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DARREN NORRIS

VIVENDO EM UMA PAISAGEM DEFAUNADA: FATORES DETERMINANTES NAS RELAÇÕES ESPACIAIS DE GRANDES MAMÍFEROS

Tese apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Área de Concentração: Zoologia).

Setembro - 2012

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Orientador: Prof. Dr. Mauro Galetti
Co-orientador: Prof. Dr. Silvio Frosini de Barros Ferraz

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Co-Orientador: Silvio Frosini de Barros Ferraz

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TÍTULO: Vivendo em uma paisagem defaunada: fatores determinantes nas relações espaciais de grandes mamíferos

AUTOR: DARREN NORRIS
ORIENTADOR: Prof. Dr. MAURO GALETTI RODRIGUES

Aprovado como parte das exigências para obtenção do Título de DOUTOR EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA) , pela Comissão Examinadora:

Prof. Dr. MAURO GALETTI RODRIGUES
Departamento de Ecologia / Instituto de Biociências de Rio Claro-UNESP

Marco A. Pizo
Prof. Dr. MARCO AURELIO PIZO FERREIRA
Departamento de Zoologia / Instituto de Biociências de Rio Claro-UNESP

Profa. Dra. MARIA LUISA DA SILVA PINTO JORGE
Departamento de Ecologia/Instituto de Biociências de Rio Claro-UNESP

Prof. Dr. ADRIANO GARCIA CHIARELLO
Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto-USP

Prof. Dr. RAFAEL DIAS LOYOLA
Depto de Ecologia-Instituto de Ciências Biológicas/Universidade Federal de Goiás

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Dedico esta tese à Fernanda

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RESUMO

Existe uma necessidade urgente de se desenvolver conhecimento ecológico de apoio à conservação e gestão da rede protegida da Mata Atlântica dentro da região biogeográfica Serra do Mar. Resultados de pesquisas anteriores mostraram variações elevadas nas abundâncias dos grandes mamíferos dentro destas grandes áreas protegidas, que são comparáveis, se não maiores, do que as encontradas nos ecossistemas fragmentados da Mata Atlântica. Neste trabalho demonstrou-se como variáveis ambientais e antrópicas influenciam grandes mamíferos em remanescentes contínuos da Mata Atlântica Brasileira na região biogeográfica da Serra do Mar. Remanescentes contínuos da Mata Atlântica apresentam um ambiente altamente heterogêneo, resultado de fatores ambientais e impactos antrópicos. Os resultados apresentados nos 4 capítulos dessa tese destacam que, embora a Mata Atlântica seja o bioma mais intensamente estudado para mamíferos no Brasil, ainda não se atingiu o conhecimento necessário para a conservação e gestão eficaz desta classe na Mata Atlântica. Estudos adicionais são necessários para permitir a definição de zonas dentro das áreas protegidas, como definido pela legislação brasileira (Lei: 9.985/2000 (SNUC)). Este zoneamento é necessário para a realização dos objetivos múltiplos das áreas protegidas (incluindo a manutenção da biodiversidade e o fornecimento dos serviços dos ecossistemas) dentro do contexto sócio-econômico em um escala regional e nacional.

Palavras-chaves: Áreas protegidas. Fatores ambientais. Impactos antrópicos. Mata Atlântica.

ABSTRACT

There is an urgent need to develop ecological knowledge to support conservation and management of the protected area network within the Serra do Mar biogeographical region. Results of previous research showed a high variation in the abundance of large mammals within large protected areas of Atlantic Forest within this region that is comparable if not greater than that found in fragmented Atlantic Forest ecosystems. This thesis shows how environmental variables and anthropogenic impacts influence large mammals within the remaining continuous Atlantic Forest remnants of the Serra do Mar. Continuous Atlantic Forest remnants are highly heterogeneous and this heterogeneity results from environmental factors and human impacts. The results presented in the four chapters of this thesis highlight that, although the Atlantic Forest is the most intensely studied biome for mammals in Brazil, the knowledge necessary for the conservation and effective management of this class in the Atlantic Forest is still lacking. Additional studies are needed to allow the establishment of zones within protected areas as defined by Brazilian legislation (Law: 9.985/2000 (SNUC)). This zoning is necessary to achieve the multiple objectives of protected areas (including the maintenance of biodiversity and the provision of ecosystem services) within the socio-economic development in a regional and national scale.

Keywords: Anthropogenic impacts. Atlantic Forest. Environmental factors. Protected areas.

SUMÁRIO

1 INTRODUÇÃO

A conservação da Mata Atlântica

As riquezas e ameaças da Mata Atlântica levaram a mesma a ser descrita por uma frase de duplo sentido: “the hottest of the hotspots” (Laurance 2009). Embora o conceito de "hotspots" tenha sido contestado (Orme *et al.* 2005), é justificável no caso da Mata Atlântica (Laurance 2009), que possui altos níveis de endemismo e ameaças (Myers *et al.* 2000, Laurance 2009, Metzger 2009). Atualmente, esse bioma está reduzido a cerca de 12% (15.719 km^2) de sua extensão original, espalhados em vários fragmentos (80% dos fragmentos são menores do que 50 ha) e poucas matas contínuas (Ribeiro *et al.* 2009). Hoje, apesar das severas restrições legais, a taxa de perda de floresta ainda é elevada, aproximando-se de 0,25% ou 350 km^2 por ano (Fundação SOS Mata Atlântica-INPE 2008) e a perda e fragmentação de hábitat são consideradas ameaças maiores do que as mudanças climáticas para espécies na Mata Atlântica (Loiselle *et al.* 2010). Portanto, uma gestão ativa para a conservação de grandes áreas florestais nesta região é reconhecida como uma prioridade para a conservação e restauração da biodiversidade e dinâmica dos ecossistemas na Mata Atlântica (Tabarelli *et al.* 2005, Galetti *et al.* 2009, Metzger 2009, Tabarelli *et al.* 2010).

O conhecimento científico é fundamental para auxiliar a gestão e conservação da biodiversidade dos remanescentes da Mata Atlântica. As iniciativas no Brasil, especialmente na Mata Atlântica, são citadas como exemplos de sucesso para a conservação da biodiversidade. Esse sucesso é proveniente da integração de proteção jurídica, gestão de áreas protegidas, e planejamento de conservação baseados na ciência (Galindo-Leal & Câmara 2003, Russo 2009, Brancalion *et al.* 2010, Tabarelli *et al.* 2010). O conhecimento científico usado para informar a gestão e conservação da Mata Atlântica é baseado em pesquisas teóricas e empíricas que podem ser divididas em duas escalas. Em uma escala ampla, os padrões espaciais de riqueza e diversidade históricas das espécies são usados para entender os padrões biogeográficos (da Silva *et al.* 2004, Quijano-Abril *et al.* 2006, Carnaval & Moritz 2008, Fouquet *et al.* 2012, Silva *et al.* 2012). Em uma escala local, os padrões espaciais de riqueza e diversidade atuais das espécies são usados para entender os impactos humanos sobre a biodiversidade da Mata Atlântica, por exemplo, urbanização (Silvano & Segalla 2005, Baptista & Rudel 2006, Izquierdo *et al.* 2011), caça (Goerck 1997, Cullen *et al.* 2001, Bernardo *et al.* 2011), e perda e fragmentação de hábitat (Tabarelli *et al.* 1999, Chiarello 2000, Pardini *et al.* 2005, Boscolo & Metzger 2011, Arroyo-Rodriguez *et al.* 2012, Braun *et al.* 2012, Suni & Brosi 2012).

A manutenção da biodiversidade da Mata Atlântica depende da proteção e da restauração das florestas nativas (Tabarelli *et al.* 2005, Baptista & Rudel 2006, Metzger 2009, Brancalion *et al.* 2010). Os poucos remanescentes florestais com mais de 10.000 ha (Ribeiro *et al.* 2009) são considerados importantes para a manutenção dos níveis de diversidade e endemismo, sendo necessários também para facilitar as atividades de restauração (Tabarelli *et al.* 2005, Metzger 2009). Embora os padrões e processos ecológicos decorrentes dos efeitos da fragmentação na Mata Atlântica são bem compreendidos, fornecendo uma base sólida para gestão e conservação (Tabarelli *et al.* 2005, Metzger 2009, Pardini *et al.* 2010), ainda existe uma grande lacuna em nosso conhecimento sobre os padrões e processos que determinam a ocorrência e abundância das espécies em remanescentes contínuos da Mata Atlântica.

A heterogeneidade e a complexidade dos hábitats são moduladores importantes da biodiversidade nas florestas tropicais (August 1983, Burnett *et al.* 1998). Comparado com hábitats menores e/ou mais fragmentados, grandes áreas contêm mais espécies e populações maiores, o que aumenta a estabilidade contra as variações demográficas, genéticas e processos ambientais (Fahrig 2003). Por conseguinte, com base em tais relações espécies/áreas, pode-se esperar que nas áreas que contêm milhões de hectares, as populações serão maiores e mais viáveis. Mas avaliações baseadas em tão ampla escala podem ignorar a heterogeneidade inerente (gradiente topográfico, por exemplo) e induzida (caça, por exemplo) nos hábitats, o que pode ter um impacto significativo sobre a distribuição e abundância das comunidades faunísticas das florestas tropicais (August 1983, Burnett *et al.* 1998, Peres 2001).

A região biogeográfica da Serra do Mar (da Silva *et al.* 2004, Silva *et al.* 2012) inclui o remanescente melhor (mais bem) conservado de Mata Atlântica (Ribeiro *et al.* 2009). Este remanescente abriga 32,2% (3.678.534 hectares) da área florestal original (Ribeiro *et al.* 2009) e, em contraste com a maioria dos remanescentes florestais de Mata Atlântica encontrados no Brasil, a Serra do Mar é um contínuo de floresta que não parece ter sido tão afetado pela degradação antrópica ou pelo efeito de borda, pois 75% da área remanescente possui distâncias maiores do que 100 m a partir da borda mais próxima da matriz e mais de 50% da floresta está mantida em áreas maiores de 50.000 ha (Ribeiro *et al.* 2009).

Mamíferos neotropicais de médio e grande porte

A base ecológica para a variação em abundância e biomassa das espécies na região biogeográfica da Serra do Mar permanece desconhecida. No entanto, para a gestão eficaz deste grande remanescente da Mata Atlântica é necessário identificar os principais fatores que podem afetar a distribuição e abundância das espécies (Aguiar *et al.* 2003, Tabarelli *et al.*

2005, Metzger 2009, Tabarelli *et al.* 2010). Mamíferos de médio e grande porte são conhecidos como um grupo chave para a manutenção e regeneração das florestas tropicais e também incluem espécies “umbrella”, “key-stone”, e “flagship” (Cuaron 2000). Portanto este grupo pode ser visto como um dos mais importantes para atividades de manejo na Mata Atlântica (Cullen *et al.* 2001, Almeida-Neto *et al.* 2008, Fonseca *et al.* 2009, Galetti *et al.* 2009, Paviolo *et al.* 2009, Redford *et al.* 2011, Suzart de Albuquerque *et al.* 2011).

Vários efeitos diretos e indiretos podem alterar o padrão espacial de regeneração nas florestas tropicais quando as comunidades de mamíferos são impactadas pelas perturbações antrópicas (Terborgh *et al.* 2008, Estes *et al.* 2011). Para evitar os impactos bem conhecidos da defaunação (Dirzo & Miranda 1990, Bascompte & Jordano 2007, Estes *et al.* 2011) e florestas vazias (Redford 1992, Terborgh *et al.* 2008, Harrison 2011) que mudariam para sempre ecossistemas e remanescentes florestais (Dirzo & Miranda 1990, Asquith & Mejia-Chang 2005, Terborgh *et al.* 2008, Estes *et al.* 2011), o primeiro passo é saber os padrões de distribuição e abundância dos mamíferos nos remanescentes contínuos da Mata Atlântica. Por exemplo, Galetti *et al.* (2009) mostram que a abundância e a biomassa de mamíferos de médio e grande porte variou em uma ordem de magnitude entre as áreas de Mata Atlântica contínua. Este variação entre remanescentes contínuos foi igual ou maior à que foi observada em fragmentos florestais de diferentes tamanhos (Chiarello 2000, Cullen *et al.* 2000, Galetti *et al.* 2009). No entanto, é necessário identificar os principais fatores que podem afetar a abundância dos mamíferos dentro desses remanescentes contínuos de Mata Atlântica (Galetti *et al.* 2009).

Muitas variáveis (não mutuamente exclusivas) têm sido levantadas para explicar a variação em abundâncias de mamíferos, incluindo: 1) diferenças nas fisionomias florestais (August 1983, Boas Goulart *et al.* 2009, Ahumada *et al.* 2011), 2) variação topográfica (Geise *et al.* 2004), 3) pressão humana atual (caça, desmatamento (Chiarello 1999, Cullen *et al.* 2001, Peres 2001) e 4) diferenças na “vulnerabilidade” de áreas protegidas (Peres & Terborgh 1995, Paviolo *et al.* 2009). A avaliação de quais destas hipóteses determinariam a abundância de mamíferos de médio e grande porte pode gerar conhecimento ecológico, e embasar a gestão eficaz de um dos maiores e mais diversos remanescentes da biodiversidade mundial. Para evitar mais perdas de biodiversidade em um “hotspot” mundial, modelos ecológicos devem ser criados para informar atividades de gestão e para assegurar a manutenção da biodiversidade local e regional. As pesquisas apresentadas nesta tese tentam contribuir para o entendimento ecológico necessário para desenvolver esses modelos.

Objetivos

O objetivo geral desta tese é avaliar a influência dos fatores antrópicos e ambientais sobre a abundância de mamíferos de médio e grande porte em áreas contínuas de Mata Atlântica, por meio de técnicas multivariadas, ecológicas (por exemplo modelagem de nicho, Distance) e geoestatísticas.

Apresentação

Capítulo 1. Embora seja o bioma com o melhor conhecimento sobre mamíferos no Brasil, ainda existem grandes lacunas em nosso conhecimento sobre os mamíferos que permanecem na Mata Atlântica. Para mostrar como a Mata Atlântica continua apresentando desafios para a mastozoologia, este capítulo apresenta como um caso de estudo uma lista de espécies de uma unidade de conservação ameaçadas pelas perturbações antrópicas. Especificamente:

- Quais espécies ocorrem na área?
- Quais dados estão faltando para o manejo eficaz dentro de unidades de conservação da Mata Atlântica ameaçadas pelas perturbações antrópicas?

Capítulo 2. Comparar e contrastar abundâncias de áreas contínuas para fornecer uma visão da influência relativa das pressões naturais e humanas sobre os padrões de abundância e de ocorrência de espécies.

- Avaliar como diferenças nas fisionomias florestais, variação topográfica e na “vulnerabilidade” de áreas protegidas influenciam as comunidades de mamíferos em duas áreas protegidas da Mata Atlântica.

Capítulo 3. Uso do *Callithrix aurita* como caso de estudo na aplicação das técnicas ecológicas (modelagem de nicho e análises Distance) para estimar a densidade de espécies com uma distribuição heterogênea.

- Como estimar a densidade de uma espécie com uma distribuição heterogênea?
- Se fatores antrópicos e ou ambientais influenciam o nicho ecológico?
- Como modelar a distribuição espacial de uma espécie rara?

Capítulo 4. Uso do *Tayassu pecari* como caso de estudo da aplicação das técnicas geoestatísticas para prever padrões de ocupação de espécies raras. Especificamente:

- Como fatores antrópicos e ambientais influenciam o nicho ecológico?
- Como modelar a distribuição espacial de uma espécie rara?
- Como melhorar o uso e inferência dos resultados das análises com dados de presença?

Declaração sobre a autoria múltipla

Eu sou o primeiro autor e principal contribuinte de cada um dos capítulos na minha tese, incluindo o desenvolvimento das perguntas, análises e conteúdo escrito. Nos parágrafos abaixo eu explico o papel de cada co-autor em cada capítulo.

Capítulo 1 foi publicado no periódico Biota Neotropica (2012, vol 12, numero 2). A versão on-line deste artigo está disponível em: http://www.biotaneotropica.org.br/v12n2/pt/abstract?inventory+bn00312022012. Eu, Mauro Galetti, José Moreira-Ramírez e Carlos Zacchi projetamos o estudo, eu e José Moreira-Ramírez realizamos o trabalho de campo, eu analisei os dados e eu, Mauro Galetti e José Moreira-Ramírez escrevemos o texto.

Capítulo 2 está em revisão no periódico Zoologia. Eu, Mauro Galetti, Carlos Zacchi, Paulo Camarero e José Moreira-Ramírez projetamos o estudo, eu e José Moreira-Ramírez realizamos o trabalho de campo, eu compilei e analisei os dados e eu, José Moreira-Ramírez, Mauro Galetti e Silvio Ferraz escrevemos o texto.

Capítulo 3 foi publicado no periódico International Journal of Primatology (2011, 32:811–829, DOI: 10.1007/s10764-011-9503-1). A versão apresentada aqui é o “accepted authors version”. A versão final deste artigo está disponível no site do Springer (http://www.springerlink.com/content/7812607jv3t86425/). Mauro Galetti, Fabiana Rocha-Mendes, Renato Marques e Rodrigo de Almeida Nobre projetaram o estudo. As perguntas foram desenvolvidas por mim e Mauro Galetti, o trabalho de campo foi realizado por Fabiana Rocha-Mendes, Renato Marques e Rodrigo de Almeida Nobre, eu compilei e analisei os dados e eu e Mauro Galetti escrevemos o texto.

Capítulo 4 foi publicado no periódico Animal Conservation (2011, 14:492–501, DOI: 10.1111/j.1469-1795.2011.00450.x). A versão apresentada aqui é o “accepted authors version”. A versão final deste artigo está disponível no site do Wiley (http://onlinelibrary.wiley.com/doi/10.1111/j.1469-1795.2011.00450.x/abstract). Mauro Galetti, Fabiana Rocha-Mendes e João Paulo Villani projetaram o estudo. As perguntas foram desenvolvidas por mim, Mauro Galetti e Silvio Ferraz, o trabalho de campo foi realizado por

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Capítulo 1

A survey of mid and large bodied mammals in
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A survey of mid and large bodied mammals in Núcleo Caraguatatuba, Serra do Mar State Park, Brazil.

Darren Norris[1,3], José Moreira Ramírez[1], Carlos Zacchi[2] & Mauro Galetti[1]

[1]*Departamento de Ecologia, Universidade Estadual Paulista Júlio de Mesquita Filho – UNESP ,*
Av. 24A, 1515, Bela Vista, CP 199, CEP 13506-900, Rio Claro, SP, Brasil
[2]*Parque Estadual da Serra do Mar – PESM, Rua Horto Florestal , 1200, 11675-730 ,*
Caraguatatuba, SP Brasil
[3]*Corresponding author: Darren Norris, e-mail: dnorris75@gmail.com*

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Abstract: We applied complementary survey techniques to obtain a baseline species list of mid and large bodied mammals in Núcleo Caraguatatuba, Serra do Mar State park, Brazil. Between May and September 2011 we surveyed the community of mid and large bodied mammals using diurnal line transect census (212.4 km), camera-traps (223.2 camera-trap days) and track-stations (478 track-station days). A total of 18 species were recorded from 14 families in eight orders. We recorded the presence of seven species considered threatened in the State of São Paulo, including Primates (*Brachyteles arachnoides*), Artiodactyla (*Mazama* cf. *americana* and *Tayassu pecari*), Carnivora (*Leopardus pardalis*, *Leopardus tigrinus* and *Puma concolor*) and Perissodactyla (*Tapirus terrestris*). Based on extrapolated (First order jackknife) species richness estimates we predict that there are between 19 and 32 species of mid and large bodied mammals in the Núcleo. Our revised Mammal Priority Index ranked Núcleo Caraguatatuba as being of medium overall importance for the conservation of mid and large bodied mammals in the Atlantic Forest. Combined with the number and diversity of species recorded, our results demonstrate that this Núcleo is an important area for mammal conservation.

Keywords: *Atlantic forest, inventory, mammals, protected area.*

NORRIS, D., RAMÍREZ, J.M., ZACCHI, C. & GALETTI, M. **Mastofauna de médio e grande porte na Núcleo Caraguatatuba, Parque Estadual Serra do Mar, SP, Brasil**. Biota Neotrop. 12(2): http://www.biotaneotropica.org.br/v12n2/pt/abstract?inventory+bn00312022012

Resumo: Nós aplicamos técnicas de amostragem complementares para obter uma lista de espécies de mamíferos de médio e grande porte no Núcleo Caraguatatuba, Parque Estadual da Serra do Mar, Brasil. As amostragens de campo realizaram-se nos meses de Maio e Setembro de 2011. Utilizou-se, censo ao longo de transectos (212,4 km), armadilhas fotográficas (223,2 armadilhas-dias) e armadilhas de pegadas (478 armadilhas-dias). Foram obtidos registros de 18 espécies, pertencentes a 14 famílias e oito ordens. Nós registramos a presença de sete espécies consideradas ameaçadas no Estado de São Paulo, incluindo primatas (*Brachyteles arachnoides*), Artiodactyla (*Mazama americana* e *Tayassu pecari*), Carnivora (*Leopardus pardalis*, *Leopardus tigrinus* e *Puma concolor*) e Perissodactyla (*Tapirus terrestris*). Com base em numa extrapolação da riqueza de espécies ("First order jackknife") nós prevemos que existem entre 19 e 32 espécies de mamíferos de médio e grande porte no Núcleo. Nosso "Mammal Priority Index" classificou o Núcleo Caraguatatuba como uma área de importância "média" para a conservação de mamíferos de médio e grande porte na Mata Atlântica. Combinado com o número e a diversidade de espécies registradas, nossos resultados demonstram que este Núcleo é uma área importante para a conservação de mamíferos no Estado.

Palavras-chave: *mata Atlântica, inventário, mamíferos, unidade de conservação.*

Introduction

The Atlantic Forest is the most intensively studied biome for Brazilian mammals (Brito et al. 2009). The sampling intensity and availability of both published and un-published studies has enabled the establishment of priority areas for the conservation of mammals across the Atlantic Forest biome (Galetti et al. 2009, Albuquerque et al. 2011). Yet these studies also highlight that there remain significant gaps not only in our understanding but also in the published data describing Atlantic Forest mammals (Brito et al. 2009, Galetti et al. 2009, Albuquerque et al. 2011). With greater attention required for the development and dissemination of studies focusing on obtaining solutions to the management problems facing wild mammal species (Brito et al. 2009).

Conservation initiatives in Brazil, particularly the Atlantic Forest, are cited as examples of the successful integration of legal protection, protected area management, and science-based conservation planning (Russo 2009, Brancalion et al. 2010, Tabarelli et al. 2010). However, despite such positive examples, the situation for the fauna and flora of the Brazilian Atlantic Forest remains precarious (Marsden et al. 2005, Tabarelli et al. 2005, Fonseca et al. 2009, Galetti et al. 2009, Teixeira et al. 2009, Tabarelli et al. 2010). Protected areas are recognized as a key part of conservation initiatives (Naughton-Treves et al. 2005, Rands et al. 2010, Stockstad 2010) with >13% of Brazilian terrestrial biomes receiving legal protection at federal or state levels (Rylands & Brandon 2005). There are >700 areas of Atlantic Forest with at least some level of legal protection (Galindo-Leal & Câmara 2003, Tabarelli et al. 2010). However, the management of protected areas for mid and large bodied mammals in the Atlantic Forest is challenging as the majority of these areas (~75%) are small i.e. <100 km^2 (Ribeiro et al. 2009) and may not retain suitable environmental conditions for endangered species (Norris et al. 2011a, Norris et al. 2011b) and threats from anthropogenic perturbations such as urbanization, illegal hunting and palm heart harvesting are ubiquitous (Galetti & Fernandez 1998, Tabarelli et al. 2005, Galetti et al. 2009, Teixeira et al. 2009, Tabarelli et al. 2010).

The Serra do Mar biogeographical sub-region is the largest area of Atlantic Forest in Brazil. More than 50% of forest cover in the sub-region is found in forest fragments >50,000 ha and it also includes the largest remnant - a continuous forest area of 1,109,546 ha that is located along the coast of São Paulo State (Ribeiro et al. 2009). The Serra do Mar State Park is embedded within this continuous area, protecting 315,390 ha of Atlantic Forest that includes a variety of habitat types from lowland (sea-level) coastal restinga to highland (>200 masl) dense mountainous ombrofilous forest (Instituto Florestal 2008, p. 11-15). The size of the protected area generates unique management challenges and to meet these challenges it was necessary to divide the area into eight administrative units or "Núcleos" (Instituto Florestal 2008, p. 13-15). Although this area is continuous, the Serra do Mar continues to suffer from intensive hunting and palm heart harvesting. The numerous highways that cross the park, and the presence of major gas and oil pipelines facilitates entry of hunters to "remote" park areas (Aguiar et al. 2003, Instituto Florestal 2008, p. 129). Additionally, park borders are densely populated and illegal hunting, palm heart and bromeliad harvesting is common place (Instituto Florestal 2008, p. 119-143).

