary forests and small fragments.

IESB et al. (2007), Cruz and Vicens (in press) included very early stages of succession, even without a forest structure present (vegetation <2 m high; Cruz, personal communication). The initial evaluations by the SOS Mata Atlântica Foundation (1986–2000) did not consider regrowth; i.e., once mapped as deforested in a recent past (~50 years), an area was never again considered as forest (SOS Mata Atlântica/INPE, 2008). They also did not consider forest fragments smaller than 100 ha. On their new report, when considering fragments >3 ha and forests at an intermediate stage of regeneration, they obtained an estimation of the remaining forest cover similar to ours (10.6%; SOS Mata Atlântica/INPE, 2008). Thus, the difference between previous estimates by SOS Mata Atlântica/INPE (1993,2000) and the present estimate is basically composed of intermediate secondary forests and/or small fragments, which correspond to approximately 32–40% of the total mapped vegetation (considering 8% and 7% of the forest cover previously mapped by SOS Mata Atlântica, respectively). The small difference between our estimates and that reported by SOS Mata Atlântica/INPE (2008) may be related to differences on the analyzed extent (slightly larger in our case to include the delimitations of BSRs by Silva and Casteleti, 2003) and because we did not excluded any fragment from the analyses.

The Atlantic forest presents a highly dynamic forest cover dynamic (Teixeira et al., 2009) and an old history of disturbance, where even the mature remnants were selective logged in a distant past, sometimes in pre-European time (Dean, 1996; Câmara, 2003). This critical scenario of the Atlantic Forest with large areas of secondary forests and small disturbed fragments is the usual pattern in most tropical regions, where 50% of them are secondary or disturbed (Wright, 2005). The implications for species conservation are huge. Even if secondary forests can sustain a significant amount of biodiversity (Viana and Tabanez, 1996; Develey and Martensen, 2006), many species need more pristine forest and large fragments to survive (Aleixo, 1999; Harris and Pimm, 2004; Develey and Martensen, 2006; Laurance, 2007; Gardner et al., 2007; Barlow et al., 2007a,b), and the replacement of mature forests by secondary ones may lead to the extinction of many species (Metzger et al., 2009).

In this landscape-structure scenario, several general guidelines can be suggested to improve or stimulate forest-species conservation in the Atlantic Forest region, particularly: (i) large mature forest fragments should be assigned a high conservation priority; (ii) smaller fragments could be used to form functionally linked mosaics; (iii) the matrix surrounding the fragments should be adequately managed to minimize edge effects; and (iv) restoration actions should be put into practice, particularly in some key structural conditions.

#### 4.2. Protecting large mature forest fragments

Particular attention should be paid to the protection of the larger remnants, especially for their capacity to maintain larger pop-

ulations and for their better prospects of sustaining species over the long term (Brooks et al., 1999; Lindborg and Eriksson, 2004). Only large fragments with mature forests are capable of preserving sensitive species, especially those with large area requirements (Ferraz et al., 2007) or with strict habitat requirements, whose survival is particularly problematic in the present fragmented state (Aleixo, 1999). Old-growth forests (Laurance, 2007; Gardner et al., 2007) are especially important because, even in excellent regeneration conditions, this process requires several decades to restore a species composition comparable to a mature stage (Dunn, 2004; Barlow et al., 2007a,b; Liebsch et al., 2008; Rodrigues et al., 2009). Moreover, the early stages of succession on abandoned lands are not protected by Brazilian environmental laws (Metzger et al., 2009), and their suppression is common and part of the rapid dynamic of the landscapes.

In the present extremely fragmented and dynamic scenario of the Atlantic Forest, the importance of the last large forest remnants increases exponentially, and their management should be cautiously designed and their transformation into nature reserves should be carefully considered. New conservation areas are most urgently needed in Pernambuco, Diamantina and São Francisco, where nature reserves protect less than 3% of the remaining forest, even if the largest fragments are not so large (e.g., <10,000 ha). Protection of at least 10% of the original habitat is recommended as a global strategy for conservation (Secretariat of the Convention on Biological Diversity, 2002), but even the Serra do Mar region does not at present fulfill this condition (8.1% of its original cover is protected in nature reserves). This kind of conservation target is subjective, and the degree of protection should vary according to the sensitivity of the system (which may differ among regions), but it is clear that the proportion of forest cover under legal protection is very low in all the BSRs, and must be enhanced.

Moreover, the largest fragments promote conservation of core areas, which are particularly uncommon since more than 70% of the remaining forest is located less than 250 m from open land, and is thus subject to edge effects. Furthermore, large mature forest fragments are vital for supporting seeds and allowing recolonization of the small surrounding fragments, and can act as source areas for restoration programs (Rodrigues et al., 2009). The distance (>25 km) of most of the remaining Atlantic Forest fragments from the existing nature reserves reduces their influence as stable sources of individuals and species for the surrounding smaller fragments. Forest regeneration in areas around nature reserves should be stimulated because of their natural regrowth potential, increasing forest cover in these regions, and reducing the present unbalanced distribution of forest cover in relation to the proximity to nature reserves.