Although challenging from a management perspective, the size and diversity of protected habitats means that we expect to find high levels of biodiversity within the Serra do Mar State park (Aguiar et al. 2003). Indeed, within such a well connected and biodiverse expanse of forest (Aguiar et al. 2003) it is not unreasonable to predict the occurrence of a significant proportion of the 45 species (De Vivo et al. 2011) of mid and large bodied terrestrial mammals recorded in São Paulo State within this park. However, even the most basic management information (i.e. which mammal species are present) is not available for the majority of the Serra do Mar Núcleos, with 6 of the 8 classified as having zero or low levels of knowledge regarding the mammalian fauna (Instituto Florestal 2008, p. 180).

Recent diurnal line transect surveys recorded a maximum of 8 mid to large bodied mammal species within 4 of the Serra do Mar Núcleos (Picinguaba, Caraguatatuba, Cunha and Santa Virginia (Galetti et al. 2009). Although standardized line transect surveys provide a powerful dataset for analysis of species abundances they are unlikely to approximate a truly representative sample of the mid and large bodied mammal fauna. This group includes rare, cryptic and illusive species that to achieve management objectives including knowledge of which species are present are best surveyed with a combination of techniques (Michalski & Peres 2007, Espartosa et al. 2011, Munari et al. 2011). The objective of the present study was to use complementary survey techniques to obtain a baseline species list and estimate the species richness of mid and large bodied mammals in Núcleo Caraguatatuba as the first step to increasing our knowledge of the regional mammalian fauna and to support the management activities within this protected area.

Material and Methods

1. *Study area*

Mammal surveys took place in Núcleo Caraguatatuba of the Serra do Mar State park (Figure 1). Núcleo Caraguatatuba protects 49,953 ha (Instituto Florestal 2008) of the pre-Cambrian Serra do Mar mountain chain (Mantovani 1993). Of the eight administrative "Núcleos" of the Serra do Mar, 5 including Caraguatatuba are coastal, with Núcleo Caraguatatuba being located in the center of the "litoral" tourist region of the state, receiving approximately 5000 visitors annually. The Núcleo is bisected by the Tamoios road, a state highway that leads to the town of Caraguatatuba (45° 25' 57" W and 23° 35' 52" S). The western portion of the Núcleo is also traversed by one of the main pipelines of the Brazilian petroleum company "Petrobras". The poorly monitored access provided by the Tamoios highway and the pipeline are the two principal vectors of anthropogenic pressure (i.e. illegal hunting and palm-heart harvesting) in the Núcleo (Instituto Florestal 2008, p. 119-143).

The regional climate is subtropical, with a mean annual temperature of 23.2 (daily means ranging from 4.6 to 36.1, data from 2010 downloaded from the Brazilian weather center http://www.cptec.inpe.br/, station ID: 83671, Lat: –21.98, Long: –47.35 m a.s.l. = 598) and annual rainfall from 1400 to 4000 mm (Mantovani 1993). Soils are predominantly nutrient-impoverished yellow-red latosol, podzols and lithosols (Brasil 1983). Forests range from coastal (≈20 m) to elevations >900 m, generating stark floristic gradients, from shrubs to well-developed montane forests (Veloso et al. 1991).

2. *Mammal surveys*

Between May and September 2011 we used complementary techniques (line transect census, track surveys and camera-traps) to sample the mid and large bodied mammal community across Núcleo Caraguatatuba (Figure 1). Surveys were conducted by two observers with a minimum of 5 years experience in monitoring neotropical mammals. Nomenclature follows that presented in De Vivo et al. (2011) except for *Alouatta guariba* which follows Groves (2005).

During 34 days we conducted a total of 212.4 km of diurnal line transect census along 13 (total km = 71.9) preexisting (established for >10 years) trails (trail length: mean, range = 4.9, 0.7-15.7 km).

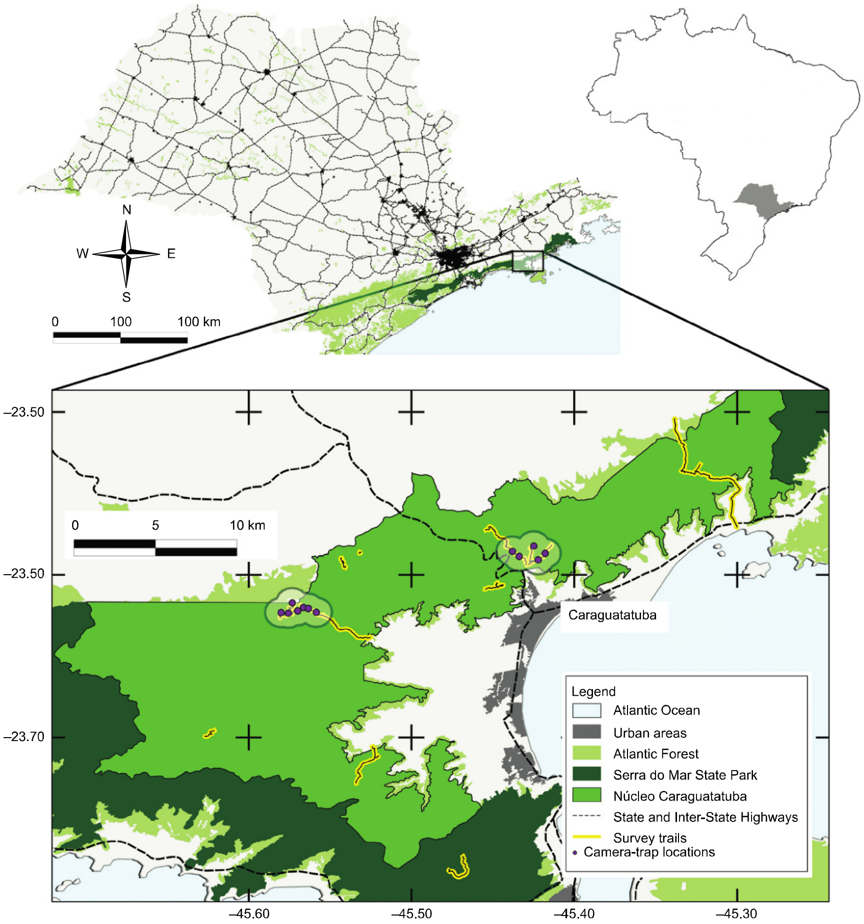

Figure 1. Study area showing locations of survey trails and camera-traps used to survey mid and large bodied mammals in Núcleo Caraguatatuba, Serra do Mar State Park, São Paulo, Brazil.

To provide a representative sample, trails were distributed throughout the Núcleo (Figure 1) and encompassed a variety of secondary and primary forest habitats. From the total of 71.9 trail km, the majority (51.9 km) were in forest dominated by early or advanced secondary successional stages, followed by primary (7.9 km) and eucalyptus and pine plantations (6.8 km).

Standard line transect protocols (Peres 1999, Buckland et al. 2010) were adapted to fit our main objective of sampling mid and large bodied mammals across the widest possible variety of habitats within the park. Census was not conducted during heavy rainfall but did occur during light showers i.e. when observers could walk comfortably without wearing protective clothing. Census was carried out during the morning (5:40 AM - 1:13 PM) and or afternoon (12:47 PM - 5:35 PM), with times varying due to logistical constraints and weather conditions. Although there was a slight overlap between the timing of morning and afternoon census, on any one day there was a minimum of 2 hours between the end of morning and start of afternoon census when we used the same trail and a minimum of 1 hour between morning and afternoon census when different trails were used. We do not consider this extension of the timing of our morning census to have biased our surveys. The standardization of census times has been determined from studies in tropical conditions where the heat during midday hours (between 12:00 AM and 2:00 PM) limits mammal activity (Peres 1999). Diurnal temperatures within our sub-tropical study area are not comparable to those in these tropical areas. At the latitude of Núcleo Caraguatatuba mammals are often seen during these "midday" hours, appearing to avoid activity during the often cold (<14 °C) early mornings. For example we did not detect any mammals before 9 AM. To enable us to survey the maximum range of habitats possible we did not follow the recommended line transect survey speed of ≈1.25 km per hour (Peres 1999, Buckland et al. 2010). Although we did pause regularly at 100 to 300 m intervals to listen for detection cues, our mean per trail census speed was above the recommended value (survey speed: mean, range = 2.4, 1.1-3.4 km per hour). Although it is possible that this increased census speed resulted in missed detections, we found no significant relationship between the number of detections recorded per km and the survey speed (Spearmans correlation, rho = –0.223, p = 0.221). We are therefore confident that our modifications of the standard census protocols did not introduce any systematic bias and that our line transect survey results are directly comparable with previous studies.

During our line transect surveys we also recorded tracks that were visible along the trails. These "ad hoc" detection events were supplemented by a total of 25 un-baited track-stations placed along two of our census trails (Figure 1). Track-stations were prepared by removing leaf litter, rocks and surface roots from a 75 × 75 cm quadrant followed by loosening, separating and smoothing the soil surface with a machete so that it would be possible to discern track impressions of mid to large bodied mammals >2 kg (tested by the gentle application of finger tips to the prepared surface). Track-stations were checked at 3-6 day intervals. Days with heavy rain were excluded from our effort, resulting in an overall effort of 478 track-station days. Observers (each with >5 years experience of surveying mid and large bodied mammals in Neotropical forests) recorded the species identity of tracks with reference to field guides (Becker & Dalponte 1991, Emmons & Feer 1997). In cases where species identity was uncertain we took photos that were sent to specialists for confirmation. Any tracks that could not be reliably identified were not included in our analysis.

From June to July 2011 we installed 12 digital camera-traps (6 Reconyx, RECONYX, Inc. Wisconsin, USA - http://www.reconyx.com/ and 6 Ecotone, ECOTONE, São Paulo, Brazil http://www.ecotonebrasil.com). Cameras were installed in two areas (Figure 1) separated by a 12.9 km straight line distance – one close to the park base (5 cameras – 103.7 camera-trap days) and one in an area that receives no visitors and has been relatively undisturbed for at least 30 years (7 cameras – 119.5 camera-trap days), providing a total effort of 223.2 camera-trap days. Cameras were operational continuously over the 24 hours diel cycle and placed at random locations between 5 and 15 m to the side of existing trails within each area, with a minimum straight line nearest neighbor distance of 530 m. However, due to the steep topography including near vertical ravines, the minimum distance between cameras for any terrestrial mammal is effectively >1400 m. We attached cameras to trees at a height of ≈ 40 cm above the ground. The area in front of cameras was cleared of green foliage and herbs to prevent sunlight reflections damaging image quality. Due to licensing restrictions cameras remained un-baited, but were checked at 2 – 9 day intervals to ensure continuous operation and for routine maintenance e.g. to change batteries.

3. *Data analysis*

To understand the relationship between species richness and our survey effort we used the "specaccum" function of the "vegan" package (Oksanen et al. 2011) in the R software (R Development Core Team 2011) to estimate the individual based rarefaction curve of mean species richness per sample day. For this analysis we summed all individuals recorded for each species using any technique by the survey date, generating a matrix of 18 species by 22 survey days (we excluded days with no mammal species records). To predict the total number of species present in the Núcleo that it would be possible to detect using the combination of survey techniques we used the "First order jackknife" estimator to extrapolate the species richness from the frequencies of species encountered per day (function "specpool", package "vegan"). Although a number of extrapolation estimators are available we chose this one to enable comparison with previous studies (Espartosa et al. 2011).

To provide a measure of the conservation importance of Núcleo Caraguatatuba we calculated the Mammalian Priority Conservation Index (Galetti et al. 2009). This index provides a comparitive measure of the importance of the site by incorporating native species richness, species threat status (based on the threat status in the State of São Paulo (Magalhães-Bressan et al. 2009), species uniqueness and body size as well as the site forest area (see Galetti et al. 2009 for full details of index calculation and interpretation). To enable comparison with previous studies (Galetti et al. 2009) we only used data from the line transect censuses to derive the index.

Results

We obtained records of 18 mid to large bodied mammal species from 14 families in 8 orders, of which seven species are considered threatened ("Vulnerable" or "Endangered") in the State of São Paulo and five (27.8%) are considered threatened internationally (Table 1). Camera-traps recorded the most species (12), followed by tracks (10), other indirect detections (7) and finally direct visual detections from diurnal line transect census (6). *Tapirus terrestris* was the only species recorded with all four classes of detection technique, whereas six species (*Didelphis aurita* - photos, *Tayassu pecari* - tracks, *Leopardus tigrinus* - photos, *Lontra longicaudis* - tracks, *Bradypus variegatus* - carcass and *Brachyteles arachnoides*- visual) were only recorded by a single class (Table 1).

The estimated curve of species richness per survey day did not reach an asymptote, with species continuing to accumulate at a rate of 0.4 species per day after 22 survey days (Figure 2). Based on the First order jackknife our extrapolated species richness was 26 species (estimate ± 95% CI = 25.63 ± 6.07).

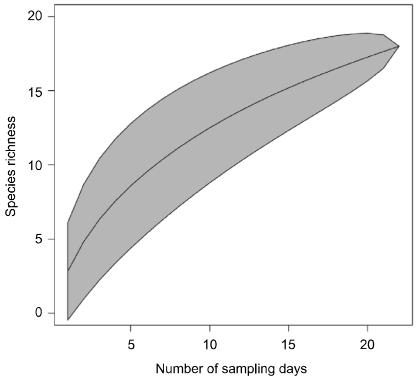

Figure 2. Mean accumulation curve and 95% confidence interval (shaded area) of the expected number of mid to large bodied mammal species in Núcleo Caraguatatuba, Serra do Mar State Park, São Paulo, Brazil.

Table 1. List of mammal species from Núcleo Caraguatatuba, Serra do Mar State Park, São Paulo, Brazil.

Order	Family	Species	Detection type[a]				Threat	Abundance[d]	
			Photo	**Track**	**Visual**	**Other**	**S[b]/Int[c]**	**LT**	**CT**
Artiodactyla									
	Cervidae	*Mazama* cf. *americana* (Erxleben, 1777)		X	X		VU/DD	0.040	
	Tayassuidae	*Pecari tajacu* (Linnaeus, 1758)	X	X		X	NT/LC		0.081
		Tayassu pecari (Link, 1795)		X			EN/NT		
Carnivora									
	Felidae	*Leopardus pardalis* (Linnaeus, 1758)	X	X			VU/LC		0.161
		Leopardus tigrinus (Schreber, 1775)	X				VU/VU		0.081
		Puma concolor (Linnaeus, 1771)	X	X			VU/LC		0.081
	Mustelidae	*Lontra longicaudis* (Olfers, 1818)		X			NT/DD		
Cingulata									
	Dasypodidae	*Dasypus novemcinctus* (Linnaeus, 1758)	X	X		X	LC/LC		0.242
Didelphimorphia									
	Didelphidae	*Didelphis aurita* (Wied-Neuwied, 1826)	X				LC/LC		0.242
Perissodactyla									
	Tapiridae	*Tapirus terrestris* (Linnaeus, 1758)	X	X	X	X	VU/VU	0.040	0.524
Pilosa									
	Bradypodidae	*Bradypus variegates* (Schinz, 1825)				X	LC/LC		
Primates									
	Atelidae	*Alouatta guariba* (Humboldt, 1812)			X	X	NT/LC	0.202	
		Brachyteles arachnoides (É. Geoffroy, 1806)			X		EN/EN	0.040	
	Cebidae	*Cebus nigritus* (Goldfuss, 1809)	X		X	X	NT/NT	1.089	0.040
Rodentia									
	Caviidae	*Hydrochoerus hydrochaeris* (Linnaeus, 1766)	X			X	LC/LC		0.081
	Cuniculidae	*Cuniculus paca* (Linnaeus, 1766*)*	X	X			NT/LC		0.040
	Dasyproctidae	*Dasyprocta* cf. *azarae* (Lichtenstein, 1823)	X	X			LC/DD		0.040
	Sciuridae	*Guerlinguetus ingrami* (Thomas, 1901)	X		X		LC/NE	0.040	0.040

[a]How species were detected. Photo = camera-trap, Track = tracks observed along trails or on prepared track-stations, Visual = diurnal line transect census, and Other = carcass, feces, or vocalizations; [b]Threat status in the State of São Paulo (Magalhães-Bressan et al. 2009, p. 599). From least to most threatened: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered; [c]International threat status following (International… 2011). NE = not evaluated, DD = data deficient, then from least to most threatened: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered; [d]Species relative abundance.LT = detections per 10 km of line transect census and CT = independent photos per 10 camera-trap nights.

Relative abundances from line transect census ranged from 0.040 (*Brachyteles arachnoides*, *Mazama* cf. *americana*, *Tapirus terrestris*, and *Guerlinguetus ingrami*) to 1.089 (*Cebus nigritus*) detections per 10 km. The relative abundances obtained from diurnal census enabled us to calculate a revised Mammalian Priority Index of 15.29, which following the thresholds established by Galetti et al. (2009) classifies the Núcleo as an area of medium overall importance for large-bodied mammals in the Atlantic Forest.

Although rarely detected during diurnal censuses *Tapirus terrestris* was the most commonly recorded species with camera-traps (0.524 independent photos per 10 camera-trap nights), followed by *Dasypus novemcinctus* and *Didelphis aurita* (0.242 independent photos per 10 camera-trap nights). The most infrequently photographed species were *Cebus nigritus*, *Cuniculus paca*, *Dasyprocta* cf. *azarae*, and *Guerlinguetus ingrami* (0.040 independent photos per 10 camera-trap nights).

Discussion

Although Atlantic Forest mammals are relatively well studied there is little comparative data available from studies of mid and large bodied mammals in continuous forest areas. In a recent compilation (Galetti et al. 2009) found that from a total of 31 mid and large bodied mammal species a maximum of only 13 (41.9%) species were recorded using diurnal line transect census in 34 mainland Atlantic Forest sites. Other studies that employ a range of techniques generally record a greater number of species on a per site basis. For example, using line transect census (241 km) in secondary forest areas of the Morro Grande Forest Reserve - a 10,870 ha protected area close to the city of São Paulo Negrão & Valladares-Pádua (2006) recorded five species of mid to large bodied mammals but when these results were combined with sand track-stations (600 track-station days) a total of 18 species were recorded in the same area (Negrão & Valladares-Pádua 2006). Other studies from the Brazilian Atlantic Forest report similar patterns with more species recorded when different techniques were applied simultaneously: a total of 16 species were recorded in a 221 ha area of semi-deciduous Atlantic Forest using visual searches and camera-traps (Abreu Junior & Köhler 2009), 23 species in a 230 ha semi-deciduous forest area using line transect census (271 km), camera-traps (336.5 camera-trap days) and track-stations (1258 track-station nights) (Gaspar 2005), 29 species in a 17 491 ha protected area using visual searches (128 km), camera-traps (1842 camera-trap nights) and nocturnal surveys along park roads (Kasper et al. 2007). However none of these studies present species richness curves/

estimates that would facilitate a between site comparison of the mid to large bodied mammal communities.

Previous studies have demonstrated the importance of protected areas for the regional conservation of Atlantic Forest mammals (De Araujo et al. 2008, Galetti et al. 2009, Paviolo et al. 2009, Norris et al. 2011a, Norris et al. 2011b). Although it is not possible to make direct comparisons with other Atlantic Forest studies our predicted species richness shows the importance of Núcleo Caraguatatuba for the conservation of regional masto-fauna. Of the 18 species recorded seven (39%) are threatened in the State of São Paulo and five (27.8%) are threatened internationally (Table 1, Magalhães-Bressan et al. 2009, International… 2011). It is worth noting that of the 18 species recorded, populations of only one (*D. novemcinctus*) are increasing (Abba & Superina 2009). From a survey of 24 secondary forest sites (some connected to the western part of the Serra do Mar forest massive) using baited camera-traps (minimum effort of 2160 camera-trap days) and baited sand track-stations (minimum effort of 1224 track-station days) Espartosa et al. (2011) recorded a total of 14 native species of mid to large bodied mammals, with species richness estimates predicting a maximum of 15 native species present in the 10 000 ha study region. We managed to record a similar number of species to Espartosa et al. (2011) using a fraction of their survey effort and time, which emphasizes the richness and diversity of the mid and large bodied mammal community in Núcleo Caraguatatuba compared with unprotected and fragmented Atlantic Forest remnants. Another important difference is that the mammal community within the Núcleo appears to be relatively intact including large bodied species such as *T. terrestris* and *T. pecari*, whereas the species recorded by Espartosa et al. (2011) represented a relatively simplified assemblage of smaller bodied generalists.

As our species richness estimate showed that we missed between 2 and 14 species we also expect further studies to add to the list of threatened species within the Núcleo. For example populations of the threatened buffy-tufted-ear marmoset (*Callithrix aurita*) have been recorded in the neighboring Núcleo Santa Virginia (Norris et al. 2011b) and it seems likely that there may be as yet undetected populations within Núcleo Caraguatatuba. We would also expect to find carnivores such as jaguar (*Panthera onca*) and the crab-eating fox (*Cerdocyon thous*) plus at least one additional cervid species - the small brocket deer (*Mazama bororo*). Indeed, cervids highlight a remaining problem in neotropical mammalogy - uncertainty in species identification and classification (Brito et al. 2009). We identified the cervid species (*M.* cf. *americana*) based on characteristic size and coloration, however similarities with *M. bororo* mean that genetic studies are necessary to confirm the species presence. The same is true for the rodent *D. azarae*, which may be confused with *D. leporina*. Although the characteristic "red-rump" of *D. leporina* was not apparent in the photo taken, further genetic studies are required to confirm the species identity within the Núcleo. Although predicting which species are likely to be detected is inherently speculative, these issues highlight that even though the Atlantic Forest is the most intensively studied biome for mammals in Brazil (Brito et al. 2009), the knowledge necessary for effective conservation and management of Atlantic Forest mammals is far from complete.

Our revised Mammal Priority Index ranked Núcleo Caraguatatuba as being of medium overall importance for the conservation of mid and large bodied mammals in the Atlantic Forest. Combined with the number and diversity of species recorded we believe this group of mammals must be considered a management priority within this protected area. Our species list provides a baseline upon which management activities can be measured and evaluated. However, future studies focusing on species ecology, habitat preferences and population densities are required to inform management activities. For example further studies are required to enable the definition of zones within the protected area as defined by Brazilian Law (Law: 9.985/2000 (SNUC)). Zonation will enable the myriad objectives of a protected area to be met efficiently and in harmony with the regional and national socio-economic context (Wells & Brandon 1993, Halpin 1997). Although species richness and diversity is a criteria for establishing the conservation value of zones within the park (Instituto Florestal 2008, p. 257), there is as yet no data to define a spatially explicit map of species distributions for any floral or faunal group within Núcleo Caraguatatuba. We hope the list of mammals presented here encourages future studies to fill such g aps.

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Capítulo 2

Anthropogenic and landscape determinants of mammal distribution in continuous Atlantic Forest remnants.

Darren Norris[1, 2]*, José Moreira-Ramírez[1,2], Silvio F. B. Ferraz[3], Carlos Zacchi[4], Paulo L. Camarero[5] and Mauro Galetti[2]

[1] Universidade Estadual Paulista (UNESP), Instituto de Biociências, Departamento de Zoologia. Caixa Postal 199, 13506-900. Rio Claro, São Paulo (SP), Brazil.

[2] Universidade Estadual Paulista (UNESP), Instituto de Biociências, Departamento de Ecologia. Caixa Postal 199, 13506-900. Rio Claro, São Paulo (SP), Brazil.

[3] Departamento de Ciências Florestais - Escola Superior de Agricultura “Luiz de Queiroz”, ESALQ, Av. Pádua Dias, 11, Piracicaba, São Paulo (SP), Brazil.

[4] PESM – Núcleo Caraguatatuba, Rua do Horto, 1200, Caraguatatuba, 11750-730 SP, Brazil.

[5] Parque Estadual Intervales, Estrada Municipal Km-25, Ribeirao Grande, São Paulo (SP), Brazil.

* Corresponding author. E-mail: dnorris75@gmail.com

ABSTRACT

Landscape attributes and anthropogenic impacts are major determinants of Neotropical mammal abundances, yet we still do not know how these factors influence the distribution of mid to large-bodied mammals in the few remaining continuous Atlantic Forest remnants. We tested hypothesis that elevation, habitat quality and vulnerability to anthropogenic impacts influenced mid- and large-bodied mammals in the largest remaining Atlantic Forest corridor. Line transect surveys were used to record direct and indirect observations of mid- and large-bodied mammal species in two protected areas, one highly vulnerable (Caraguatatuba) and the other less vulnerable (Intervales) to anthropogenic impacts. Multivariate analysis of associations between community composition and landscape attributes were conducted using non-metric multidimensional scaling (nMDS), cluster and indicator group analysis. The influence of landscape and anthropogenic variables on community and functional composition was examined using generalized additive models (GAMs). GAMs were also used to model the influence of landscape and anthropogenic variables on the relative abundance of the six most frequently recorded species (*Pecari tajacu, Puma concolor, Panthera onca, Tapirus terrestris, Alouatta guariba,* and *Sapajus nigritus*). We obtained 406 detections of 19 mid- and large-bodied mammal species. Our results showed clear but variable trends in community and species responses to landscape and anthropogenic gradients. Altitude was the most important explanatory variable independent of the measure of community composition. However predictions from habitat quality and vulnerability hypothesis were only weakly supported by the distribution of mid and large-bodied mammal communities. The distribution of individual species was also highly variable with predictions from all 3 hypotheses (elevation, habitat quality and vulnerability) being strongly supported by at least one of the species. Our results highlight the importance of considering the differential distribution of mid- to large-bodied mammals for the effective management of the remaining areas protecting the largest expanses of Atlantic Forest.

Key-words: altitudinal gradient; diversity; distribution; protected area; vulnerability

INTRODUCTION

Latitude and altitudinal gradients are recognized as determinants of biogeographically important areas of Neotropical vertebrate endemism (da Silva *et al.* 2004, Loyola *et al.* 2009, Silva *et al.* 2012). These coarse scale analyses are important for continental scale assessments yet may not be informative for regional or local scale conservation activities. For example, more detailed investigations have shown that abundances of mid- to large-bodied mammals differ by orders of magnitude between large (> 10 000 ha) areas of Atlantic Forest within the same biogeographic regions (Galetti *et al.* 2009). This presents a challenging paradigm for conservationists – how to conserve widely distributed yet locally rare species in anthropogenically dominated biodiversity hotspots.

In a human-dominated world, anthropogenic influences, particularly the introduction of exotic species, hunting and habitat fragmentation continue to drastically alter the distribution of species (Pereira *et al.* 2010, Rands *et al.* 2010, Estes *et al.* 2011). This is particularly relevant in species-rich ecosystems, where a myriad diversity of species have been affected by and are likely to suffer from as yet unquantified losses resulting from anthropogenic perturbations (Kuussaari *et al.* 2009, Pereira *et al.* 2010, Estes *et al.* 2011). Faced with such challenges protected areas are a rare success for global biodiversity conservation (Stokstad 2010), however the effective protection of biodiversity hotspots located within rapidly developing nations remains highly contentious (Pereira *et al.* 2010, Rands *et al.* 2010).

The Brazilian Atlantic forest encapsulates 21st century challenges to biodiversity conservation. In a time of global economic recession the Brazilian economy has continued to grow and at the same time conservation initiatives in the Brazilian Atlantic Forest have been often cited as examples of the effective integration of legal protection, protected area management, and science-based conservation planning (Galindo-Leal & Câmara 2003, Tabarelli *et al.* 2010). Although deforestation rates are generally declining across Brazil, the Atlantic Forest still loses approximately 133km^2 annually (Fundação SOS Mata Atlântica & INPE 2012). This is a substantial amount considering i) that only ≈ 12% of the original Atlantic Forest remains and many remnants retain only early sucessional forest stages (Ribeiro *et al.* 2009, Tabarelli *et al.* 2010) and ii) the threats posed by legislative changes in Brazil (Michalski *et al.* 2010). Within this context the effective management of the few remaining large (>10 000 ha) Atlantic Forest areas is particularly important not only for conservation within this biodiversity hotspot but also for future restoration activities (Laurance 2009, Metzger 2009).

The Serra do Mar biogeographic region retains the largest remaining Atlantic Forest remnant (Ribeiro *et al.* 2009). The size of the protected areas within this region (typically > 10 000 ha) and their proximity to areas of human development (e.g. urban areas and agricultural monocultures) generates substantial management challenges (Instituto Florestal 2008, 2009). Zonation has been proposed as one solution for effective biodiversity conservation within the regional socio-economic context (Wells & Brandon 1993). However, effective zonation requires a spatially explicit understanding of the distribution of "features" (species and or habitats) of conservation value.

Understanding the spatial determinants of species diversity and distribution is vital for effective conservation management in rapidly changing environments. Due to their importance for both conservation activities and ecosystem functioning mid- to large bodied mammals are often used as a focal group for biodiversity management activities. For example within the Atlantic Forest this group has been used for broad scale biogeographic analysis (Silva *et al.* 2012) to regional and local scale studies that highlighted the conservation implications and ecological impacts of forest fragmentation and hunting across the Atlantic Forest biome (Chiarello 1999, Cullen *et al.* 2000, Galetti *et al.* 2009). Due to the drastic consequences of anthropogenic changes, most attention has been given to the spatial distribution of species in fragmented Atlantic Forest landscapes (Chiarello 1999, Cullen *et al.* 2000, Espartosa *et al.* 2011), but there is increasing evidence that anthropogenic impacts can also permeate throughout continuous forest areas. However we still do not know the spatial determinants (e.g. relative importance of landscape attributes and anthropogenic influences) on the distribution of mid- to large bodied mammals in the few remaining continuous Atlantic Forest areas.

Our objective was to test predictions that topographic, floristic and vulnerability gradients would influence the community of mid- to large-bodied mammals within protected areas of the Serra do Mar biogeographic region. To test these predictions we examined the effects of altitude, floristic composition and vulnerability to anthropogenic perturbations on mid- to large-bodied mammal species in two continuous protected Atlantic Forest remnants. We hypothesize that community diversity and richness will increase with altitude as a result of anthropogenic disturbances at lower altitudes (Tabarelli *et al.* 2010). We also expect to find differences in community composition between different floristic types. Based on intense human interventions we also hypothesize that increasing vulnerability will simplify mammal communities both within and between the protected areas (Wilson *et al.* 2005, Suzart de Albuquerque *et al.* 2011).

MATERIAL AND METHODS

Study sites

Surveys of mid- to large bodied mammals took place in two protected Atlantic Forest areas in the State of São Paulo, Brazil: Núcleo Caraguatatuba, of the Serra do Mar State Park (hereafter Caraguatatuba) and Intervales State park (hereafter Intervales). These two areas were preselected due to differences in their "vulnerability" (Table 1). The protected areas are within the same biogeographical range (da Silva *et al.* 2004, Silva *et al.* 2012), and have similar climatic ("Cfa" warm temperate, fully humid with a hot summer based on the revised Koppen classification (Rubel & Kottek 2010)), and physiognomic conditions (Instituto Florestal 2008, 2009), and we therefore assume the mammal communities were originally composed of similar species. We expect Caraguatatuba to be more vulnerable to the loss of mammals than Intervales due to elevated exposure to and intensity of anthropogenic interventions (Table 1). Caraguatatuba is bisected by a major state highway that leads to the town of Caraguatatuba (45° 25' 57" W and 23° 35' 52" S) a populous (> 100,000 inhabitants) urban center bordering the park. The western portion of the protected area is also traversed by a >40 km access road for one of the main pipelines of the Brazilian petroleum company "Petrobras". The highway and the pipeline facilitate access to "remote" regions of the park and are the two principal vectors of anthropogenic pressure (i.e. illegal hunting and palm-heart harvesting - Instituto Florestal 2008, p. 119-143).

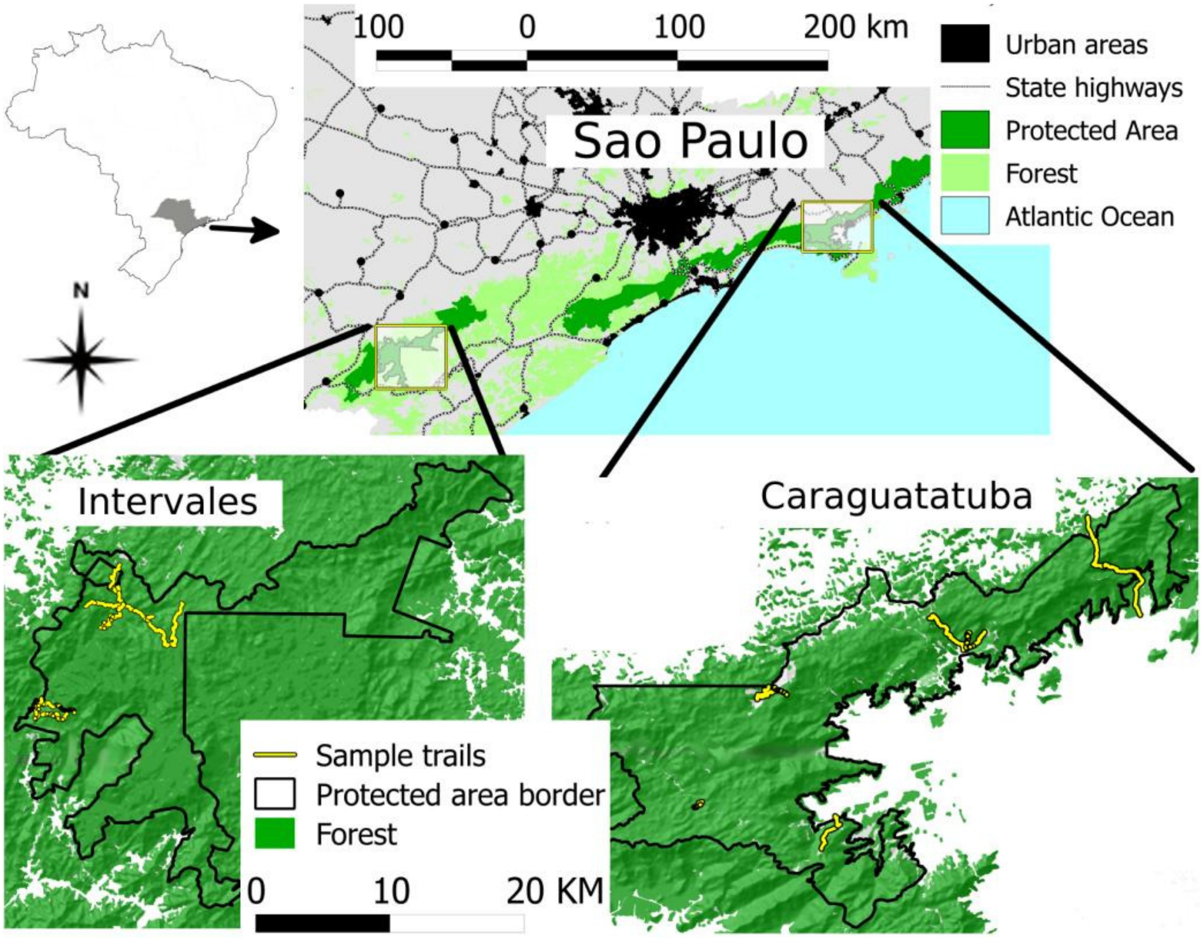

Figure 1 Locations of mid- and large bodied mammal surveys two continuous Atlantic Forest remnants. Surveys took place in two study areas with different vulnerability to human impacts within protected area networks of the Serra do Mar biogeographic region, São Paulo State, Brazil. Relief maps show the distribution of transects within Intervales (less vulnerable) and Caraguatatuba (highly vulnerable). Forest areas include primary and secondary sucessional stages.

Data collection

Between April and November 2011 we used diurnal line transect census to survey the mid- to large-bodied mammal fauna in the protected areas. Surveys were conducted by two observers with a minimum of 5 years experience in monitoring Neotropical mammals. We recorded all direct (visual and vocal encounters) and indirect (feces, tracks, carcasses) detections encountered during the surveys. Nomenclature follows that presented in (Paglia *et al.* 2012). Standard line transect protocols (Peres 1999, Buckland *et al.* 2010) were adapted to fit our main objective of sampling mid- and large-bodied mammals across the widest possible variety of habitats within the parks (Norris *et al.* 2012). To provide a representative sample, we walked preexisting trails that were distributed throughout the areas (Figure 1) and that encompassed the full altitudinal range (20 – 874 and 219 – 992 m a.s.l, Caraguatatuba and Intervales respectively) and a variety of secondary and primary forest habitats.

Landscape and anthropogenic attributes

We used a combination of landscape and anthropogenic attributes to model patterns of community and species abundance. Based on published descriptions of predictors of mid- and large-bodied mammal species distributions in the Atlantic Forest (Galetti *et al.* 2009, Norris *et al.* 2011a, Norris *et al.* 2011b, Suzart de Albuquerque *et al.* 2011) we selected different variables to model community and species patterns. We used 4 variables to understand patterns in community composition across the 2.4 km transect sections: mean altitude, maximum distance to park border, proportion of mature forest (primary and advanced secondary stages), and altitudinal forest class. Altitudinal forest class was included as a 3 level factor based on altitudinal limits that take into consideration differences in soil and vegetation types (Oliveira-Filho & Fontes 2000).

Species abundances were modeled using the same continuous variables but “location” a two level factor (Intervales and Caraguatatuba) replaced altitudinal forest class as we expected that differences in vulnerability to human intervention between protected areas should influence species responses.

Table 1 Characteristics of the 2 protected areas included in the present study

	Caraguatatuba	Intervales
Protected area formed	[a, b]1977	[c] 1995
Size (size of total connected protected area)	[b] 49,953 ha (≈315,390 ha)	[c] 41,704 ha (≈120,000 ha)
[d] Human density (mean/range)	80.4 (7.9–211.8)	19.9 (3.7–43.8)
Number of park guards 2011	12	[c] 14
[e] Exposed perimeter (km)	160.2	191.7
[f] Proximity to urban area (km)	6.7 (3.6)	22.4 (3.4)
[f] Proximity to road (km)	6.3 (3.3)	17.4 (6.0)
[f] Altitude (m a.s.l)	608.6 (280.5)	602.0 (233.4)

[a] Includes ≈ 14 000 ha that has been legally protected since 1956

[b] (Instituto Florestal 2008) pp. xvii, 11-15, and “anexo 1”

[c] (Instituto Florestal 2009) pp. 5 - 15

[d] Human population density (ind. per km^2) within administrative regions (municipalities) surrounding the protected areas. Values relate to 2011 and were collated by the Brazilian Institute for Geography and Statistics (“Instituto Brasileiro de Geografia e Estatística” - IBGE), available at http://www.ibge.gov.br/home/download/estatistica.shtm

[e] Length of park perimeter (km) that does not border another protected area derived from GIS analysis

[f] Values (mean and standard deviations in parenthesis) within the protected areas derived from GIS analysis

Data analysis

All analysis were conducted using R (R Development Core Team 2011) and functions from associated packages (“ggplot2” (Wickham 2009), “FD” (Laliberté & Shipley 2011), "indicspecies" (De Caceres & Legendre 2009), and “vegan” (Oksanen *et al.* 2012)). Differences in survey effort resulting from logistical constraints (e.g. differences in the number and length of transects) resulted in differences in the cumulative effort between transects and areas which could potentially bias analysis. It is likely that differences in the number of visits per transect (mean±SD = 6±3.7), also influenced the number of species detected, however there was no significant association between the number of visits and species richness (Spearman correlation, rho = 0.370, $P = 0.070$). As such we assume that differences in survey visit numbers are not biasing our sample of patterns of species richness or community composition.

To obtain representative relative abundances from a standardized survey effort for the comparison of communities within and between parks we applied a resampling approach to a subset of the surveyed transects. The subset of transects comprised only those which had been visited at least once per trimester (i.e. a minimum of three times). We used the shortest transect length walked to divide all transects into sections of equal length (2.4 km). We generated a data matrix of species relative abundances (i.e. counts of detections per species (Pearce & Ferrier 2001)) per visit for each 2.4 km section and then used a resampling approach to derive values from a standardized effort. Standardized (resampled) values were generated for each section from a bootstrapped sample of 5000 visits. Species abundances were then summed for five randomly selected visits, providing abundances per 12 km walked (5 x 2.4 km). This was repeated 1000 times and we then calculated the mean value (i.e. mean number of detections per 12 km for each species) from the sample generated by 1000 iterations for each section.

Multivariate Community composition

Multivariate analysis of associations between community composition and environmental attributes were conducted using non-metric multidimensional scaling (nMDS), cluster analysis and indicator group analysis (Borcard *et al.* 2011). To represent community association patterns a Bray–Curtis dissimilarity matrix was derived from species abundances. Ordination (nMDS) was used to understand the relationships between community association (dissimilarity distances) patterns and environmental variables using ANOSIM (Clarke 1993) and BIOENV (Clarke & Ainsworth 1993) procedures. Mantel correlations and correlograms were used to examine spatial correlations in the multivariate association patterns (Borcard *et al.* 2011) pp. 234. Cluster and indicator group analysis were used to identify community types and indicator species across the survey areas and in relation to altitudinal gradients (De Caceres & Legendre 2009, Borcard *et al.* 2011).

Univariate metrics of community composition

We selected 4 weakly correlated (supplemental material S1) univariate measures of community composition and functioning. Species richness and Shannon diversity (H) were used to represent community composition. Functioning of the mid- to large-bodied mammal communities was represented by functional richness (Villéger *et al.* 2008) and functional dispersion (Laliberté & Legendre 2010). To derive the functional indices we selected 11 traits (Jones *et al.* 2009) to represent species resource use, environmental niche and sensitivity to anthropogenic impacts (supplemental material S2). Morans I was used to examine spatial correlations in these univariate responses.

Modeling univariate metrics of community composition and species distribution

We used Generalized additive models (GAMs) to examine the influence of environmental predictors on the responses of 4 univariate measures of community composition and the relative abundance of the six most frequently recorded species (*Pecari tajacu, Puma concolor, Panthera onca, Tapirus terrestris, Alouatta guariba, Sapajus nigritus*). With the ability to model non-linear relationships GAMs have been shown to be useful for modeling spatial distribution patterns of various faunal and floral groups (Barry & Welsh 2002, Venables & Dichmont 2004, Meynard & Quinn 2007). Different approaches were used to model community and species responses with GAM models using the package "mgcv" (Wood 2010) with package defaults unless otherwise specified.

To compare the relative influence of spatial and environmental gradients all 4 univariate community responses were modeled (family = Gaussian, link=identity) with and without controlling for first order spatial correlation (i.e. by regressing against x, y coordinates and using residuals as a response). By comparing the results from both models for each response this approach enables us to determine the significance of the GAM models and examine how spatial correlations influence this significance.

The relative influence of spatial and environmental gradients on species relative abundance (counts per 12 km from the standardized effort) was modeled (family = negative binomial, link=log) including the geographic location as a covariate in the GAMs. This approach accounts for trends in the data across geographical distances enabling us to model the shape of species responses taking into consideration the spatial relationship between samples.

GAM model evaluation

We adopted a two stage approach to identify the relative importance of the environmental variables in the GAMs. Firstly the inclusion of smooth variables in the GAM model was determined via null space penalization (using gam option “select = TRUE”). The appropriateness of these models was evaluated by examination of residuals (function “gam.check”) and the percent deviance explained was used as an indicator of model performance (i.e. how well the model fitted the data). Spatial autocorrelation was investigated for all models by examining residuals from final GAMs with Moran’s I correlograms. We then evaluated variable importance based on their information content, as measured by AICc –Akaike’s Information Criterion corrected for small sample sizes. This was done via a model averaging approach implemented in the R package “MuMIn” (Barton 2011) following (Michalski *et al.* 2011). This approach evaluates the relative importance of variables as measured by the variables’ Akaike weights (Burnham & Anderson 2002) pp. 75-77, 167-172), which is a scaled measure of the likelihood ratio that ranges between 0 (least important) and 1 (most important).

RESULTS

Mammal Communities

We obtained 406 detections of 19 mammal species (supplemental material Table S4) from a total of 88 survey days (61 days in Caraguatatuba and 27 in Intervales). Tracks (213, 52.5%) and feces (100, 24.6%) were the most frequently recorded types of detection. The total of 406 detections included 53 (13.1%) visual detections of 8 species recorded during our line transects census effort of 610.5 km (351.6 km in Caraguatatuba and 258.9 km in Intervales). Subsequent results refer to analysis of the standardized (resampled) relative abundances from the 2.4 km transect sections (17 sections in Caraguatatuba, 22 sections in Intervales).

Rarefied species richness curves showed that the number of species detected reached an asymptote in both areas (Fig. 2). Caraguatatuba had higher average values for all richness and diversity metrics examined (Fig. 2), however there was no significant difference in species or functional richness and diversity between the two areas (Wilcoxon, $P > 0.18$ for all four metrics). There was also no significant difference in the community composition dissimilarities between Caraguatatuba and Intervales (ANOSIM $R = 0.302$, $P = 0.587$).

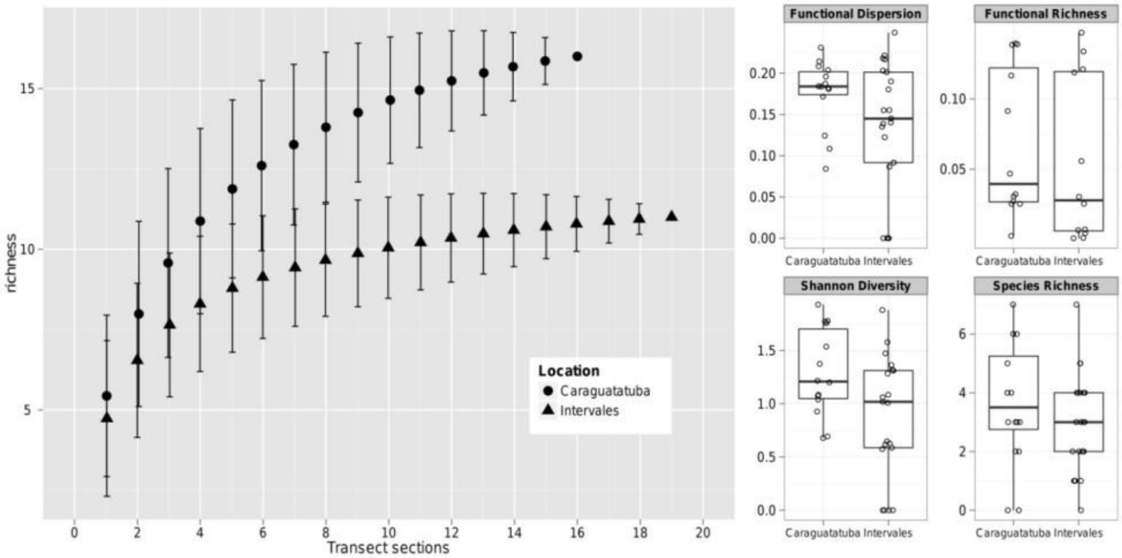

Figure 2 Species richness and diversity of non-volant mammals in two continuous Atlantic Forest remnants. Mean rarified species accumulation curves with 95% confidence intervals (vertical lines) of mid and large bodied mammal species recorded along 2.4km transect sections in highly vulnerable (Caraguatatuba) and less vulnerable (Intervales) protected areas of the Serra do Mar biogeographic region, Brazil. Boxplots compare richness and diversity metrics between the two areas.

Analysis of Ward clusters supported the ANOSIM results. Results examining cluster fusion levels and silhouettes suggested that three groups could be separated that were an ecologically meaningful compromise between too many and too few groups (supplemental material S3). One of these three groups included seven transect sections from Caraguatatuba and the other two groups comprised a mix of sections from both Caraguatatuba and Intervales (Fig 3). The nMDS ordination (stress = 0.177) of Bray-Curtis dissimilarities again showed no clear separation of mammal communities between Caraguatatuba and Intervales (Fig 3b). Examination of the species association patterns across these three groups showed that *P. tajacu* and *S. nigritus* were the most prominent (i.e. indicator) species in mammal communities of group 1, whereas *S. nigritus*, *T. terrestris* and *P. onca* were the most prominent species in communities of groups 2 and 3 (“multipatt” function, $P < 0.05$ for all species).