Protecting the last largest blocks of forests of all BSRs should definitely be a conservation priority. However, only in the Araucaria, Bahia, and especially the Serra do Mar regions can large fragments still be found. The Interior Forest also has a few large fragments, which together with the large tracts of forests still existing in Argentina (Giraud, 2003) and Paraguay (Cartes and Yanosky, 2003; Huang et al., 2007) constitute a better conservation prospect for this BSR. All the other BSRs lack large fragments, which may severely compromise species conservation (Silva and Casteleti, 2003). In these regions, alternative conservation practices should be implemented for the existing remnants.

#### 4.3. Creating functionally linked mosaics

The conservation of small fragments should not be neglected, because they constitute a large fraction of the remnants (83.4% with <50 ha), and are essential in enhancing connectivity between the larger ones. The mean distance between fragments for the Atlantic Forest is around 1400 m, considering the small fragments.

This is a considerable separation for most forest species (Laurance and Gómez, 2005), which avoid edge areas (Hansbauer et al., 2008; Lopes et al., 2009) and in some cases do not even cross roads or small gaps in the canopy (Develey and Stouffer, 2001; Laurance, 2004; Laurance and Gómez, 2005). As the distances between fragments increase, connectivity decreases, and individual crosses became less frequent (Hanski, 1994; Haddad, 1999). However, clusters of neighboring fragments (<200 m) that form large tracts of forest (>50,000 ha) are common ( $n = 12$ ; 4,992,700 ha; 32% of the total remaining forest), and should be considered in conservation policies as important potential mosaics for conservation. They can play an important role in animal movement through landscapes, either functioning as stepping stones (Castellón and Sieving, 2005; Sekercioglu et al., 2006; Uezu et al., 2008; Boscolo et al., 2008), or forming networks of functionally connected areas, which could allow species to persist in disturbed landscapes (Martensen et al., 2008). They can also act as stable sources of seeds and individuals for nearby, smaller fragments.

Especially in cases where no large fragment is left, one option is to consider functionally linked mosaics of smaller fragments (Uezu et al., 2005; Martensen et al., 2008). This is especially the case in the Pernambuco, Diamantina and São Francisco BSRs. These BSRs are naturally fragmented (Fig. 1), and the advanced forest destruction intensified this pattern, increasing the number of small fragments, reducing the forest cover to <15% and thus threatening the biodiversity that depends on this forest.

Matrix permeability is a key connectivity component (Fonseca et al., 2009). Different regions of the Atlantic Forest have suffered for centuries under poor soil management and extensive destruction and simplification of the forests, which has intensified in recent decades (Fig. 6S), with agricultural mechanization and the use of pesticides and herbicides (Brannstrom, 2001; Durigan et al., 2007). Recent expansions of *Eucalyptus* (Bacha and Barros, 2004; Baptista and Rudel, 2006; Fig. 6S) and sugar-cane plantations (Rudorff and Sugawara, 2007; Nassar et al., 2008; Fig. 6S) have caused huge social, economical and environmental impacts, and their influences in reducing patch connectivity have been suggested and need to be better understood (Fonseca et al., 2009).

Matrix management is especially important in a scenario where short movements through the matrix can promote fragment connections. Increasing matrix permeability can allow species to persist in fragmented situations and can be an interesting option for conservation of some species (Ricketts, 2001; Baum et al., 2004; Antongiovanni and Metzger, 2005; Umetsu et al., 2008; Uezu et al., 2008; Pardini et al., 2009; Vieira et al., 2009). Matrix management could be employed in the Araucaria Forest, where functionally connected areas increase stability through improved gap-crossing abilities; and in the Bahia region, where a large network of fragments are functionally linked by distances of 100 m of open areas. In all these cases, inter-forest management can improve connectivity. The implementation of forested pastures, where trees are scattered in different densities, or disposed in lines along fences, has been suggested as one easy option to improve connectivity in traditional pasture areas, while also promoting additional economical gains to the landowner, as well as work in wind blocking (Harvey et al., 2004). The establishment of small agroforest patches, with the presence of trees dispersed in agricultural fields is also suggested as important to improve landscape connectivity (Uezu et al., 2008). Moreover, sugar cane has been expanding over former pastures, where scattered trees were common (Nassar et al., 2008). The suppression of these trees should be avoided, because they can have a disproportional effect in biodiversity conservation (Harvey et al., 2004). Finally, different management options in the plantations of exotic trees are also pointed out as vital to enhance connectivity, as well as in harboring some extremely demanding species, what could be severely

limited with traditional forest management practices (Fonseca et al., 2009).