Multivariate mantel correlation tests between similarity distance matrices showed that mammal communities were correlated with the environmental variables mean altitude, distance to park border and proportion of mature forest (Mantel statistic r: 0.225, P=0.001). BIOENV analysis (Table 2) showed that altitude and the proportion of mature forest were the two environmental variables most significantly correlated with community similarity. However, only altitude was significantly correlated with the detrended community distance matrix (Table 2). Cluster analysis identified 3 interpretable groups from the elevation data. Following (Oliveira-Filho & Fontes 2000) these 3 groups were classified as “lowland” (n=7, median altitude of 209.8 m a.s.l), “sub-montane” (n=12, median altitude of 642.7 m a.s.l) and “lower montane” (n=16, median altitude of 742.1 m a.s.l). Examination of the species association patterns across these three groups showed that *P. tajacu* was the most prominent (i.e. indicator) species in mammal communities of lowland (group 1) transect sections, whereas *P. onca* was the most prominent species in communities of sub-montane (group 2) (“multipatt” function, $P < 0.05$ for both species). Of the species associated with 2 groups, *S. nigritus* was a prominent species in lowland and sub-montane transect sections (groups 1 and 2) and *T. terrestris* in the higher altitude sub and lower montane sections (groups 2 and 3) (“multipatt” function, $P < 0.05$ for both species).

Table 2 Correlations between environmental variables and mammal abundance based on results of BIOENV analysis with up to three environmental variables. Two sets of correlations were run, one ("Mantel") without controlling for first order spatial correlations and the second ("DetMantel") controlling for first order correlations with a detrended species similarity matrix. Bold face denotes the best subset of environmental variables with maximum rank correlation with community similarities from BIOENV analysis.

Number of variables	[a]Variables	Mantel r (*P*)	DetMantel r (*P*)
1	Alt	**0.342 (0.001)**	**0.148 (0.031)**
1	Forest_M	0.132 (0.006)	-0.035 (0.746)
1	Dist_B	-0.111 (0.923)	-0.060 (0.724)
2	Alt, Forest_M	**0.327 (0.001)**	**0.091 (0.087)**
2	Alt, Dist_B	0.327 (0.001)	0.091 (0.087)
2	Forest_M, Dist_B	0.041 (0.243)	-0.070 (0.814)
3	Alt, Forest_M, Dist_B	**0.225 (0.001)**	**0.032 (0.322)**

[a] Alt = mean altitude, Forest_M = proportion (%) of mature forest, Dist_B = maximum distance from protected area border.

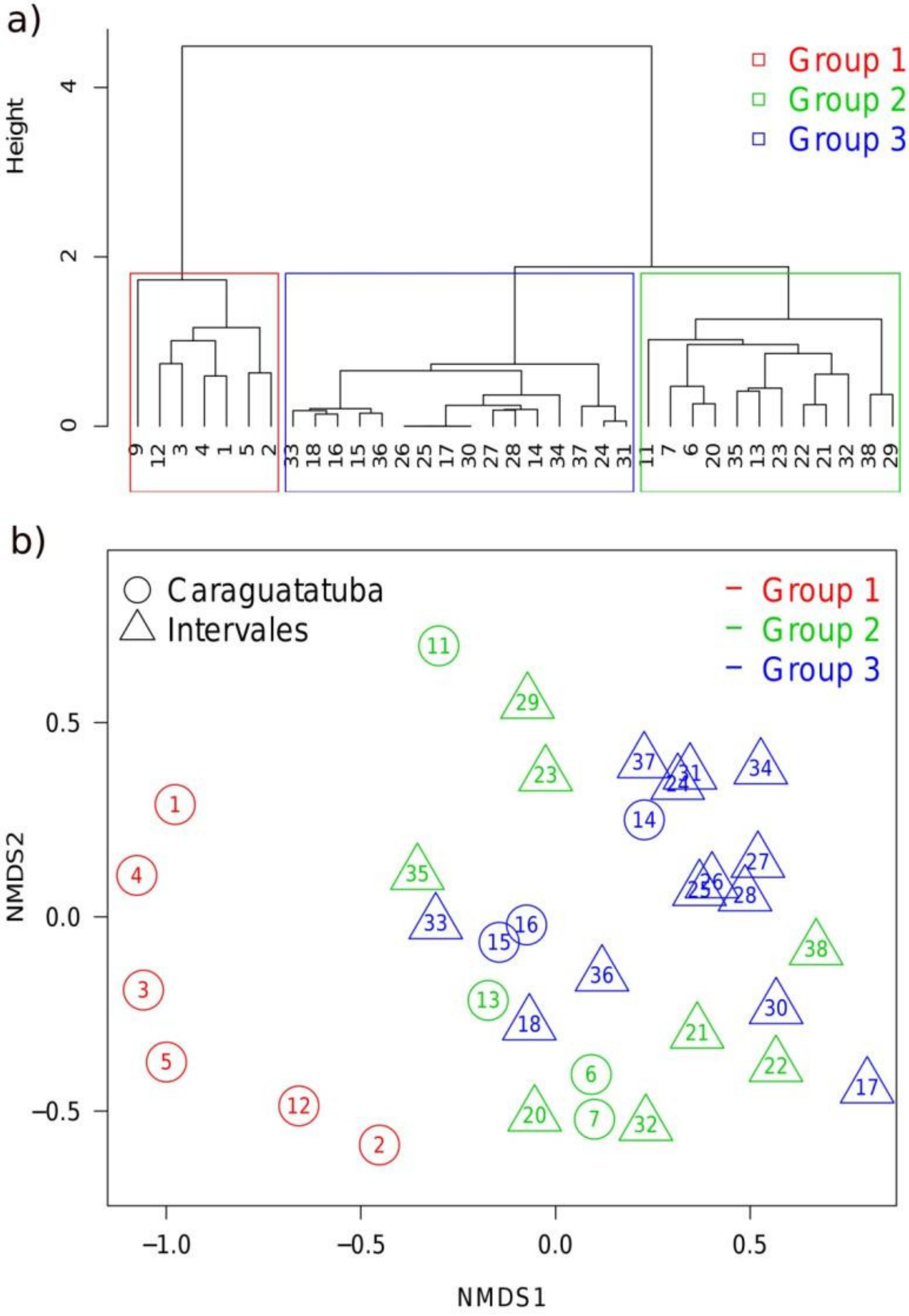

Figure 3 Dendrogram (a) and nMDS ordination (b) of the mid- and large-bodied mammal community in two continuous Atlantic Forest remnants.

Correlograms showed patterns of spatial correlation differed between the multivariate and univariate measures of community composition (Fig 4). The Mantel correlogram showed significant spatial correlation for the distance matrix of species similarities, and Moran's I correlograms showed significant correlation for community Shannon diversity and Functional Dispersion values. However, there was no significant spatial correlation for species richness or Functional Richness (Fig 4). Species similarities were positively correlated and distances < 2km, as were Shannon diversity values (Fig 4). The correlograms also showed significant spatial correlation between distances of 5 and 10 km for both Shannon diversity and Functional dispersion (Fig 4).

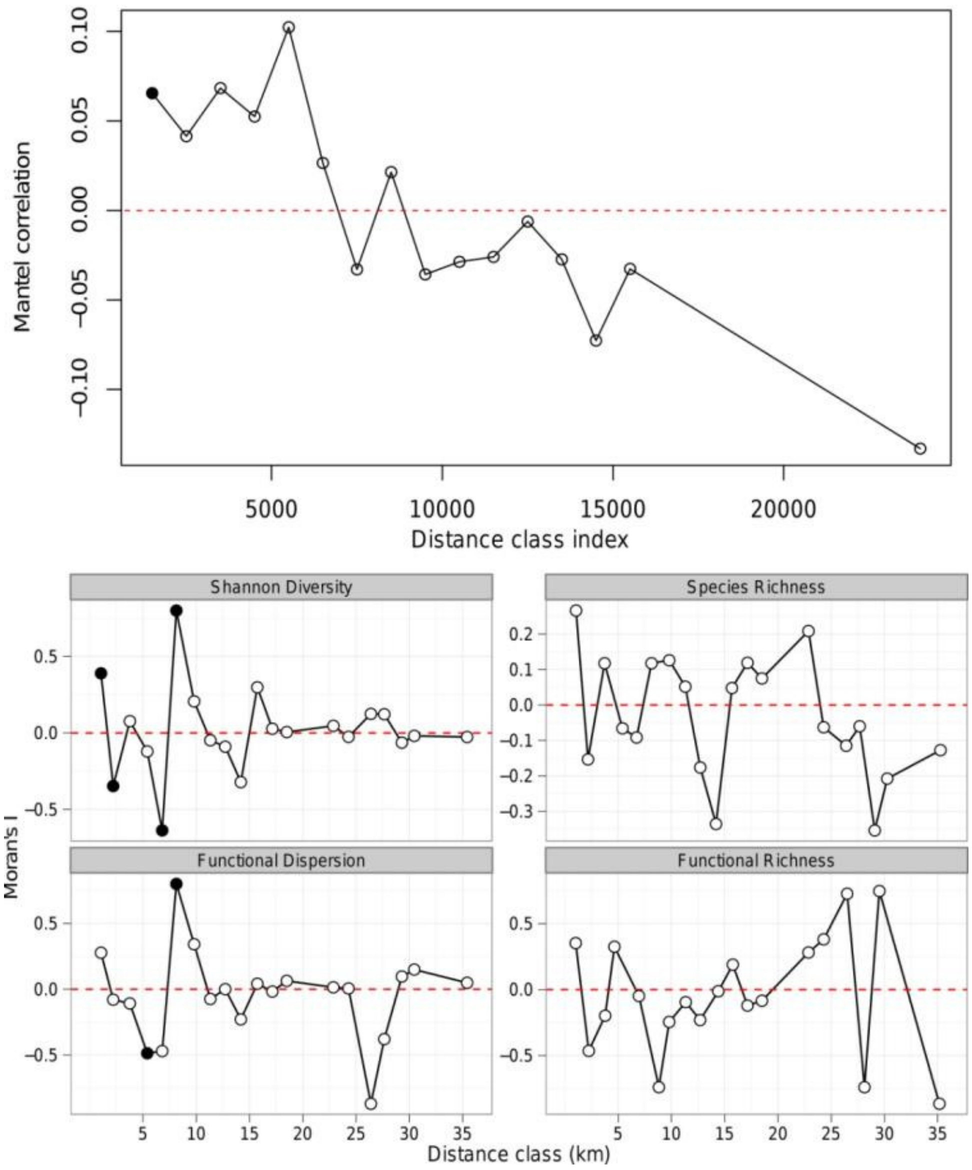

Figure 4 Spatial structures in mid and large bodied mammal communities in continuous remnants of Atlantic Forest. Correlograms show spatial correlation in the detrended multivariate (multi-species distance matrix – Mantel) and univariate (Moran's I) measures of species richness and diversity. Solid black circles indicate distance classes with significant correlations.

Analysis of the 4 univariate measures of community composition showed that all but one (detrended functional dispersion) of our full GAMs explained significant percentages of the deviance (Table 3). The information theoretic analysis (Table 3) showed that the relative importance of the explanatory variables depended on both the responses and their associated spatial correlations. Mean altitude was the most important of the variables with the highest relative weight of evidence in all models ($\sum w_i$ range 0.61 – 0.97). The proportion of mature forest was of intermediate importance ($\sum w_i$ range 0.13 – 0.46) with the remaining variables (distance from park border and altitude class) only weakly supported ($\sum w_i$ range 0.06 – 0.34).

Visual inspection of the GAM predictions showed that detrended responses of species richness followed the predicted inverted "U" shape of the mid-domain hypothesis. However, none of the other 3 responses followed the predicted pattern. Both Shannon diversity and functional diversity showed a non-linear decline above altitudes of 600 m a.s.l and functional richness declined linearly with increasing altitude.

Species distribution

Our landscape and anthropogenic variables explained a significant percentage of GAM model deviance for all species (Table 4). The relative importance of all variables differed between species, with all variables weighted > 0.7 for at least one species (Table 4). Altitude was the most important explanatory variable of species relative abundances ($\sum w_i$ range 0.54 – 1.00) and was the variable with the highest weight of evidence for 3 of the 6 species evaluated (*P. concolor*, *P. onca* and *A. guariba,* Table 3*)*. Mature forest was weighted 1.00 for *S. nigritus* and spatial trends weighted 1.00 for *T. terrestris*. Distance from border was weighted 0.89 for *P. tajacu.* With all detections recorded in Intervales (supplemental material Table S4), Location (Caraguatatuba vs

Intervales) was weighted 0.79 for *P. onca*. All other species-variable combinations received weak or intermediate support (Table 4, $\sum w_i$ range 0 – 0.6).

Table 3 Model covariate weights from information-theoretic analysis of mid and large bodied mammal communities in continuous Atlantic Forest remnants. Generalized additive models were used to examine the influence of 3 non-parametric smoothed variables and one parametric factor on the responses of four univariate measures of community composition. Two models were run for each response, one (^{sm}) without controlling for first order spatial correlations and the second (^{rm}) controlling for first order correlations with detrended responses.

Model factor	Species richness		Shannon Diversity		Functional Dispersion		Functional Richness	
	$^{sm}\sum w_i$ (rank ^{a})	$^{rm}\sum w_i$ (rank ^{a})	$^{sm}\sum w_i$ (rank ^{a})	$^{rm}\sum w_i$ (rank ^{a})	$^{sm}\sum w_i$ (rank ^{a})	$^{rm}\sum w_i$ (rank ^{a})	$^{sm}\sum w_i$ (rank ^{a})	$^{rm}\sum w_i$ (rank ^{a})
^{S} Mean altitude (m a.s.l)	0.97* (1)	$0.63^{\ddagger}$ (1)	0.87* (1)	0.61* (1)	0.81 (1)	0.67 (1)	0.89** (1)	0.78* (1)
^{S} Distance from border	0.06 (4)	0.17 (3)	0.07 (4)	0.11 (3)	0.02 (4)	0.14 (4)	0.34* (3)	0.34* (3)
^{S} Mature forest %	0.23 (2)	0.22 (2)	0.41 (2)	0.13 (2)	0.30 (2)	0.20 (3)	0.36* (2)	0.46* (2)
Altitude class (compared to lowland)	0.11 (3)	0.10 (4)	0.19 (3)	0.10 (4)	0.25 (3)	0.27 (2)	0.07* (4)	0.07 (4)
Full model deviance explained (%)	64.9***	67.6***	53.4***	75.0***	39.6*	27.3	78.2***	65.3***
^{c} Residual correlation	No	No	Yes	No	Yes	No	No	No

Model/Variable significance: *** < 0.001, ** < 0.01, * < 0.05, ‡ < 0.1

[a] Variable ranked importance based on the sum of Akaike weights ($\sum w_i$) for all models within our set of candidate models with a given variable. Model averaging was carried out using the full set of confidence models i.e. when a variable was not present in the model its value was set to 0 (Burnham and Anderson 2002, pp. 152).

[c] Significant spatial autocorrelation in residuals from final GAMs (from Moran's I correlograms)

[S] non-parametric smoothed term

Table 4 Model covariate weights from information-theoretic analysis of mid and large bodied mammal species in continuous Atlantic Forest remnants. Generalized additive models were used to examine the influence of 4 non-parametric smoothed variables and one parametric factor on the relative abundance of six mid- and large-bodied mammal species.

	Species	c Residual correlation	Full model deviance explained (%)	^{S} Mean altitude (m a.s.l) $\sum w_i$ (rank ^{a})	^{S} Distance from border $\sum w_i$ (rank ^{a})	^{S} Mature forest % $\sum wi$ (rank ^{a})	^{si} Spatial $\sum w_i$ (rank ^{a})	Location $\sum w_i$ (rank^{a})
Artiodactyla	*Pecari tajacu*	No	59.3***	0.88* (2)	0.89* (1)	0.07 (5)	0.46 (3)	0.18 (4)
Carnivora	*Puma concolor*	No	39.2**	1.00* (1)	0.00 (5)	0.00 (5)	0.00 (5)	0.33 (2)
	Panthera onca	No	51.7***	0.90* (1)	0.00 (5)	0.24 (3)	0.00 (5)	0.79 (2)*
Perissodactyla	*Tapirus terrestris*	No	84.2***	0.54** (2)	0.00 (5)	0.00 (5)	1.00* (1)	0.12 (3)
Primate	*Alouatta guariba*	No	31.6*	0.98* (1)	0.60 (2)	0.00 (5)	0.51 (3)	0.16 (4)
	Sapajus nigritus	No	25.7*	0.68 Ɨ (2)	0.00 (5)	1.00* (1)	0.00 (5)	0.20 (3)
^{b} Overall variable importance				0.89 (1)	0.00 (5)	0.04 (4)	0.23 (2)	0.19 (3)

Model/Variable significance: *** < 0.001, ** < 0.01, * < 0.05, Ɨ < 0.1

[a] Variable ranked importance based on the sum of Akaike weights ($\sum w_i$) for all models within our set of candidate models with a given variable. Model averaging was carried out using the full set of confidence models i.e. when a variable was not present in the model its value was set to 0 (Burnham and Anderson 2002, pp. 152).

[b] median of variable sum of Akaike weights ($\sum w_i$) across all species.

[c] Significant spatial autocorrelation in residuals from final GAMs (based on Moran's I correlograms)

[S] non-parametric smoothed term

[si] non-parametric smoothed interaction term of transect section coordinates (easting and northing of section center point)

Visual inspection of the GAM predictions showed that only *P. tajacu* followed predictions of the mid-domain effect (lower abundances at low and high altitudes). Relative abundances of *T. terrestris* increased non-linearly with altitude. Both *S. nigritus* and *A. guariba* showed a linear decline with increasing altitude. Abundances of both *P. onca* and *P. concolor* tended to increase at lower altitudes but remained constant after 400 m a.s.l.

DISCUSSION

The purpose of this study was to evaluate if a group of mid- to large-bodied mammals responded to landscape and anthropogenic gradients in continuous Atlantic Forest remnants and whether these responses fit predictions from hypothesis relating to the diversity and distribution of this group. Our data indicate clear but variable trends in community and species responses to landscape and anthropogenic gradients. The results presented help to fill the gap between previous broad scale evaluations (Galetti *et al.* 2009, Suzart de Albuquerque *et al.* 2011) and studies focusing on regional / local scale species responses (de Oliveira *et al.* 2008, De Angelo *et al.* 2011, Norris *et al.* 2011a, Norris *et al.* 2011b); thereby providing a first step towards a more detailed understanding of the local scale distribution of mid- to large bodied mammals and the development of effective management strategies for the remaining areas protecting the largest expanses of Brazilian Atlantic Forest.

Community responses

Our results present the first empirical demonstration of the relative influence of landscape and anthropogenic variables on the distribution of mid- and large-bodied mammal communities in continuous Atlantic Forest remnants. Previous studies have shown how landscape and anthropogenic attributes influence mammal communities throughout the Brazilian Atlantic Forest (Galetti *et al.* 2009, Suzart de Albuquerque *et al.* 2011). Our results showed that variation in mammal communities was influenced by these attributes and spatial correlations. However altitude was the most important explanatory variable independent of the measure of community composition or spatial correlation.

Our findings agree with previous studies that have shown the importance of altitudinal gradients on patterns of Neotropical mammal richness and diversity from biogeographic (Costa *et al.* 2000, Quijano-Abril *et al.* 2006, Loyola *et al.* 2009, Silva *et al.* 2012) to local scales (Geise *et al.* 2004, Caceres *et al.* 2011). Our multivariate and univariate analysis showed that the influence of altitude differed depending on the measure of community composition. Our measures of species and functional richness and diversity capture distinct aspects of the studied communities (Villeger *et al.* 2008, De Caceres & Legendre 2009, Laliberte & Legendre 2010) and the different patterns of responses suggests that there is no "optimum" altitude and that different aspects of mammal community composition are maintained across the altitudinal range studied.

Only one of the community responses (species richness) followed predictions from the mid-domain hypothesis. Values of the other three metrics (Shannon Diversity, Functional Richness and Functional Dispersion) did not increase and all declined after 600 m a.s.l. The majority of Atlantic Forest < 800 m has been drastically affected by anthropogenic impacts (Tabarelli *et al.* 2010) that have reduced the Atlantic Forest to 12% of its original extent (Ribeiro *et al.* 2009). We would therefore expect a reduction in functional diversity (functional richness and dispersion) at lower altitudes which typically experience higher levels of anthropogenic pressure such as urbanization, agriculture, logging, hunting and palm heart harvesting (Galetti & Fernandez 1998, Tabarelli *et al.* 2005, Galetti *et al.* 2009, Teixeira *et al.* 2009, Tabarelli *et al.* 2010). Why then was this expected pattern not found?

Our indicator species analysis suggests an explanation for the unexpected reduction in functional diversity at higher altitudes. Across our study sites lower altitudes were characterized by relatively smaller bodied species that have been shown to persist in habitats influenced by anthropogenic activities such as the predominantly arboreal *S. nigritus* and *A. guariba* (de Araujo *et al.* 2008, de Oliveira *et al.* 2008, Arroyo-Rodriguez & Dias 2010). However some large bodied species such as *T. terrestris* were also recorded at low altitudes (albeit at lower abundances). We believe that it was these low altitude areas retaining a mix (i.e. more functionally diverse communities) of small and large sized species that influenced the patterns of functional diversity, with higher altitudes retaining communities of larger bodied species such as *P. onca*, *P. concolor*, and *T. terrestris* but either lacking or with a reduced number of the smaller bodied generalists/arboreal species. The reduction in functional diversity may therefore be due to a type of convergence in species traits at higher altitudes. However before any firm conclusions can be made regarding how the community of mid and large bodied mammals respond to altitude further studies are required that incorporate the full altitudinal range (from sea level to ≈ 2000 m a.s.l) of continuous Atlantic Forest remnants.

None of the other landscape or anthropogenic attributes examined significantly explained variation in the multivariate or univariate measures of community composition. There are numerous possible explanations for this result. However, we believe that the most likely are 2 non-mutually exclusive explanations. Firstly due to > 500 years of human interventions the remaining mid- to large-bodied mammal communities in the study areas are dominated by species that are relatively persistent to anthropogenic impacts and secondly the survey technique adopted did not detect rare and elusive species (Michalski & Peres 2007, Munari *et al.* 2011, Norris *et al.* 2012). Although it is impossible to know how species abundances have changed over 500 years perhaps the most revealing result was the lack of differences between communities in the two study areas, one of which is highly vulnerable to anthropogenic impacts. This lack of difference suggests that the majority of the transect sections may contain species that are relatively resilient to anthropogenic impacts. Although we only detected 19 of the 45 species of mid- to large-bodied mammals known to occur in the State of São Paulo (de Vivo *et al.* 2011), we believe that the variety of species encountered provides a representative sample for comparison of the communities present in the study areas.

(Espartosa *et al.* 2011) conducted studies in Atlantic Forest fragments close to Intervales, the area we consider less vulnerable to anthropogenic impacts. Through intensive track and camera-trap surveys (Espartosa *et al.* 2011) found an impoverished community of small bodied generalist terrestrial mammal species. Within the protected area we detected species ranging from paca (*Cuniculus paca*) to jaguar (*P. onca*), which as shown in previous studies demonstrates the importance of protected areas compared with unprotected forest fragments (Marsden *et al.* 2005, Paviolo *et al.* 2009, Norris *et al.* 2011a). Yet the lack of difference between communities in the two protected areas suggests that the most commonly detected species are a relatively resilient subset and that we may be witnessing the protection of "half-empty" (Harrison 2011, Wilkie *et al.* 2011) remnants of continuous Atlantic Forest in Brazil and/or have yet to witness the collection of "unpaid" extinction debts (Kuussaari *et al.* 2009).

Species responses

Results from our GAMs of the responses of the 6 most commonly encountered species provided additional insight into the relative importance of landscape and anthropogenic attributes. Of the 6 species 4 (*P. tajacu*, *P. concolor*, *P. onca* and *T. terrestris*) remain widely distributed across Neotropical biomes (IUCN 2012) and 2 (*A. guariba* and *S. nigritus*) are found throughout the remaining Brazilian Atlantic Forests (Paglia *et al.* 2012). All 6 species are threatened in the State of São Paulo (Magalhães-Bressan *et al.* 2009) yet they all retain traits that may facilitate their persistence e.g. in the absence of hunting they are able to persist in a variety of habitats and even in close proximity to humans (Sanderson *et al.* 2002, de Araujo *et al.* 2008, Norris *et al.* 2008, Arroyo-Rodriguez & Dias 2010, De Angelo *et al.* 2011).

Populations of *P. onca* were severely impacted by hunting across the Serra do Mar (Leite *et al.* 2002) and it was therefore not surprising that we did not detect this species in Caraguatatuba. However the more resilient *P. concolor* (De Angelo *et al.* 2011) has returned to areas in Caraguatatuba where it was at one time hunted. Both felid species were recorded in the less vulnerable Intervales, highlighting that although vulnerability did not significantly influence community composition the relative isolation of this protected area appears to have contributed to patterns in species occupancy and abundance.

Pecari tajacu was the only species where distance from park border significantly influenced abundances. This species remains a preferred target of hunters around both protected areas (D. Norris, pers. obs) and this result suggests that although continuous remnants are thought to be resilient to edge effects (Ribeiro *et al.* 2009, Tabarelli *et al.* 2010), continued hunting could be generating a significant edge effect. A similar result was also found for the white-lipped peccary (*Tayassu pecari* - (Norris *et al.* 2011a) in a protected area neighboring Caraguatauba. It would therefore appear that species may be able to recover where hunting is reduced e.g. as in the case of *P. concolor* whereas continued hunting could be triggering substantial changes in the distribution of target species which may have (as yet un-quantified) cascading influences on Atlantic Forest floristic structure and biodiversity conservation (Terborgh *et al.* 2008, Wilkie *et al.* 2011).

Conclusions

In no way can the mid to large-bodied mammal community documented in the present study be considered similar to the resplendent historic diversity reported from Brazilian Atlantic Forests (Dean 1997, Câmara 2003). Although some authors consider the Serra do Mar as a region retaining “complete species assemblages” (Galindo-Leal & Câmara 2003) pp. 7) our results show that mid- to large-bodied mammal community composition presents substantial variation in continuous forest remnants within this biogeographic region due to local scale differences in landscape and anthropogenic attributes.

Differences in the composition of mid- to large-bodied mammal communities means that from a management perspective there are multiple “assemblages” that must be considered by management plans if conservation objectives of the protected areas are to be met. For example both the protected areas have been divided into zones defined by linear distances to borders of the protected area (Instituto Florestal 2008, 2009). Our results suggest that at the very minimum a 3 dimensional zonation is required that integrates both topographic variation and spatial gradients such as distance from the border of the protected area for the effective management of mid to large-bodied mammals within the largest Atlantic Forest corridor.

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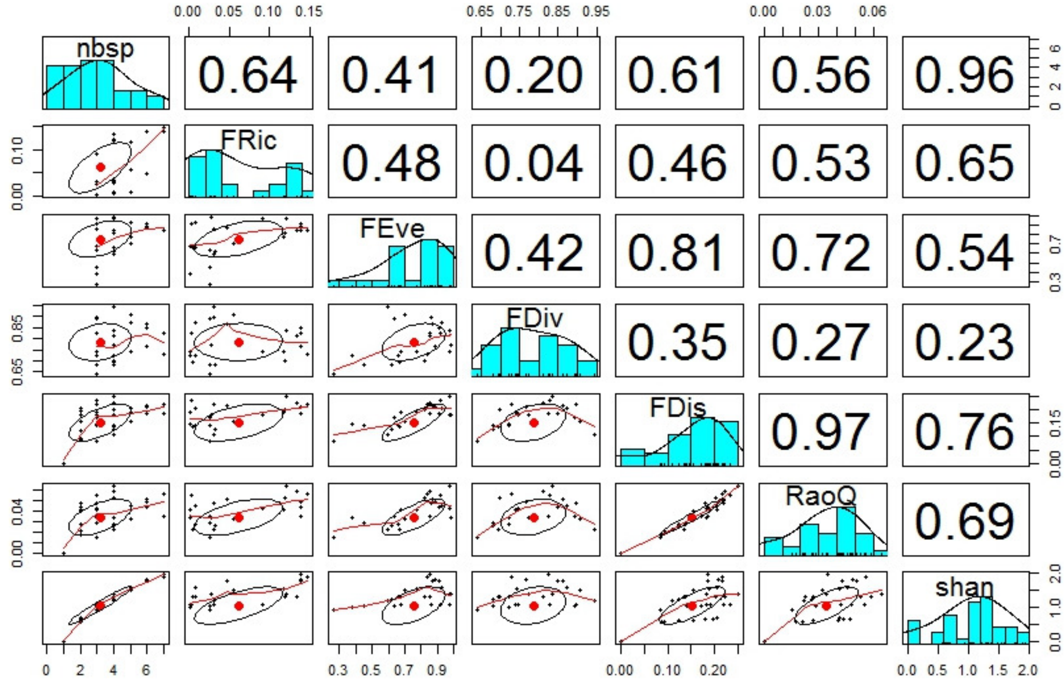
SUPPLEMENTAL MATERIAL

S1 Correlation between species richness and diversity metrics across 38 transect sections

We selected 4 metrics that were weakly correlated and characterized distinct aspects of species richness and functioning (Villéger *et al.* 2008, Laliberté & Legendre 2010).



nbsp = number of species, FRic = Functional Richness, FEve = Functional Evenness, FDiv = Functional Diversity, FDis= Functional Dispersion, RaoQ = and shan = Shannon's diversity index

S2 Species traits

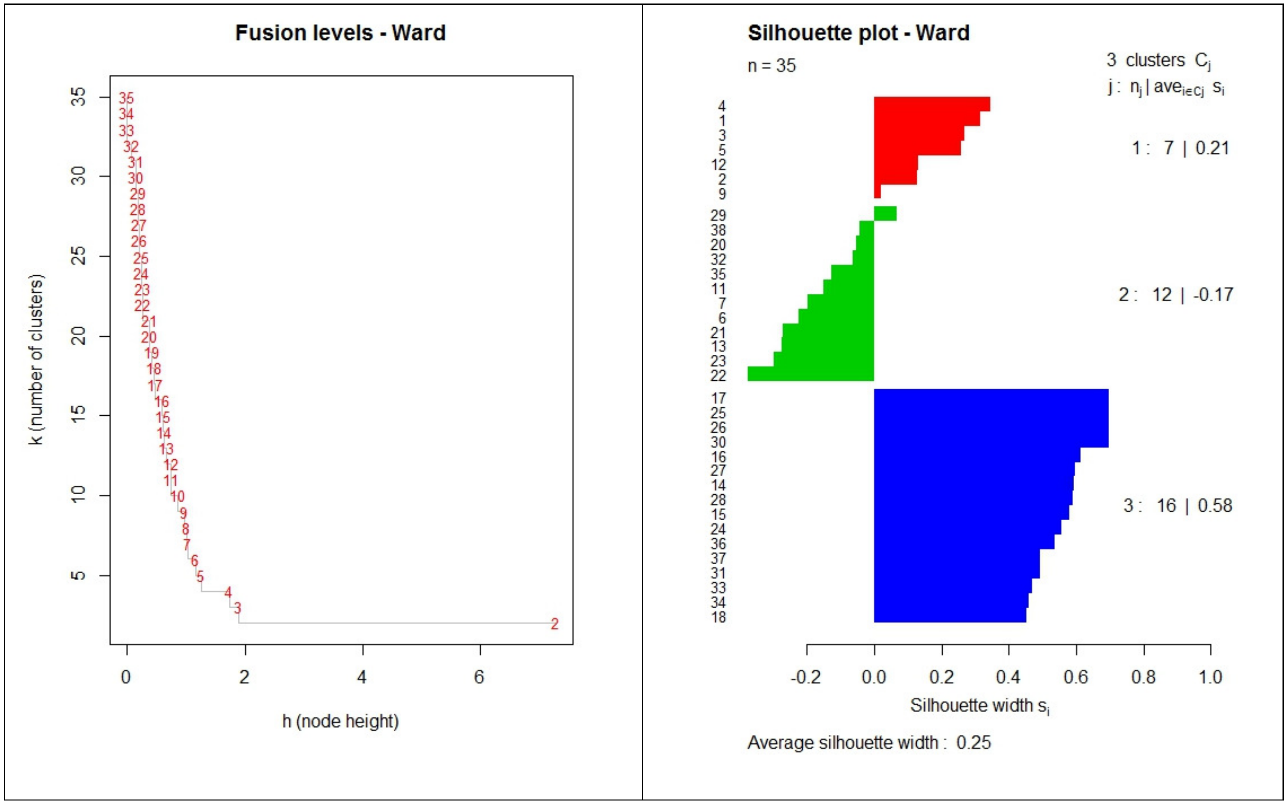
Eleven species traits used to measure non-flying mammal functional diversity (FD). Traits represent different demographic aspects plus resource and habitat use. Traits were selected to represent: 1) ecological niche dimensions of the species, 2) demographics / susceptibility to anthropogenic perturbations and 3) include the most complete and well documented traits for the studied species.

Trait type	[a]Trait	Scale
Resource Quantity / Demographic	1. (5-1) Adult Body Mass (g)	Continuous
Resource Quantity / Demographic	2. (9-1) Gestation (days)	Continuous
Resource Quantity / Demographic	3. (15-1) Litter size	Continuous
Resource Quantity / Demographic	4. (17-1) Longevity (months)	Continuous
Resource Quantity / Demographic	5. (10-2) Social Group Size	Continuous
Diet / Environmental niche	6. (6-1) Diet breath (number of diet categories)	Continuous
Diet / Environmental niche	7. (6-2) Trophic level (herbivore < omnivore < carnivore)	Categorical - ordered
Activity / Environmental niche	8. (1-1) Activity cycle (nocturnal, crepuscular/cathemeral, diurnal)	Categorical
Activity / Environmental niche	9. (12-1) Habitat breath (number of habitat layers)	Continuous
Activity / Environmental niche	10. (12-2) Terrestriality (fossorial/ground dwelling, above ground)	Categorical
Activity / Environmental niche	11. (22-1) Home range area (km^2)	Continuous

[a] text in parenthesis corresponds to the PanTHERIA database (Jones *et al.* 2009) column heading, data available at: http://esapubs.org/archive/ecol/E090/184/default.htm

S3 Partition of clusters

Fusion levels and silhouette plots were used to determine the number of interpretable and ecologically meaningful clusters (Borcard *et al.* 2011). Results for the analysis of species associations across 36 transect sections are presented. The same process was adopted to cluster the transect sections based on an independent environmental variable (section altitudes).



S4 Mammal species from Intervales State Park and Núcleo Caraguatatuba, Serra do Mar State Park, São Paulo, Brazil

									Intervales				Caraguatatuba			
Order	Family	Species	Authority	[a]Threat IUCN	[b]Threat SP	Total detections	Resampled ranked abundance	[d] Number of 2.4 km sections	[c]visual	[c]tracks	[c]feces	[c]other	[c]visual	[c]tracks	[c]feces	[c]other
Artiodactyla	Cervidae	*Mazama spp*				17	4	10		X				X		
		Mazama cf. *americana*	Erxleben (1777)	DD	VU	1		1					X			
	Tayassuidae	*Pecari tajacu*	Linnaeus (1758)	LC	NT	31	3	14		X	X			X	X	X
		Tayassu pecari	Link (1795)	NT	EN	2	17	1						X		
Carnivora	Canidae	*Cerdocyon thous*	Linnaeus (1766)	LC	LC	1	14	1						X		
	Felidae	*Leopardus pardalis*	Linnaeus (1758)	LC	VU	6	8	5		X				X		
		Puma concolor	Linnaeus (1771)	LC	VU	12	5	9		X				X	X	
		Panthera onca	Linnaeus (1758)	NT	CR	12	6	7		X						
		Puma yagouaroundi	Geoffroy (1803)	LC	LC	1	15	1		X						
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Linnaeus (1758)	LC	LC	2	12	2						X		X
Perissodactyla	Tapiridae	*Tapirus terrestris*	Linnaeus (1758)	VU	VU	249	1	30	X	X	X	X	X	X	X	X
Pilosa	Bradypodidae	*Bradypus variegatus*	Schinz (1825)	LC	LC	1	16	1								X
Primates	Atelidae	*Alouatta guariba*	Humbolt (1812)	LC	NT	11	7	8	X				X			X
		Brachyteles arachnoides	Geoffroy (1806)	EN	EN	5	11	4	X							
	Callitrichidae	*Callithrix* cf. *aurita*	Geoffroy (1812)	VU	VU	1	13	1								X
	Cebidae	*Sapajus nigritus*	Goldfuss (1809)	NT	NT	42	2	18	X			X	X			X
Rodentia	Caviidae	*Hydrochoerus hydrochaeris*	Linnaeus (1766)	LC	LC	1	18	1							X	
	Cuniculidae	*Cuniculus paca*	Linnaeus (1766)	LC	NT	5	9	3		X				X		
	Dasyproctidae	*Dasyprocta* spp				5	10	3						X		
	Erethizontidae	*Sphiggurus villosus*	Cuvier (1823)	LC	LC	1	19	1								X

[a] International threat status following (IUCN 2012). DD = data deficient, then from least to most threatened: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered

[b] Threat status in the State of São Paulo (Magalhães-Bressan et al. 2009, p. 599). From least to most threatened: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered

[c] Detections. Track = tracks observed along trails, Visual = diurnal line transect census, Feces and Other = carcass, or vocalizations.

[d] total number of the 36 survey transect sections with species detections

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Capítulo 3

Density and Spatial Distribution of Buffy-tufted-ear Marmosets (*Callithrix aurita*) in a Continuous Atlantic Forest

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Density and Spatial Distribution of Buffy-tufted-ear Marmosets (*Callithrix aurita*) in a Continuous Atlantic Forest

**Darren Norris · Fabiana Rocha-Mendes ·
Renato Marques · Rodrigo de Almeida Nobre ·
Mauro Galetti**

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Abstract The continued degradation of forest habitats and isolation of fragmented populations means that the conservation of endemic marmosets in the Brazilian Atlantic forest depends on human interventions including legal protection. Population monitoring is required to ensure effective management and appropriate allocation of conservation resources; however, deriving estimates of population metrics such as density within heterogeneous environments is challenging. We aimed to quantify the population density and spatial distribution of buffy-tufted-ear marmosets (*Callithrix aurita*) in the northern region of Serra-do-Mar State Park. We incorporated habitat suitability as quantified by a niche modeling algorithm (MAXENT) to refine density estimates obtained via distance methods. We used 6 environmental predictors to model the distribution of *Callithrix aurita* and used the resulting MAXENT niche model to identify environmental conditions that represent suitable habitat for this species. We used 877.7 km of line transect surveys and distance methods to derive estimates of 2.19 groups or 7.55 individuals/km^2 from direct observations (n=40), providing an overall population estimate of 1892 (95% CI=1155–3068) individuals in 250.7 km^2 of Atlantic forest. Our refined density estimate, obtained by combining distance methods and a niche model, yielded a result of 1386 individuals. Suitable habitat was not uniformly distributed across the study area and was most strongly associated with altitude and the type of vegetation cover. We provide a review of previous surveys and find this is the largest known population of *Callithrix aurita.* Our refinement of density estimates provides a simple and informative addition to the primatologist's toolbox.

Electronic supplementary material The online version of this article (doi:10.1007/s10764-011-9503-1) contains supplementary material, which is available to authorized users.

D. Norris (✉) · F. Rocha-Mendes · R. Marques · R. de Almeida Nobre · M. Galetti
Laboratório de Biologia da Conservação, Departamento de Ecologia,
Universidade Estadual Paulista (UNESP), Caixa Postal 199, Rio Claro, SP 13506–900, Brazil
e-mail: dnorris75@gmail.com

F. Rocha-Mendes
Instituto Neotropical: Pesquisa e Conservação, CP 19009, CEP 81531–980 Curitiba, PR, Brazil

Keywords Atlantic forest · Callitrichidae · Distance sampling · Line transect · MAXENT · Population density · Presence-only distribution modeling · Spatial distribution

Introduction

Eastern Brazilian marmosets (*Callithrix* species) are small-bodied (<500 g) primates possessing specialized dentition for gouging and extracting gums from tree trunks and branches (Coimbra-Filho and Mittermeier 1976; Rylands and Faria 1993). This specialization enables them to occupy a variety of forest habitats across the Atlantic forest, Caatinga, and Cerrado biomes. *Callithrix* have been separated into ecological groups based on differences in gum-gouging specialization and geographic distribution (Rylands and Faria 1993). Specialization in gum gouging enables the invasive *Callithrix jacchus* and *C. penicillata* to survive periods of food scarcity and occupy drier areas of Cerrado and Caatinga as well as a variety of upland and lowland Atlantic forest types (Coimbra-Filho and Mittermeier 1977; Fonseca and Lacher 1984; Rylands *et al.* 2009). In comparison, the other 4 (less specialized) species of *Callithrix—C. kuhlii*, *C. geoffroyi*, *C. flaviceps*, and *C. aurita*— have a much narrower distribution that is restricted to the Brazilian Atlantic forest (Rylands *et al.* 2009).

Callithrix aurita (buffy-tufted-ear marmosets) are endemic to the Atlantic forest of São Paulo, Rio de Janeiro, and Minas Gerais states (Muskin 1984). They occur in monogamous or polygonous groups of 3–11 individuals (Bernardo and Galetti 2004; Corrêa *et al*. 2000; Coutinho and Corrêa 1995). Across their restricted range, *Callithrix aurita* are found in both Atlantic rain forest and Atlantic semideciduous forest types (Cerqueira *et al.* 1998; Olmos and Martuscelli 1995; Rylands and Faria 1993). Although historically *Callithrix aurita* may have been distributed across lowland altitudes, today their distribution is limited to upland montane or submontane forests >500 m (Rylands and Faria 1993). *Callithrix aurita* are poorly adapted for gum-gouging (Rylands and Faria 1993; Rylands *et al.* 1996), but supplement their omnivorous diet with gum feeding from ungouged exudates during months of low fruit availability (Corrêa *et al.* 2000; Martins and Setz 2000; Rylands and Faria 1993). Populations of *Callithrix aurita* are threatened by continued habitat destruction (Atlantic forest habitats currently experience an annual deforestation rate of 0.25% or 350 km^2 [Fundação SOS Mata Atlântica and INPE 2008]), and competition and inbreeding with introduced congeners (*C. jacchus* and *C. penicillata*) that is causing (as yet unquantified) demographic and genetic degradation of the remaining fragmented populations (Rylands *et al*. 2008).

Previous researchers demonstrated that *Callithrix aurita* is nowhere common and may be rare even in large forest areas (Cerqueira *et al.* 1998; Coimbra-Filho 1984; Muskin 1984). For example, in a forest fragment of *ca.* 1450 ha, the population was estimated at ≤8–12 individuals (Milton and de Lucca 1984); this low estimate is supported by more recent surveys in the same area that were unable to provide density estimates owing to a severely limited number of detections: 4 sightings from

274.8 survey km (Martins 2005). Although uncommon, their small body size and dietary flexibility enables populations of *Callithrix aurita* to persist in forest fragments as small as 17 ha (Martins 2000; Martins and Setz 2000). The long-term viability of these small and isolated populations is very uncertain, particularly as small, isolated populations are more susceptible to stochastic or deterministic extinctions (Harrison 1991).

With more than 83.4% of Atlantic forest areas <50 ha in size (Ribeiro *et al.* 2009), it seems likely that the majority of the <10,000 remaining *Callithrix aurita* (Rylands *et al*. 2008) are found in populations that are both fragmented and isolated (Cerqueira *et al.* 1998; Olmos and Martuscelli 1995; Rylands *et al.* 2009). Based on the predictions from metapopulation theory (Hanski 1998; Harrison 1991; Hastings and Harrison 1994), the long-term genetic and demographic persistence of these fragmented populations will depend on the ability of individuals to disperse between fragments and colonization/translocation of individuals from source populations (Harrison 1991).

A detailed understanding of the spatial relationships between species and their environments is essential to prioritize research and conservation needs (Morrison *et al*. 2006). The fragmented nature of populations of *Callithrix aurita* means that it is vital to quantify the densities and the local scale spatial distribution of populations in the few remaining large areas of Atlantic forest, as it is these populations that will provide a source for the effective conservation and restoration of the species in fragmented areas. It is well known that demographic parameters such as population densities and birth rates are lower in less suitable habitats (Felton *et al*. 2003; Hazell *et al*. 2004) and one of the key factors required to understand if a population can be considered a source is the spatial distribution of population densities (Heinrichs *et al*. 2010; Kareiva *et al*. 1990). Yet raw density estimates of sampled populations are not necessarily accurate in heterogeneous environments where species presence and abundance can be strongly influenced by environmental factors (Morrison *et al*. 2006; Thomas *et al*. 2010; Van Horne 1983). Thus incorporating environmental heterogeneity in estimating densities is useful to refine estimates of population size and provide more accurate information.

The majority of population studies of *Callithrix aurita* have been conducted in small forest fragments (Bernardo and Galetti 2004; Martins 2005), and basic information regarding population numbers and spatial distribution of potential source populations in larger (>10,000 ha) forest areas remains poor. We, therefore, aimed to 1) quantify the population density of *Callithrix aurita* and 2) establish the environmental conditions that represent suitable habitat for this species in the largest remaining fragment of Atlantic forest: the Serra-do-Mar forest massif (Ribeiro *et al.* 2009). By integrating information on population densities and habitat suitability derived from an extensive line transect survey effort, we generate information relevant to the management of this endangered species. This novel approach provides a simple way to accommodate known difficulties in extrapolating densities across heterogeneous environments (Thomas *et al*. 2010).

Methods

Study Area

We conducted surveys between 2002 and 2008 in the Serra-do-Mar State Park (Parque Estadual da Serra-do-Mar [PESM]). The PESM was created in 1977 and covers *ca.* 3190 km^2 of Atlantic forest. The park is divided into 8 administrative regions called Núcleos. We conducted surveys in 2 Núcleos in the northern portion of the park (Fig. 1): Núcleo Cunha/Indaiá (23°13′–23°16′S and 45°02′–45°05′W) and Núcleo Santa Virgínia (23°17′– 23°32′S and 45°03′–45°11′W). The region has a subtropical climate, with an average annual precipitation of 1850 mm, and altitudes within the 2 Núcleos vary from 800 m to 1600 m (Instituto Florestal 2008 and Table I).

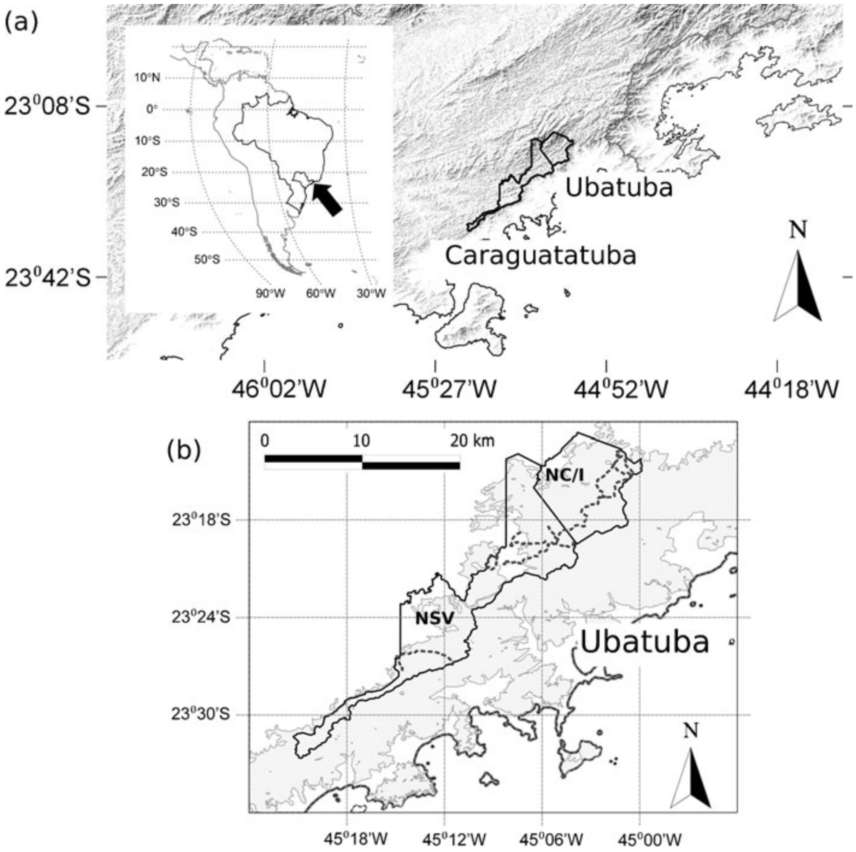

Fig. 1 **a** Shaded relief of the northern coast of São Paulo state with the location of Núcleos Santa Virgínia (NSV) and Cunha (NC/I) in Serra-do-Mar State Park (black outlines). **b** Location of survey transects (dotted dark gray lines) within the protected areas (solid black outline) of coastal Atlantic forest (primary and secondary vegetation: light gray shading).