#### 4.4. Reducing edge effects

Because the remaining Atlantic Forest is severely fragmented in small patches edge effects increase in importance. Tropical species, particularly the strictly forest ones, are well known to be highly sensitive to edge alterations, especially because of their high niche specialization (Kapos, 1989; Murcia, 1995; Hansbauer et al., 2008; Lopes et al., 2009). Kapos (1989), Laurance et al. (2007), Laurance (2008) showed that some edge effects in the Amazon Forest can extend as far as 300–400 m into the forest. In the Atlantic Forest, almost half of the remaining forest is located less than 100 m from open areas, and more than 70% of the remaining forest is located less than 250 m from open land, i.e., is subject to strong edge-effect influences.

Because most of the present forest is directly influenced by nearby land use, matrix influences should also be particularly investigated and their management carefully conducted (Umetsu and Pardini, 2007; Umetsu et al., 2008; Uezu et al., 2008; Fonseca et al., 2009; Pardini et al., 2009; Vieira et al., 2009). Forested or agroforestry matrixes are suggested as efficient in reducing microclimate changes caused by edge conditions (Didham and Lawton, 1999), and thus, to reduce edge-effect influences (Cullen Junior et al., 2004). In some cases, strip of trees are planted forming a buffer around the remaining patches in order to reduce edge effects (Cullen Junior and Fenimore, 2002; Cullen Junior et al., 2004).

#### 4.5. Stimulating restoration actions in key structural conditions

The present small amount of remaining forest generates a scenario where rapid restoration actions should be undertaken to allow species conservation in the near future (Rodrigues et al., 2009). In this case, careful site selection is necessary in order to maximize restoration achievements. Priority should be given to the bottlenecks of the large clusters of fragments. In the Serra do Mar region, for example, small disruptions (<100 m) break apart a potential larger fragment of more than 2.8 million ha, and restoration of these connections should be a conservation priority. In this region, roads are also a key element in breaking apart large fragments, and mitigation policies should be analyzed and employed to restore connectivity. Complementarily, efforts should be allocated to create new reserves between the large fragments of the Serra do Mar, enhancing reserve sizes and width, especially in areas where forest areas are relatively narrow and disruption of these fragments could occur in the future.

Another key characteristic of the Serra do Mar region is the presence of large fragments that extend into the Interior and Araucaria regions. Maintenance or linkage restoration of these inter-region fragments is also vital to maintain the biological evolutionary processes, which could be particularly important in the present scenario of climate changes. These linkages may be especially important in the case of the Araucaria BSR, since these inter-region fragments are also the largest ones found in this BSR, and the region has been undergoing profound impacts from the recent changes in land use, with the expansion of *Eucalyptus* plantations (Bacha and Barros, 2004; Baptista and Rudel, 2006).

The northern Atlantic Forest is presently in worst state of conservation compared to the southern part, except for the large mosaic in the south of the Bahia region. This mosaic should be a key target for biological conservation, and the restoration of forest connections should be a main concern in this region. The absence of forest in the area between Bahia and the Serra do Mar makes it particularly difficult for individual animals to pass between the southern and northern Atlantic Forests, which could severely impact

evolutionary processes and could be particularly deleterious in a climate-change scenario.

Finally, restoration priority should also be given to link the smaller fragments surrounding larger ones, especially in the cases where these large fragments are nature reserves. Enhancing the connectivity between fragments, especially linking to a large one that can act as a source of individuals, can improve conservation possibilities in highly fragmented regions (Uezu et al., 2005; Martensen et al., 2008).

## 5. Conclusion

This report quantifies for the first time the extremely degraded state of the Atlantic Forest distribution, showing that most fragments cover less than <50 ha, almost half the remaining forest is <100 m from forest edges, and the present conservation network is insufficient to support the long-term survival of this rich and endangered tropical forest. Urgent conservation and restoration actions should be implemented to mitigate this situation, based on careful planning and with clear targets.

The management of the region as a whole must begin with the transformation of the large mature forest tracts into conservation reserves and the reestablishment of key connectivity linkages, especially between the larger remnants. The matrix, mainly between and surrounding these large fragments, is also important to manage, since a large fraction of the forest is influenced by the close proximity to edges. In sections where not a single large fragment remains, which is common in most sub-regions, management should focus on the reestablishment of functionally connected clusters of fragments, enhancing landscape connectivity. In the present critical conservation scenario of the Atlantic Forest, every remnant is important for species conservation. The clear differences in the amount of forest remaining and how they are organized in each sub-region must be considered when planning biodiversity conservation.

## Acknowledgments

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bioco.2009.02.021.

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