Table I Environmental predictors used to determine habitat suitability for *Callithrix aurita* in a 250-km^2 area in the north of the Serra-do-Mar State Park, Brazil

Variable	Description/ecological characteristic	Grid[a]	Study area values: mean (range)	Transect values: mean (range)	Source/ instrument
DEM	Digital elevation model: topography	30	1066 (770–1623) m	1005 (783–1202 m)	Aster[b]
TWI	Topographic wetness index	30	–15.25 (−18.93 to 4.18)	–12.33 (−18.55 to 3.50)	From DEM
Lc.C	Land cover in 2 categories: forest and nonforest	30	0–1	0–1	Landsat 5 TM[c]
Veg.C	Vegetation class: 3 categories	30	0–2	0–2	Landsat 5 TM[c]
NDVI	Normalized difference vegetation index	250	0.88 (0.69–0.92)	0.88 (0.77–0.92)	MODIS[d]
EVI	Enhanced vegetation index	250	0.55 (0.38–0.71)	0.55 (0.43–0.65)	MODIS[d]

[a] Native cell resolution (meters) of raster grid.

[b] ASTER global digital elevation model (product of METI and NASA 2009), distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (lpdaac.usgs.gov). Downloaded via: https://wist.echo.nasa.gov.

[c] Downloaded via: http://glovis.usgs.gov/.

[d] Distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (lpdaac.usgs.gov). Downloaded via: https://wist.echo.nasa.gov

Núcleo Cunha/Indaiá was created in 1974 and became part of the PESM in 1977. It protects 140 km^2, with 66.50% covered by dense ombrophylous forests, 20.60% by secondary vegetation, and the remaining 12.90% bare ground (Instituto Florestal 2008). The neighboring Núcleo Santa Virgínia was created simultaneously with the PESM in 1977 and encompasses 170 km^2, with 57.80% of its area covered by dense ombrophylous forests, 29.70% by secondary vegetation, and the remaining 10.80% by anthropogenic developments and plantations of *Eucalyptus* (Instituto Florestal 2008; Villani 1998).

Line-transect Census

We conducted diurnal line transect census following standardized protocols (Peres 1999) for a total of 158 survey days distributed evenly from June 2002 to October 2008 such that km walked and days of survey were equal across the austral winter (June–October) and summer (November–May). We walked a total of 877.7 census km during the morning or afternoon along 69.35 km of preexisting trails that had been established for >3 yr before surveys (n=16, mean transect length=4.34 km, range 1.10 to 8.60 km; Table I) distributed throughout both Núcleos (Fig. 1, Table I). Although we did not implement a systematic design in transect placement (opening an equivalent 69 km of random transects within a protected area was not an option), our extensive coverage and survey effort enabled us to obtain a representative sample of the population of *Callithrix aurita* across the broad range of environmental conditions in the Núcleos (Table I, electronic supplement S1), satisfying the 2 basic principles of line transect survey design, i.e., randomization and replication (Buckland *et al*. 2010; Thomas *et al*. 2010). Three different observers received standardized training in the sampling methodology following Buckland *et al*. (2001) and Peres (1999), and conducted censuses with no temporal overlap: observer 1: 417.5 km, June 2002–January 2004; observer 2: 227.2 km, August 2004–January 2005; observer 3: 233 km, September 2007–October 2008.

Environmental Predictors

We used 6 environmental predictors derived from remotely sensed data sources to predict habitat suitability for *Callithrix aurita* within the Núcleos (Table I). We chose variables relating to habitat characteristics that are known to be important for this species: altitude, land cover, and vegetation type (Cerqueira *et al.* 1998; Geise *et al.* 2004; Muskin 1984; Olmos and Martuscelli 1995; Pinto *et al.* 2009; Rylands *et al.* 2009). We downloaded a digital elevation model (DEM) from the Advanced Spaceborne Thermal Emission and Reflectance Radiometer (Aster) global digital elevation data set (https://wist.echo.nasa.gov) and used this to provide elevation data (masl [meters above sea level]) and a topographic wetness index (TWI, generated via SAGA GIS [Boehner *et al.* 2002; Wang and Liu 2006]).

We conducted surveys in protected areas, so vegetation cover should not differ across the years of the study. We therefore chose scenes from one year (2007) to derive measures of land cover and vegetation type. We quantified spatial patterns of vegetation cover using normalized difference (NDVI) and enhanced vegetation (EVI) indices, which we derived from a yearly average of atmospherically corrected MODIS surface reflectances (Huete *et al*. 2002) obtained from the Land Processes Distributed Active Archive Center (https://wist.echo.nasa.gov). We derived forest cover and primary and secondary vegetation classes from a Landsat 5 TM image (cloud free scene 220/077, June 4, 2007, bands 3, 4, and 5, downloaded from: http://glovis.usgs.gov/) following Michalski *et al*. (2008).

Data Analysis

Unless otherwise stated, we used R (R Development Core Team 2009) for our statistical analysis.

Density Estimation We used distance methods to estimate the population density of *Callithrix aurita* from our line-transect surveys (Thomas *et al*. 2010). As different observers can bias density estimates derived from distance sampling, we tested if detection distances, group sizes, or detection rates varied between observers before estimating densities. We limited this analysis to 2 transects that were surveyed by all 3 observers to prevent any confounding influence of habitat or topological

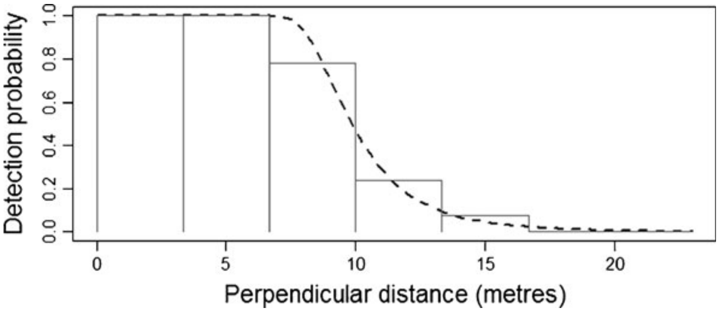

Fig. 2 Detection probability of *Callithrix aurita*. Observed values for 40 detections in a continuous area of Atlantic forest. The dashed line shows expected values from the Distance detection function (hazard-rate with polynomial series expansion).

differences. We used analysis of variance (ANOVA, $\alpha=0.05$) to test whether 1) detection distance ($n=24$) or 2) group size ($n=24$) were influenced by observer. We transformed data (detection distance was square root transformed; group size was $\log_{10}$ transformed) to meet assumptions of normality (Shapiro-Wilk: $p=0.066$ for transformed detection distance, $p=0.061$ for group size) and homoscedasticity (Fligner-Killeen, df=2: $\chi^2=1.2974$, $p=0.5227$ for transformed detection distance and $\chi^2=1.32$, $p=0.516$ for group size).

We divided the total survey effort over 2 transects (total of 369.3 census km) walked by all 3 observers into 4-km stretches (the shortest distance walked by any observer) to test if detection rates differed between observers. We then applied a generalized linear model (GLM: family=quasipoisson, link=log) to test if the response of number of detections over 4 km varied between observers.

We calculated densities using the DISTANCE 6.0.2 (Thomas *et al.* 2009), grouping detections into 7 distance intervals and truncating at 23 m, which excluded an extreme detection of 45 m (Fig. 2). We applied a global detection function (hazard rate with polynomial series expansion) to estimate densities for each transect in the study area. We used the mean number of individuals per group from 40 detections to estimate the density of individuals. As we used standardized line-transect protocols that include limited observation time (Buckland *et al.* 2001; Peres 1999), our survey group sizes are not directly informative for the social structure of *Callithrix aurita* (Buckland *et al.* 2010); however, we present these data to allow comparison with previous studies.

Spatial Distribution We used a maximum entropy algorithm with MAXENT (Phillips and Dudik 2008) to predict habitat suitability for *Callithrix aurita*. MAXENT uses presence-only data to model species potential geographic distribution and performs well with small sample sizes (as little as 5 total records), particularly, as in our case, where the focal species has "small geographic ranges and limited environmental tolerance" (Hernandez *et al.* 2006). We chose this presence-only approach because, although it would be theoretically possible to model our data as presence/absence based on repeated visits along the same transects, the combination of environmental heterogeneity and the small-bodied, secretive nature of our study species means that even with statistical advances in occupancy models that correct for detection probability including Bayesian hierarchical and state space models (MacKenzie *et al*. 2006), we cannot reliably infer absences across the broad environmental gradients (Table I) in our study area.

We used 6 environmental predictors (Table I) to model habitat suitability for *Callithrix aurita* in MAXENT. We used the default settings, with 25% of points ($n=10$) used for cross-validation. To evaluate the models we used a receiver operating characteristic (ROC) analysis, which has been widely used for model evaluation, and is part of the MAXENT output (Elith *et al*. 2006). The ROC generates a single measure of model performance: area under the curve (AUC). We ran 10 bootstrap iterations to derive an average representation of the contribution of our environmental variables and an average overall AUC.

MAXENT produces a habitat suitability index (HSI) map with values ranging from 0 to 1 and computes response curves showing how the model predictions of habitat suitability depend on the environmental variables (Phillips *et al*. 2006). We used these response curves to identify which values of the most important environmental variables (variables that contributed >10% to the MAXENT model) correspond to the most suitable habitat conditions. Because the curves were derived from a MAXENT model created using only the corresponding variable, they quantify dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables (Buermann *et al.* 2008; Phillips *et al.* 2006; Wiley *et al.* 2003).

Integrating Density Estimates and Habitat Suitability We integrated results from our abundance estimates and analysis of the environmental niche of *Callithrix aurita* to provide an approximation of a realized density estimate for the study area, i.e., a density estimate that includes information of the shape and nature of a species environmental response (Guisan and Zimmermann 2000). This requires a positive correlation between the habitat suitability as defined by our niche models and density estimates, i.e., that there are more individuals along transects in more suitable habitat. We tested this by correlating the mean HSI (habitat suitability index) values within a 23-m buffer of the transect line and the mean density estimates for each transect.

We rescaled density estimates by HSI values to calculate a refined density estimate (D_r) for each grid cell:

$$D_r = D_{\min} + D_{adj}$$

where D_{min} is the lower 95% CI density estimate, and D_{adj} is the adjusted density obtained from:

$$D_{adj} = (HSI_c - HSI_{\min}) \times \left(\frac{\Delta D}{\Delta HSI}\right)$$

where HSI_c is the cell HSI value and HSI_{min} is the lowest HIS value; in our case we chose 0.125 to represent a widespread starting point (because HSI values start at 0, a value of 0.125 indicates that the majority of the habitat will be suitable at least to some extent, i.e., the species will have a widespread distribution) for a realized distribution (Boubli and de Lima 2009; Soberón and Peterson 2005). ΔHSI is the range of HSI values from the region of interest (maximum $HSI - HSI_{\min}$) and ΔD is the 95% CI range of density estimates scaled to cell size (upper 95% CI – lower 95% CI). We then obtained an overall density by summing D_r over the study area (see electronic supplement S2 for an illustrated example).

Results

Population Density

We obtained 41 detections from an overall survey effort of 877.7 km. The overall encounter rate was 0.47 (range=0–1.83) groups/10 km (Table II). We pooled results from all observers to estimate densities and detection probabilities, as there was no significant influence of observers on mean detection distance ($F_{2,21}$: 0.18, $p=0.83$) or group size ($F_{2,21}$: 0.47, $p=0.63$) and only a marginally significant influence on detections per 4 km compared with the null model (GLM: deviance explained=8.52%, $p=0.037$). We found no significant relationship between detection rate (groups/10 km) and total kilometers walked per transect (Pearson correlation: $n=16$, $r=0.07$, $p=0.79$), which provides evidence that our effort per transect was sufficient to ensure that distance walked did not influence detection rate per transect.

Table II Summary of diurnal line transect census effort and density estimates for C*allithrix. aurita* in a 250-km^2 area in the north of the Serra-do-Mar State Park, Brazil

Transect ID	Núcleo	Transect length (km)	Total dist. (km)/no. of surveys	Abundance (groups/10 km)	Density (95% CI)
1	NC/I	4.50	27.50/17	0	
2	NC/I	1.10	27.40/25	1.83	30.07 (23.20–39.00)
3	NC/I	5.95	70.00/12	0	
4	NC/I	8.45	84.50/10	0	
5	NC/I	1.50	9.00/6	1.11	18.31 (14.12–23.74)
6	NSV	6.30	150.00/24	0.53	8.80 (6.78–11.40)
7	NSV	4.50	24.30/6	0.41	6.78 (5.23–8.79)
8	NSV	2.80	59.50/22	0.34	5.54 (4.27–7.18)
9	NSV	5.40	38.80/8	0.77	12.74 (9.83–16.52)
10	NSV	2.15	62.40/30	0.32	5.28 (4.07–6.85)
11	NSV	2.45	19.50/8	0.51	8.45 (6.52–10.96)
12	NSV	8.60	17.20/2	0	
13	NSV	5.30	31.80/6	0.31	5.18 (4.00–6.72)
14	NSV	2.50	27.50/11	0	
15	NSV	3.00	9.00/3	0	
16	NSV	4.85	219.30/46	0.78	12.02 (9.27–15.60)
Totals		69.35	877.70/226	0.47	7.55 (4.61–12.24)

We found considerable differences in relative abundance (detections per 10 km of census) between transects, ranging from no detections in 6 transects (consisting of 33 transect km and 235.7 census km) to 1.82 groups per 10 km. The mean group size from 40 detections was 3.43 (95% CI=2.94–3.99), providing an overall density of 2.19 (95% CI=1.35–3.57) groups or 7.55 individuals (95% CI=4.61–12.24) per square kilometer. Therefore our overall estimate without taking spatial variation into consideration is 549 (95% CI=338–894) groups or 1892 (95% CI=1155–3068) individuals in the 250.7 km of Atlantic forest (primary and secondary) in Núcleo Cunha/Indaiá and Núcleo Santa Virgínia.

Spatial Distribution

The predicted distribution of suitable habitat for *Callithrix aurita* is not homogeneous in our study area (Fig. 3). The mean AUC value was 0.813 (range: 0.746–0.875), which is a good score for the model validation (Phillips *et al.* 2006; Soberón and Peterson 2005). Of our 6 original variables those with the highest predictive value and % contribution when used in isolation were: altitude (DEM=26.2%), the presence of primary or secondary forest (For.C=26.0%), the vegetation cover class (Veg.C=21.2%), and NDVI (15.1%), which jointly contributed 88.5% to the average MAXENT model.

Most of our study area (75%) comprised areas with a HSI <0.5 (Fig. 3b). The map of HSI values revealed that there appear to be several isolated "hotspots" of the most suitable habitat (totaling 31.1 km^2, HSI >0.5, Fig. 3a), whereas the majority of the study area contains less than optimal habitat for this species as measured by our environmental variables. Response curves for the 4 most important environmental variables revealed that the following environmental conditions are necessary for >50% predicted probability of suitable habitat: altitude between 608 and 1023 m (Fig. 4a); and NDVI between 0.87 and 0.91 (Fig. 4b). We also found a 15% probability of suitable habitat in nonforest areas (Fig. 4c), which was a result of a single observation of a group of 3 *Callithrix aurita* within an area of plantation of *Eucalyptus*. On average the secondary forest class had a higher probability compared with primary ombrophylous forest (Fig. 4d, 64% and 51% secondary and primary respectively).

Integrating Density Estimates and Habitat Suitability

We found a significant positive correlation between mean transect HSI and density estimates (Pearson correlation: n=16, r=0.84, p<0.001). Our refined density estimate (sum of D_r) within the primary and secondary forest of both Núcleos was 1386 individuals and overall within both Núcleos (including areas of reforestation) was 1456 individuals.

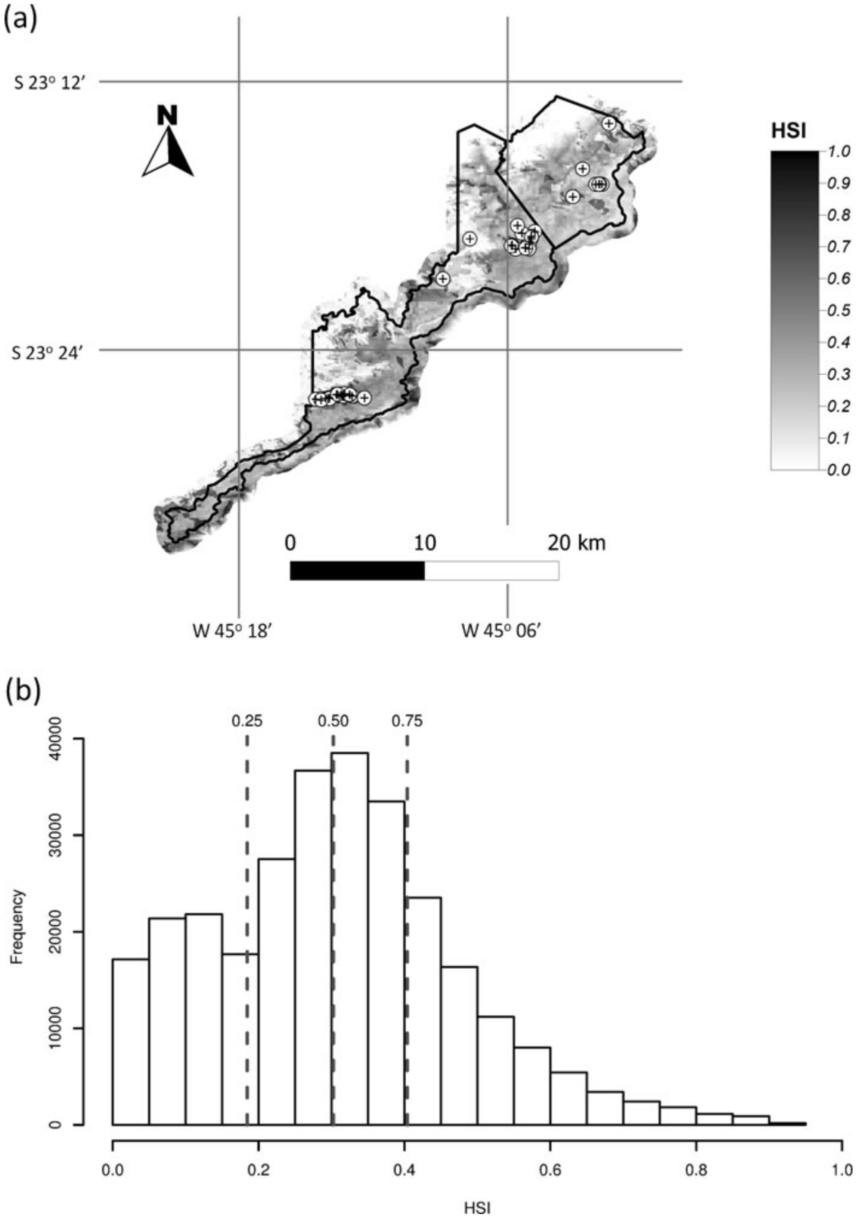

Fig. 3 Distribution of suitable habitat. We calculated a habitat suitability index (HIS: least 0–1 most suitable) from 40 locations of *Callithrix aurita* using a maximum entropy method. **a** The spatial distribution of suitable habitat and location of observations (white circles) in Núcleos Santa Virginia and Cunha (black lines) and **b** frequency of HSI values with 25%, 50%, and 75% quartiles (dashed vertical lines).

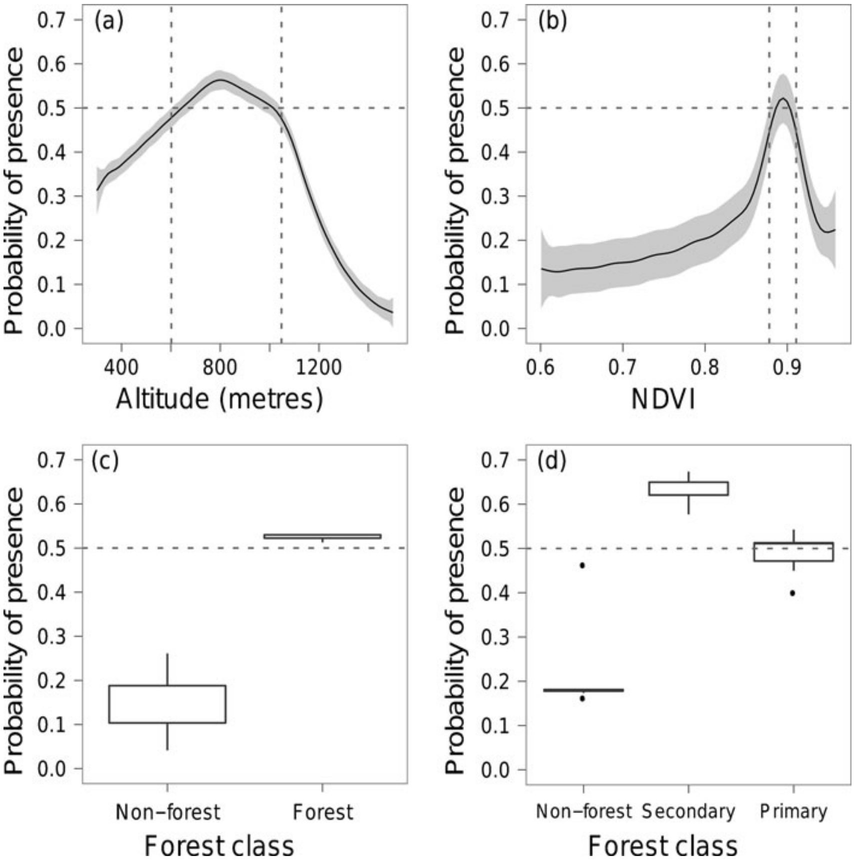

Fig. 4 Influence of environmental predictors on occurrence of *Callithrix aurita*. Plots illustrate how the predicted probability of suitable conditions obtained via MAXENT vary with the 4 most important environmental variables.

Discussion

Population Density

We conducted our surveys in part of the largest (1,109,546 ha) remaining area of Atlantic forest (Ribeiro *et al*. 2009). The population of *Callithrix aurita* in our study area is the largest recorded population of this species. Though a number of studies describe populations of *Callithrix aurita* throughout its Atlantic forest habitat (Raboy *et al*. 2008 and Table III), density estimates are generally not directly comparable due to methodological differences, and we were able to find only 1 study in the past 20 yr, which reported values that are directly comparable to out density estimates (Bernardo and Galetti 2004). Nevertheless, based on comparisons of our results with 1) surveys conducted since 1990 and 2) a review including older accounts (Rylands *et al*. 2008), it seems unlikely that populations of *Callithrix aurita* >1000 individuals will be found anywhere else.

Table III Population density estimates of *Callithrix aurita* in the Atlantic forest obtained from the literature since 1990

Location (state)	Forest area (ha)	Altitude (m)	Forest type	Density inds/km^2: mean (95% CI)	Encounter rate per 10 km: mean (range)		Method	Dist. (km)
					Individuals	Groups		
[1]RF Morro Grande (SP)	10,870	860–1075	Atlantic rain forest	—	—	0.54 (0–1.9)	Line transect	241.0
[2]PFE Rio Doce (MG)	35,000	230–515	Atlantic semideciduous	—	0.26 (0–0.8)	—	Line transect	300.0
[3]FSJ Mata São José (SP)	230	630	Atlantic semideciduous	3.5 (2.8–4.6)	—	0.56	Line transect	125.0
[4]FBR Viraeiro/Tabatinguera (SP)	1450	450–586	Atlantic semideciduous	—	—	0.23	Line transect	131.4
[4]FBR Sara (SP)	501	450–586	Atlantic semideciduous	—	—	0.15	Line transect	68.3
[5]Fazenda Santa Isabel (SP)	920	700–1200	Atlantic semideciduous	—	—	1.41	Playback	85.0
[5]RB/EE Mogi-Guaçu (SP)	137–619	300–600	Cerrado, gallery forests, eucalyptus	—	—	0.83	Playback	48.1
[6]PESM Cunha (SP)	14,000	800–1600	Atlantic rain forest	20–23	—	—	Individuals×area	—

RF = Reserva Florestal; PFE = Parque Florestal Estadual; FSJ = Fazenda São José; FBR = Fazenda Barreiro Rico; RB = Reserva Biológica; EE = Estação ecológica; SP = São Paulo, MG = Minas Gerais.

References: [1] Negrão and Valladares-Pádua (2006); [2] Stallings *et al.* (1990); [3] Bernardo and Galetti (2004); [4] Martins (2005); [5] Olmos and Martuscelli (1995); [6] Corrêa (1995).

Our 95% CI values from transects within Núcleo Cunha/Indaiá were the highest recorded throughout our surveys and overlap values obtained from the same area by extrapolating area use by individuals (Corrêa 1995). Although methodologies differ, this overlap in density estimates between our results and those reported in 1995 strongly suggests that the number of individuals is stable, at least within this Núcleo. Populations of *Callithrix aurita* are declining across its range; our finding of a relatively large and apparently stable population is noteworthy for both conservation and management. The number of individuals and apparent stability of the population of *Callithrix aurita* suggests that it could serve as a source for conservation and management actions; however, further studies are required to quantify habitat specific mortality and productivity within our highly heterogeneous study region before firm conclusions can be drawn (Heinrichs *et al.* 2010; Van Horne 1983).

Spatial Distribution

Our results are based on the assumption that the locations we obtained through direct observation of *Callithrix aurita* represent the environmental requirements for this species in upland coastal Atlantic forest, though the predicted distribution might show areas where the species could occur but it is not present because of other unmeasured variables, including anthropogenic perturbations and biotic interactions like predation (Phillips and Dudik 2008; Soberón and Peterson 2005). It is also possible that some of the locations of *Callithrix aurita* are from less than suitable habitat, i.e., areas that groups were simply traveling through; therefore our estimates of habitat suitability are likely to be higher in terms of the total area covered than is truly the case.

In accordance with previous studies (Muskin 1984; Rylands and Faria 1993), we found that suitable habitat for *Callithrix aurita* is strongly dependent on topography and forest type. For example, secondary forest was more suitable than primary forest, which agrees with previous studies that have shown a preference for secondary habitats with bamboo and vines that provide shelter (Rylands 1996) and predictable food sources, such as fungi and gum (Corrêa *et al.* 2000; Martins 2000; Rylands and Faria 1993). This may also help explain how populations of *Callithrix aurita* persist in small forest fragments, as edge effects are known to generate an early sucessional forest composition and structure that is similar to secondary forest in areas <100 ha (Santos *et al.* 2008; Tabarelli *et al.* 2008). However, the results of our niche model depend on correlations between the environmental variables; therefore, it seems likely that the suitability of secondary habitat for *Callithrix aurita* will also depend on other factors such as altitude and the presence of primary forest. A further consideration is that in forest fragments where *Callithrix jacchus* and *C. aurita* co-occur there may also be a significant competitive advantage for the invasive species (*C. jacchus*) in degraded secondary habitats that may facilitate the displacement of *C. aurita* (Cerqueira *et al*. 1998).

Altitude also limited the probability of suitable habitat for *Callithrix aurita*. The probability of suitable habitat declines after 800 m, and there appears to be an altitudinal limit of *ca.* 1000 m. This information is important for the management of the remaining populations of *Callithrix aurita* across its range. Our results suggest a more restricted range than previous results from São Paulo state where the species was recorded between altitudes of 600–1200 m (Olmos and Martuscelli 1995). However, museum specimens collected in Rio de Janeiro state also show an altitudinal limit of *ca.* 1000 m (Cerqueira *et al.* 1998; Geise *et al*. 2004).

Although the Serra-do-Mar can be considered a continuous forest area, the distribution of *Callithrix aurita* within the forest does not appear to be continuous. The forest extends to the north of our study areas, into Rio de Janeiro state and Bocaina National Park. It is thought that *Callithrix aurita* occur at low densities within this park (Coimbra-Filho 1984); however, there are no recent studies to support this conclusion. Similarly, the existence of populations in the more southerly Núcleos of PESM, to the southeast of the city of São Paulo is at best uncertain, as *Callithrix aurita* is not known to occur outside Núcleo Santa Virgínia and Núcleo Cunha/Indaiá (Instituto Florestal 2008). Following the precautionary principle (Cooney and Dickson 2005), it therefore seems inappropriate to extrapolate distribution or density predictions outside of our study area, owing to the high probability of commission errors, i.e., plotting the species where they will not be found, particularly as our models did not consider anthropogenic perturbations or species interactions, which are likely to restrict further suitable habitat.

Integrating Density Estimates and Habitat Suitability

We are not aware of other studies that have integrated primate density estimates and habitat suitability. Our intention is not to substitute the use of statistical techniques to predict species densities or distributions (Elith and Leathwick 2009; Hengl *et al.* 2009; MacKenzie *et al.* 2006) but rather to apply a simple and informative addition to the primatologist's toolbox. Integrating information from density and habitat suitability seems particularly relevant for situations (all too common in the primatological literature) where it is necessary to extrapolate a local (i.e. transect) abundance estimate to a regional (i.e. a representatively sampled study area) density estimate for management and conservation applications but the target species is not uniformly distributed.

Conservation Implications

Conservation initiatives in Brazil, particularly the Atlantic forest, are cited as examples of the successful integration of legal protection, protected area management, and science-based conservation planning (Brancalion *et al.* 2010; Galindo-Leal and Câmara 2003; Russo 2009; Tabarelli *et al.* 2010). However, despite such positive examples, the case of *Callithrix aurita* highlights just how precarious the situation remains not only for primates but also for the rest of the endemic fauna and flora in the Brazilian Atlantic forest (Metzger 2009; Tabarelli *et al.* 2010).

Current Brazilian legislation actively promotes biodiversity conservation through the maintenance of connectivity via riparian corridors (there is a legal minimum of 30 m of forest cover around rivers) and the restoration of degraded forest areas (Brancalion *et al*. 2010). Although the benefits of maintaining connectivity are well documented (Beier and Noss 1998; Hanski 1999), there are also possible negative effects for species such as *Callithrix aurita*. Increased connectivity will allow dispersal between populations and facilitate the maintenance of populations and genetic diversity (Hanski 1999). However, increased connectivity may also allow the spread of invasive species (Crooks and Suarez 2006) such as *Callithrix jacchus* and *C. penicillata* that could cause local extinctions of *C. aurita* through competition and or hybridization (Rylands *et al*. 2008). Although the lack of data means these issues are speculative, they highlight the need for conservation planning to be informed by the continued monitoring of densities and distributions of *Callithrix* spp. throughout the Atlantic forest. Therefore, there is an urgent need to fill gaps in our understanding of population densities, particularly in the state of Rio de Janeiro, where no results have been published in the last 20 yr, and monitoring populations of *Callithrix aurita* outside of protected areas should be considered a priority, especially in light of proposed changes to Brazilian environmental laws that are likely to reduce connectivity between forest areas (Michalski *et al*. 2010).

There are >700 areas of Atlantic forest with at least some level of legal protection (Galindo-Leal and Câmara 2003; Tabarelli *et al.* 2010). However, it is unlikely that protected areas can maintain populations of *Callithrix aurita* in the long term because 1) the majority (~75%) are small (<100 km^2 [Marsde*n et al*. 2005]), and 2) >50% of land covered by protected areas is above 1200 masl (Tabarelli *et al*. 2010). Based on our niche analysis, habitat suitability of *Callithrix aurita* declines after 800 m masl. It therefore appears that the majority, in terms of both the number and area, of protected areas do not encompass suitable habitat for this species. The conservation of *Callithrix aurita* is therefore dependent on effective conservation planning to develop a strategy that manages populations both in and outside protected areas.

The minimum viable population size to ensure the long-term survival of a species is thought to be 3000–5000 individuals (Traill *et al*. 2007). Based on our density estimates and review of the literature no individual population of *Callithrix aurita* can be considered viable in the long term. Therefore the conservation of *Callithrix aurita* will depend on effective monitoring and management within a meta-population framework where individual movements are facilitated by human interventions including legal protection of the species and its habitats, and possibly, should populations continue to decline, the introduction and translocation of individuals.

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Electronic Supplementary Material 1

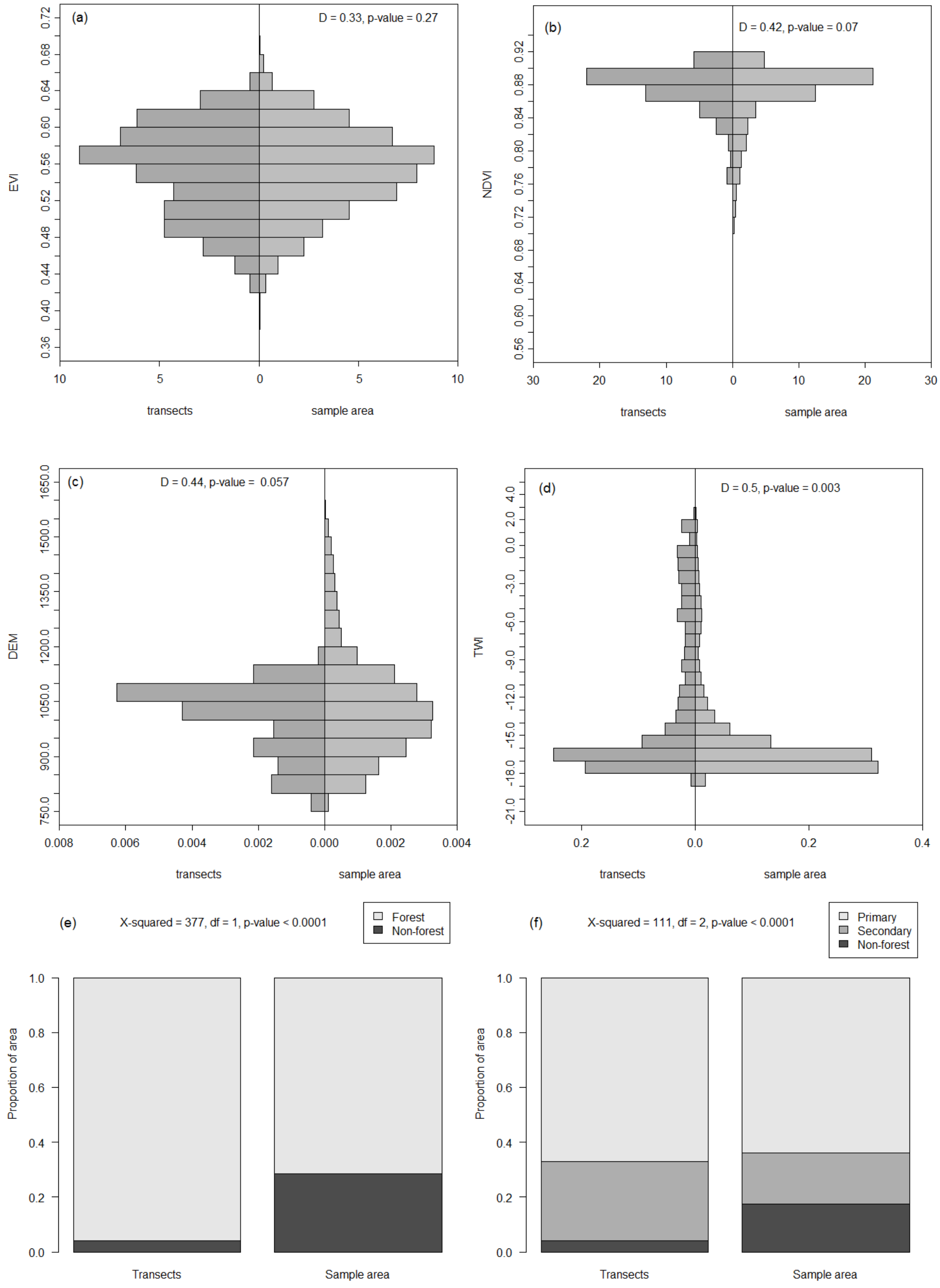
Density and Spatial Distribution of Buffy-tufted-ear Marmosets (*Callithrix aurita*) in a Continuous Atlantic Forest

Darren Norris · Fabiana Rocha-Mendes · Renato Marques · Rodrigo de Almeida Nobre · Mauro Galetti

Distribution and Coverage of Environmental Variables

To determine how well our extensive census encompassed the environmental gradients in the study areas we compared the distribution of the 6 environmental predictors used to determine habitat suitability for *Callithrix aurita* between the area covered by our overall line-transect survey effort and the sample area (Núcleo Cunha/Indaiá and Núcleo Santa Virgínia).

For our 4 continuous variables [**(a)** = EVI (enhanced vegetation index), **(b)** = NDVI (normalized difference vegetation index), **(c)** = TWI (topographic wetness index), and **(d)** = DEM (digital elevation model)] we compared the probability distribution of the environmental variables surveyed 1) over 877.7 km of diurnal line-transect census and 2) throughout the sample area using the nonparametric Kolmogorov-Smirnov test. We used Pearson's χ^2 test to compare the frequency distributions of our categorical variables [**(e)** = land cover and **(f)** = vegetation class].


(a)
D = 0.33, p-value = 0.27
EVI
0.36
0.40
0.44
0.48
0.52
0.56
0.60
0.64
0.68
0.72
10
5
0
5
10
transects
sample area
(b)
D = 0.42, p-value = 0.07
NDVI
0.56
0.60
0.64
0.68
0.72
0.76
0.80
0.84
0.88
0.92
30
20
10
0
10
20
30
transects
sample area
(c)
D = 0.44, p-value = 0.057
DEM
750.0
900.0
1050.0
1200.0
1350.0
1500.0
1650.0
0.008
0.006
0.004
0.002
0.000
0.002
0.004
transects
sample area
(d)
D = 0.5, p-value = 0.003
TWI
-21.0
-18.0
-15.0
-12.0
-9.0
-6.0
-3.0
0.0
2.0
4.0
0.2
0.0
0.2
0.4
transects
sample area
(e)
X-squared = 377, df = 1, p-value < 0.0001
☐ Forest
■ Non-forest
Proportion of area
0.0
0.2
0.4
0.6
0.8
1.0
Transects
Sample area
(f)
X-squared = 111, df = 2, p-value < 0.0001
☐ Primary
▨ Secondary
■ Non-forest
Proportion of area
0.0
0.2
0.4
0.6
0.8
1.0
Transects
Sample area

Electronic Supplementary Material 2

We derived a refined density estimate (D_r) for each grid cell by rescaling density estimates by the habitat suitability index (HSI) calculated via MAXENT:

$$D_r = D_{min} + D_{adj}$$

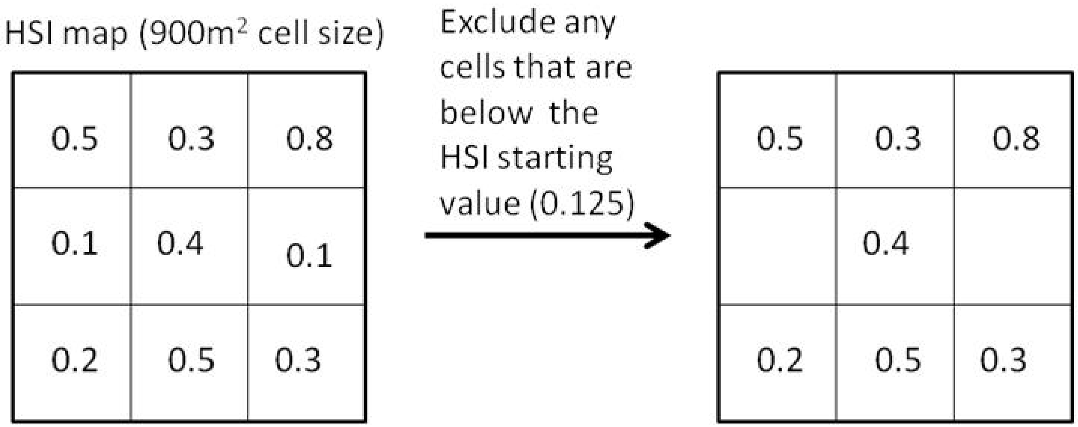
where D_{min} is the lower 95% CI density estimate scaled to the cell size (in our case 4.61 inds/km^2 = 0.0041 inds/900 m^2) and D_{adj} is the adjusted density obtained from:

$$D_{adj} = (HSI_c - HSI_{min}) \times \left(\frac{\Delta D}{\Delta HSI}\right)$$

where HSI_c is the cell HSI value produced by MAXENT, HSI_{min} is the lowest HSI value (in our case we chose 0.125 to represent a widespread starting point for a realized distribution), ΔHSI is the range of HSI values from the region of interest (maximum $HSI - HSI_{min}$) and ΔD is the 95% CI range of density estimates scaled to cell size (upper 95% CI – lower 95% CI). We then obtained an overall density by summing D_r over the study area.

The process can be separated into 4 calculation steps:

1) Derive HSI map and establish minimum (starting) HSI value.



HSI map (900m² cell size)

0.5	0.3	0.8
0.1	0.4	0.1
0.2	0.5	0.3

Exclude any cells that are below the HSI starting value (0.125)

0.5	0.3	0.8
	0.4	
0.2	0.5	0.3

2) Convert range of 95% CI density estimates to correspond to the grid size.

4.61 – 12.24 individuals / km² ⟶ 0.0041 – 0.0110 individuals / 900m²

3) Calculate density adjustment: $\boldsymbol{D_{adj} = (HSI_c - HSI_{min}) \times \left(\frac{\Delta D}{\Delta HSI}\right)}$**.**

$\Delta D = 0.0110 - 0.0041 = 0.0069$

$\Delta HSI = 0.8 - 0.2 = 0.6$

$$\frac{\Delta D}{\Delta HSI} = 0.0115$$

$$\begin{array}{c} HSI_c - HSI_{min} \\ \begin{array}{|c|c|c|}\hline 0.3 & 0.1 & 0.6 \\ \hline & 0.2 & \\ \hline 0.0 & 0.3 & 0.1 \\ \hline \end{array}\end{array} \xrightarrow{X\ 0.0115} \begin{array}{c} D_{adj} \\ \begin{array}{|c|c|c|}\hline 0.00345 & 0.00115 & 0.00690 \\ \hline & 0.00230 & \\ \hline 0.00000 & 0.00345 & 0.00115 \\ \hline \end{array}\end{array}$$

4) Calculate the refined density in the sample area.

$$\begin{array}{c} D_{min} \\ \begin{array}{|c|c|c|}\hline 0.0041 & 0.0041 & 0.0041 \\ \hline & 0.0041 & \\ \hline 0.0041 & 0.0041 & 0.0041 \\ \hline \end{array}\end{array} + \begin{array}{c} D_{adj} \\ \begin{array}{|c|c|c|}\hline 0.00345 & 0.00115 & 0.00690 \\ \hline & 0.00230 & \\ \hline 0.00000 & 0.00345 & 0.00115 \\ \hline \end{array}\end{array} = \begin{array}{c} D_r \\ \begin{array}{|c|c|c|}\hline 0.00755 & 0.00525 & 0.00110 \\ \hline & 0.00640 & \\ \hline 0.00410 & 0.00755 & 0.00525 \\ \hline \end{array}\end{array}$$

Capítulo 4

How to not inflate population estimates? Spatial density distribution of white-lipped peccaries in a continuous Atlantic forest

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How to not inflate population estimates? Spatial density distribution of white-lipped peccaries in a continuous Atlantic forest

D. Norris[1], F. Rocha-Mendes[1,2], S. Frosini de Barros Ferraz[3], J. P. Villani[4] & M. Galetti[1]

1 Laboratório de Biologia da Conservação, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil
2 Neotropical Institute: Research and Conservation, Curitiba, PR, Brazil
3 Departamento de Ciências Florestais, Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo, Piracicaba, SP, Brazil
4 Parque Estadual da Serra do Mar – Núcleo Santa Virgínia, São Luiz de Paraitinga, SP, Brazil

Keywords
Atlantic forest; ENFA; MAXENT; presence only; protected area management; spatial prediction; species distribution monitoring; *Tayassu pecari*.

Correspondence
Darren Norris, Laboratório de Biologia da Conservação, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), Caixa Postal 199, Rio Claro, 13506-900 SP, Brazil. Tel/Fax: + 55 51 3332 0762
Email: dnorris75@gmail.com

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Abstract

In a world with poor biological inventorying and rapid land-use change, predicting the spatial distribution of species is fundamental for the effective management and conservation of threatened taxa. However, on a regional scale, predicting the distribution of rare terrestrial mammals is often unreliable and/or impractical, especially in tropical forests. We apply a recently developed analytic process that integrates density estimation (kernel smoothing), niche-analysis and geostatistics (regression-kriging) to model the occupancy and density distribution of a threatened population of white-lipped peccaries *Tayassu pecari* in a Brazilian Atlantic forest. Locations ($n = 45$) within a protected area of the Serra-do-Mar state park were obtained from diurnal line transect census (233 km), camera-trapping (751 camera-trap days) and surveys (>626 km) conducted by park rangers. Niche modelling (environmental niche-factor analysis and MAXENT) revealed a restricted niche compared with the available habitat as defined by seven environmental variables. From the occupancy model obtained from regression-kriging, we found that 72% of a 170 km^2 protected area is likely to be used by peccaries. We demonstrate that the distribution of large mammals can be restricted within continuous areas of Atlantic forest and therefore population estimates based on the size of protected areas can be overestimated. Our findings suggest that the generation of realized density distributions should become the norm rather than the exception to enable conservation managers and researchers to extrapolate abundance and density estimates across continuous habitats and protected areas.

Introduction

On a broad scale, the distribution of mammal species is largely predictable, making them appropriate subjects for landscape-scale analysis (Soares-Filho *et al*., 2006; Galetti *et al*., 2009). Yet, such broad-scale assessments overlook inherent and induced habitat heterogeneity, which can have a significant impact on faunal communities. For example, Galetti *et al.* (2009) found that the abundance and biomass of mid- and large-bodied mammals varied by orders of magnitude among continuous areas of Atlantic forest, a variation equal to or greater than that recorded between forest fragments of different sizes (Chiarello, 2000; Cullen, Bodmer & Valladares-Pauda, 2000). On a regional scale, the cryptic nature, low abundances and heterogeneous distribution of mammalian species mean that predicting their distribution is often unreliable and or impractical, with some authors reporting that it is not possible to establish conservation priorities as it is not possible to detect patterns in species occurrence throughout the remaining areas of Atlantic forest (Verdade & Martins-Kierulff, 2006).

The Serra-do-Mar region (São Paulo state) contains the largest conserved area of Atlantic forest in Brazil, covering 32.2% (3 678 534 hectares) of the original forest area (Ribeiro *et al*., 2009). The urgent need for conservation of this forest continuum is recognised as a national and international priority to enable the restoration of biodiversity in fragmented areas and the maintenance of the dynamic Atlantic forest ecosystem (Galetti *et al*., 2009; Loyola *et al*., 2009; Metzger, 2009; Ribeiro *et al*., 2009). However, the most basic data for effective conservation management decisions, that is the spatial distribution of threatened species within these remaining continuous areas of Atlantic forest remain poorly understood and sparsely documented.

Mammals are key components of tropical forest ecosystems (Asquith, Wright & Claus, 1997), with large mammals such as white-lipped peccaries *Tayassu pecari* (hereafter 'peccaries') considered ecosystem engineers (Beck, 2006;

Keuroghlian & Eaton, 2009). Assessing the spatial variation in the diversity and community composition of key mammalian species is therefore often a high research priority, especially in light of threats from habitat loss, habitat degradation, forest fragmentation and hunting (Laurance, Vasconcelos & Lovejoy, 2000; Peres, 2001).

Peccaries are one of the neotropical mammals most affected by hunting and habitat loss (Reyna-Hurtado *et al.*, 2008). For example, from a survey of 26 mammal species in a recent deforestation frontier, peccaries were the only species where a negative response to hunting pressure was found (Michalski & Peres, 2007). Not only are peccaries a preferred target of hunters throughout the neotropics, but they also require large areas to maintain viable populations (Fragoso, 1998; Keuroghlian, Eaton & Longland, 2004; Beck, 2006; Reyna-Hurtado, Rojas-Flores & Tanner, 2009), such that they may well be one of the first species to disappear as a result of human perturbations (Leopold, 1959; Peres, 1996).

Peccaries are considered threatened or critically threatened across the Atlantic forest (Bergallo *et al.*, 2000; Chiarello *et al.*, 2007), and it is paramount to increase protection throughout the region to prevent population collapses such as those reported from mesoamerica (Reyna-Hurtado *et al.*, 2010). Monitoring the spatial distribution of these 'ecosystem engineers' (Jones, Lawton & Shachak, 1994; Beck, 2006) should therefore be a priority for protected area managers. However, as in many other tropical forest regions, conservation activities are limited by a lack of reliable information on the spatial distribution of threatened species.

The negative effects of failing to account for spatial dependence in conservation biology are well documented (Carroll & Pearson, 2000). A wide variety of techniques are available to predict the distribution of plants and animals (Elith *et al.*, 2006). However, the generation of realized distribution models, models that incorporate findings of the shape and nature of species response (Guisan & Zimmermann, 2000), including spatial dependencies, from presence-only data remains a challenge (Lobo, 2008; Elith & Leathwick, 2009; Hengl *et al.*, 2009).

Recent advances that integrate techniques from geostatistics and ecological modelling show great promise for the generation of species distribution models from presence-only data (Hengl *et al.*, 2009). New geostatistical techniques provide a framework within which it may be possible to accurately represent the spatial density distribution of rare and cryptic species from occurrence-only data (Hengl *et al.*, 2009). Incorporating geostatistical techniques into ecological analysis could therefore provide management information that until now has been lacking for managers and researchers. Here, we aim to firstly document the habitat suitability of a continuous Atlantic forest for peccaries and secondly predict occupancy and density distribution from presence-only data via the integration of density estimation (kernel smoothing), niche-analysis and geostatistics (regression-kriging). We demonstrate novel techniques that can be used to provide spatially explicit models that are generally applicable for the management and conservation of rare and threatened species.

Methods and study area

Study area

Our study was conducted in Núcleo Santa Virgínia (170 km^2) and neighbouring Núcleo Cunha (140 km^2), administrative units located in the north of the Serra-do-Mar State Park, São Paulo state, Brazil (Fig. 1). The majority of our survey effort was within Núcleo Santa Virgínia (79.4 km of the 83.7 km of trails utilized). The region has a subtropical climate, with an average annual precipitation of 1850 mm, and altitudes within Núcleo Santa Virgínia vary

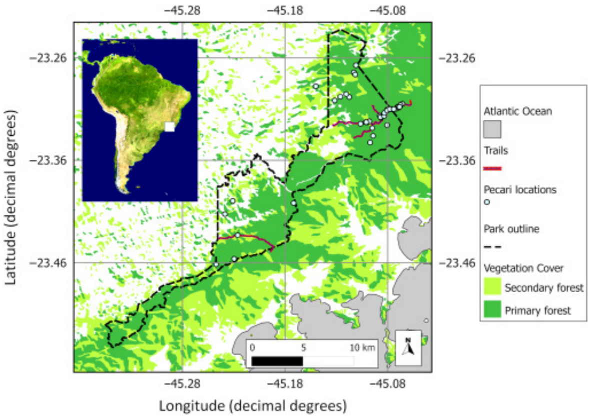

Figure 1 Location of Núcleo Santa Virgínia of the Serra-do-Mar state park. The 45 locations of *Tayassu pecari* recorded within our "modeling grid" are shown. Trails used by park guards are not shown for security reasons.

from 780 to 1600 m (Instituto Florestal, 2008, Table 1). Núcleo Santa Virgínia was created simultaneously with the Parque Estadual da Serra do Mar in 1977, with *c.* 57.80% of its area covered by dense ombrophylous forests, 29.70% by secondary vegetation and the remaining 10.80% by anthropogenic developments and Eucalyptus plantations (Villani, 1998; Instituto Florestal, 2008). Núcleo Santa Virgínia is bisected by an asphalt road, which may act as a barrier between the southern and the northern sections of the Núcleo; however, we consider this a continuous area due to connections to the north (which stretch until the Bocaina National Park in Rio de Janeiro state) and the south (with the 499 km^2 Núcleo Caraguatatuba of the Serra-do-Mar State Park).

Although we did not implement a systematic survey design, by combining data from complementary sources, we obtained a representative sample across the broad range of environmental conditions in the Núcleo (Table 1, supporting information Appendix S1). We reduced the impact of analytic edge effects by extending the study area with a 5000 m buffer around the border of the Santa Virgínia unit, generating a 774 km^2 modelling area.

Diurnal line transect census

A series of line transect censuses were conducted following standardized protocols (Peres, 1999; Chiarello, 2000). A total of 233 census kilometres were conducted during the morning or afternoon along four long established (>5 years) trails (totalling 14.1 km in length and ranging from 2000 to 4100 m long – Fig. 1). Census surveys were distributed evenly from September 2007 to October 2008.

Camera trapping

Between March and June 2008, 28 Leaf River® camera-traps (Taylorsville, MS, USA) were distributed at 400 m intervals along sections (selected at random) of our four census trails. Cameras were positioned without bait and remained active over 24 h for 7 days, after which time, they were moved to a new location, yielding a total effort of 751 camera-trap days.

Park ranger surveys

We used peccary locations recorded by park rangers between 2007 and 2009. Park rangers cover 69.6 km of trails [mean length (range): 3.6 (0.5–15.3) km] that are otherwise closed to the public and researchers. Although the total kilometres walked by rangers is not recorded, all trails are surveyed a minimum of three times a year, providing a minimum effort of 626.4 km. These locations were georeferenced in relation to the distance from known locations of rivers and trail intersections.

Environmental predictors

We used seven environmental predictors, selected based on published descriptions of determinants of peccary occurrence. Peccaries require forest areas, and prefer areas close to rivers, swampy locations and locations with fruiting

Table 1 Environmental predictors used to determine habitat suitability for *Tayassu pecari* in the Serra do Mar State Park, Brazil

Variable	Description/ecological characteristic	Grid[a]	Study area values: mean (range)[b]	Transect values: mean (range)[b]	Source/instrument
DEM	Digital elevation model – altitude above sea level/floristic structure and composition	30	984 (781–1602) m	1023 (785–1434)	ASTER[c]
TWI	Topographic wetness index/floristic structure and composition	30	11.4 (8.8–19.6)	9.01 (8.9–19.2)	From DEM
Slope	Topographic morphometry/suitability for quadraped locomotion	30	11.5 (0–27.2)	8.7 (0.1–22.7)	From DEM
distRoad	Distance from asphalt road/human accessibility		6169.3 (61.6 – 15268.3)	5174.5 (77.8–15268.3)	Derived from road network vector[d]
distBord	Distance from park border/human accessibility and disturbance (negative values outside/ positive inside)		1187.1 (−28.5–4506.5)	1160.9 (4.6–4385.9)	Derived from park boundary vector[e]
Veg2	Vegetation cover – two categories: forest and non-forest	30	(0–1)	(0–1)	Landsat 5 TM[f]
Veg5	Vegetation cover – five categories	30	(1–5)	(1–5)	Landsat 5 TM[f]

[a] Native cell resolution (metres) of raster grid.

[b] Values calculated with resampled grids (300 × 300 m cell resolution).

[c] ASTER global digital elevation model (product of METI and NASA 2009), distributed by the Land Processes Distributed Active Archive Center (LP DAAC), located at the US Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center (lpdaac.usgs.gov). Downloaded via https://wist.echo.nasa.gov

[d] From the remote-sensing centre (CSR – Centro de Sensoriamento Remoto) of the Brazilian environmental agency (IBAMA). Downloaded via http://siscom.ibama.gov.br/shapes/

[e] Compiled and maintained by the Brazilian environment agency (IBAMA). Downloaded via http://www.ibama.gov.br/zoneamento-ambiental

[f] Downloaded via http://glovis.usgs.gov/

palms (Kiltie & Terborgh, 1983; Keuroghlian *et al.*, 2004; Keuroghlian & Eaton, 2008; Desbiez *et al.*, 2009; Reyna-Hurtado *et al.*, 2009). The dominant palm species in the study area is *Euterpe edulis* (palmito-juçara), whose distribution and fruiting phenology is also known to vary with wetness and elevation (Castro, Galetti & Morellato, 2007).

We therefore selected (see Table 1 for sources and value ranges): (1) forest cover (derived from a supervised classification of Landsat 5 TM bands 3, 4 and 5) – comprising five classes, four forest types (primary, secondary, reforestation and lowland coastal) and other (including agricultural development and bare ground); (2) primary forest cover and non-primary forest; (3) elevation (ASTER global digital elevation model); (4) topographic wetness index (TWI); (5) slope. Both slope and TWI were generated from our digital elevation model with SAGA GIS (Wang & Liu, 2006). We also included two proxies for human disturbance and accessibility: (6) distance from asphalt road and (7) distance from the park border. All predictors were projected to the same coordinate system (SAD69, UTM zone 23S) and resampled (mean values for our continuous variables and nearest-neighbour values for categorical variables) to a 300 × 300 m grid (selected subjectively to account for uncertainty in locations obtained from park rangers) within SAGA GIS.

Principal component transformation of our environmental grids (supporting information Appendix S2) was used to avoid multicolinearity in regression analysis. Component loadings and visual inspection revealed that the four axes with eigenvalues >1 (PC1, PC2, PC3 and PC4) generally represented primary forest cover, slope and altitude, topographic wetness and forest cover and classes of vegetation cover, respectively, and PC5 represents distance from asphalt road and park border, but it was not possible to identify any unambiguous interpretation for the remaining axes (supporting information Appendix S2).

Modelling framework

Unless otherwise stated, analyses were conducted in the R-software (R Development Core Team, 2009). Based on the combination of environmental heterogeneity (Table 1, supporting information Appendix S1), the rare and secretive nature of our study species and the use of different survey techniques, we chose a presence-only approach to predict peccary distribution. Our modelling process (Fig. 2) is based on a subset of a more general analytic framework that is fully presented and described in Hengl *et al.* (2009). Pseudo-absences were generated and then presence–pseudo-absence locations were modelled with regression-kriging [a hybrid technique that uses kriging to make spatially explicit predictions from regression models and the residual variogram (Hengl, 2009)] to predict: (1) species occupancy (with presences and pseudo-absences) and (2) density distributions (with Kernel smoothed densities and pseudo-absences).

Estimation of peccary potential distribution and pseudo-absences

To generate the niche model of potentially suitable habitat required to derive pseudo-absences, we applied environmental niche-factor analysis (ENFA) implemented in the adehabitat package (Hirzel *et al.*, 2002; Calenge, 2006). The appropriateness of our ENFA analysis was determined via evaluation of the niche as described by the marginality and specialization using Monte Carlo simulation with 999 iterations (see Calenge (2006) and Basille *et al.* (2008) for further details of ENFA analysis and interpretation).

ENFA is recognized as robust with respect to the quality and quantity of occurrence locations used (Hirzel, Helfer & Metral, 2001; Hirzel & Guisan, 2002); however, to ensure that the resulting habitat suitability map used to generate pseudo-absences was representative and not a result of analytic bias, we compared the ENFA results with the potential niche derived from a maximum entropy algorithm using the software MAXENT (Phillips & Dudik, 2008; supporting information Appendix S3).

We combined niche models and the distance from locations to generate pseudo-absences (Chefaoui & Lobo, 2008; VanDerWal *et al.*, 2009). By combining these two sources of information, we derived a probability weights map used to generate a random point pattern of 45 pseudo-absences (Baddeley, 2008) located both far from occurrences and in areas of low habitat suitability. The pseudo-absences were overlaid on a medium-resolution image (Landsat 5 TM: 30 m

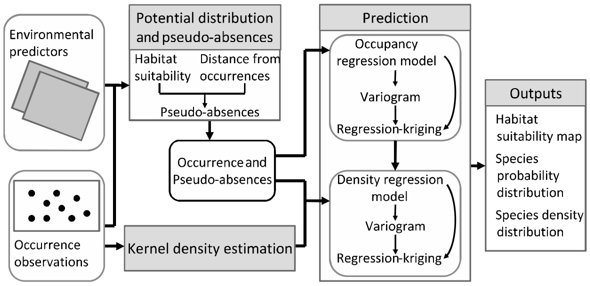

Figure 2 Process flow of techniques used to model the occupancy and probability distribution of *Tayassu pecari* from occurrence-only data: adapted from Hengl *et al.* (2009).

grid resolution) and assessed by three experts to determine their validity (supporting information Appendix S4).

Prediction of peccary density distributions

The occurrence locations are used to derive the density of a species for a given area via point pattern analysis based on a kernel smoother (Baddeley & Turner, 2005). To determine the kernel smoothing parameter (bandwidth) objectively, we followed Berman & Diggle (1989), obtaining a value of 305 m.

A generalized linear model (GLM, family = binomial, logit = 'link') was used to model occupancy across the modelling area. To avoid problems of model saturation, we used only the first three PCA axes to predict the binary response of peccary presence–pseudo-absences. The residuals of the GLM are then analysed for autocorrelation by fitting a variogram. The final predictions are generated by combining GLM and variogram parameters (Pebesma, 2004; Bivand, Pebesma & Rubio, 2008; Hengl, 2009). The same process (regression–variogram–regression-kriging) was also used to model peccary density distribution (log transformed). Predictions of the density distribution were calculated for our modelling area where the probability of occurrence (as defined by our occupancy model) was >0.5.

The final results of the regression-kriging were evaluated using the 10-fold cross validation method (Pebesma, 2004), where the model predictions for our 90 presence–pseudo-absence locations are separated into $n = 10$ parts. For all observations in a part, predictions are then made based on the remaining $n-1$ parts; this is repeated for each of the n parts. The results from this cross-validation were then used to derive a summary estimate of the map accuracy (Bivand *et al.*, 2008).

Relevance for population density estimates

To quantify the degree to which spatial dependencies are considered when extrapolating density estimates, we reviewed the published literature to determine the extent to which conservation biologists consider spatial relationships. We limited our search to terrestrial mammals as this is a widely studied group and population estimates for these charismatic species often make headline impacts. We evaluated publications from the conservation biology literature (Conservation Biology, Animal Conservation, Biological Conservation, Oryx and Biodiversity and Conservation) published since 2005 to compare the frequency of density estimates published with and without considering spatial relationships (supporting information Appendix S6).

Results

We obtained 45 peccary locations from camera-traps ($n = 18$), diurnal line transect census ($n = 7$) and park ranger surveys ($n = 20$). Our overall sampling intensity was 0.06 points per square kilometre within our 774 km^2 modelling area.

Peccary potential distribution

The ENFA habitat suitability analysis showed that peccaries have a restricted habitat niche (Fig. 3). Preliminary analysis of the eigenvalues revealed that only one axis accounted for the main part of specialization. With an

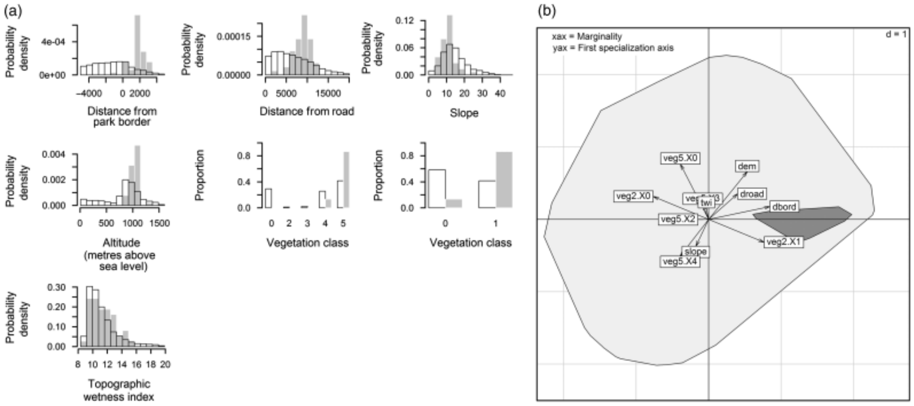

Figure 3 Niche-environment system of white-lipped peccary *Tayassu pecari* in a coastal Atlantic forest: (a) histograms comparing the distribution of available (white fill) and used (grey fill) environmental resource units of white-lipped peccary measured with seven environmental variables. (b) biplot of the ENFA, in the plane formed by the marginality axis (*x*-axis) and the first specialization axis (*y*-axis). The light and dark areas correspond to the minimum convex polygon enclosing all the projections of the available and used points, respectively. The arrows show the projections of the correlations between environmental variables and niche axis.

eigenvalue of 113.9, this specialization (y-axis, Fig. 3b) indicates that the variance of the available habitat was 113.9 times that of the ecological niche in this dimension, that is, the ecological niche is much narrower than the habitat available as defined by our environmental predictors. Monte Carlo simulations revealed that both statistics were highly significant ($P = 0.001$ and $P = 0.001$, marginality and specialization, respectively). The ENFA HSI map (Fig. 4a) mainly follows the patterns of distance from the park border, primary forest cover, distance from road and altitude, with areas of primary forest within a relatively narrow range of higher elevations over 2 km from roads and within the park border (Fig. 3a) being more suitable for peccaries.

Our ENFA results were supported by MAXENT analysis run with the same peccary locations and seven environmental predictors (supporting information Appendix S3). The mean AUC value for the MAXENT test data were 0.928 (range: 0.897–0.961), which is a good score for the model validation (Soberón & Peterson, 2005; Phillips, Anderson & Schapire, 2006). From our seven original variables, four variables had a high predictive value and contribution (98.6%) when used in isolation: distance from park border (63.6%), distance from road (28.4%), the vegetation cover class (Veg2 – 5.0%) and altitude (1.6%).

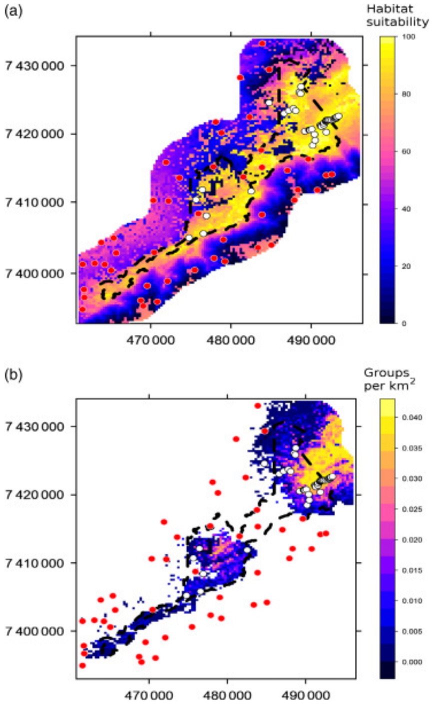

Figure 4 Spatial prediction of *Tayassu pecari* in the Núcleo Santa Virgínia of the Serra do Mar State Park: (a) Habitat Suitability Index (0–100%) from occurrence-only data (white circles) using ENFA, which was used to derive pseudo-absence locations (red circles), (b) the final predictions of group density produced using regression-kriging.

Peccary–realized density distribution

Regression analysis of the log-transformed kernel density (response) derived from the occurrence-only data showed that the nine PCA variables explained 58.1% of the model variation. After including the pseudo-absences, the explained variation increased to 80.1%.

From the total of grids where the probability of occurrence was > 0.5, our occupancy model provides an estimate of 241 km^2 (33.6%) and 120 km^2 (72%) of the modelling area and protected area of Núcleo Santa Virgínia, respectively, that is likely to be used by peccaries. The 10-fold cross validation of the density distribution (Fig. 4b) shows that the model is highly precise, explaining 94% of the original variance.

Relevance for population density estimates

We identified a total of 24 studies that reported density estimates based on our selection criteria (supporting information Appendix S6). These studies encompassed a broad spectrum of species (from rodents to tigers) and techniques (distance sampling, home-range-based estimates, mark–recapture and others including total counts). Only four (16.7%) incorporated spatial dependencies before estimating densities (Fig. 5).

Discussion

Here, we apply a general framework incorporating (1) density estimation (kernel smoothing); (2) niche-analysis (ENFA); (3) geostatistics (regression-kriging) to deliver new sources of information previously unavailable to researchers and protected area managers. We were able to produce: (1) an HSI map showing the potential habitat (Fig. 4a) and (2) the species' distribution (density) map (Fig. 4b). Previous authors have demonstrated the actual species' distribution map (density) quantifies the spreading of the species and can also be used to identify realized hotspots for research and or management activities (Hengl *et al.*, 2009; Singh *et al.*, 2009). We also suggest that realized species distributions should become integral to extrapolating population densities.

Peccary spatial density distribution

For the first time, we demonstrate that the potential niche of peccaries is restricted by a combination of environmental and anthropogenic factors in a coastal Atlantic forest. Peccary populations used to be widely distributed across

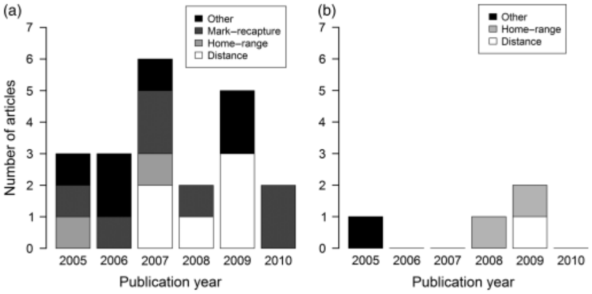

Figure 5 Frequency of publications that: (a) do not or (b) do consider spatial dependencies when estimating population densities.

the Atlantic forest; however, the synergistic effects of hunting and fragmentation have restricted their range to large forest areas and, where they do occur, they are found at low abundances (Chiarello, 2000; Cullen *et al.*, 2000; Keuroghlian & Eaton, 2008; Galetti *et al.*, 2009). Peccaries therefore characterize the difficulties in modelling species occurrences on a regional scale that are commonly encountered by conservation biologists: a dispersed, spatially non-random (autocorrelated) distribution and low abundances that limit the ability of researchers to derive robust and reliable management information for population monitoring via 'traditional' abundance and density estimation (i.e. using camera-traps and line transect census).

Our ENFA and MAXENT niche models revealed that distance from park border, distance from roads, primary forest and altitude constrained the amount of suitable habitat within an area that from a broad-scale assessment of the amount of secondary and primary forest (67% of our modelling area and 89% of the protected area) might well be assumed to be largely suitable. Predictions from our occupancy model showed that only 34% of our modelling area and 72% of our study area had a >50% occurrence probability; this difference between the forest areas 'available' and likely occupied in the modelling and study area (Núcleo Santa Virgínia) emphasizes the importance of protected areas for the conservation of mammals in the Atlantic forest (Galetti *et al.*, 2009). The density distribution obtained from presence–pseudo-absences showed further contraction of the occupied range with clear concentrations of areas with higher densities. It therefore seems likely that peccaries are not distributed uniformly across our Atlantic forest study area.

The finding that peccaries are unlikely to occur in a uniform distribution within continuous forest agrees with results from Atlantic forest fragments (Keuroghlian *et al.*, 2004) and Amazonian forests (Fragoso, 1998). Peccaries are known to be highly mobile in space and time (Fragoso, 1998; Keuroghlian *et al.*, 2004; Reyna-Hurtado *et al.*, 2009), with previous studies documenting requirements for different habitats during different fruiting periods (Kiltie & Terborgh, 1983; Keuroghlian & Eaton, 2008; Reyna-Hurtado *et al.*, 2009) and prolonged absences from continuous areas of the Peruvian Amazon (from Madre de Dios between 1978 and 1990; Silman, Terborgh & Kiltie, 2003). As such, there is likely to be a degree of uncertainty in modelling peccary presences, which must be addressed before ecological mechanisms and accurate absolute density values can be derived (Hengl *et al.*, 2009; Kearney & Porter, 2009). Despite such an uncertainty, our results, from an extensive field campaign, do show a restricted range within a continuous forest area and demonstrate the importance of incorporating realized spatial distributions into protected area management and research.

Relevance for population density estimates

The spatial model presented here can be an important tool for the conservation of threatened and hard to census species in continuous forests. The integration of geostatistical analysis and ecological niche modelling enables researchers to capture the strengths of both groups of techniques (Bahn & McGill, 2007) and the framework is general enough to enable application for a variety of faunal and floral species and sampling techniques. From a management perspective, the application of freely available software and data sources is obviously attractive, and from a research perspective, incorporating both exogenous autocorrelation (spatial structure in the niche variables) and endogenous autocorrelation (based on the dispersal/movement patterns of organisms) can potentially help to counteract the known effects of sampling bias on predictions from niche models (Phillips, 2008; Costa *et al.*, 2010).

Despite a rapid increase in the application of species distribution models over the past decade, the generation of realized species distribution maps remains a challenge (Elith *et al.*, 2006; Tsoar *et al.*, 2007; Elith & Leathwick, 2009). The spatial relationships between observations are not commonly used in calculations of abundances or densities; instead, researchers usually extrapolate estimates throughout the sampled area or strata in a uniform fashion. To date, we are not aware of any example from the tropics where realized distributions have been used to provide abundance or density estimates. Although the study species is perhaps an extreme example, our results suggest that to provide effective and precautionary (Cooney & Dickson, 2005) management information, the spatial distribution of observations must be used to inform both the design and also the resulting abundance and density estimates reported from faunal and floral surveys.

Global population estimates such as those presented in the IUCN redlist (http://www.iucnredlist.org/) are generally extrapolated from local- and regional-scale abundance and density estimates from the primary literature (Rodrigues *et al.*, 2006), which, from our review of the conservation biology literature, are unlikely to include realized distributions. It seems possible that such estimates are likely to be overestimates and to ensure a more precautionary approach the generation of realized density distributions should become the norm rather than the exception to enable conservation managers and researchers to extrapolate abundance and density estimates to 'realized' population sizes. For example, from a preliminary examination of the habitat available within our modelling area, we would assume that peccaries were distributed throughout primary and secondary forests types, which equate to an area of 483 km^2; however, our occupancy model indicates that only 241 km^2 is used by peccaries. If we assume a density of 0.5 individuals per square kilometre, population estimates would decline from 241 to 121 individuals. We therefore recommend the inclusion of geostatistics in the conservation toolbox to ensure the generation of informed management decisions across uncertain landscapes (Burgman, Lindenmayer & Elith, 2005).

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Supporting Information

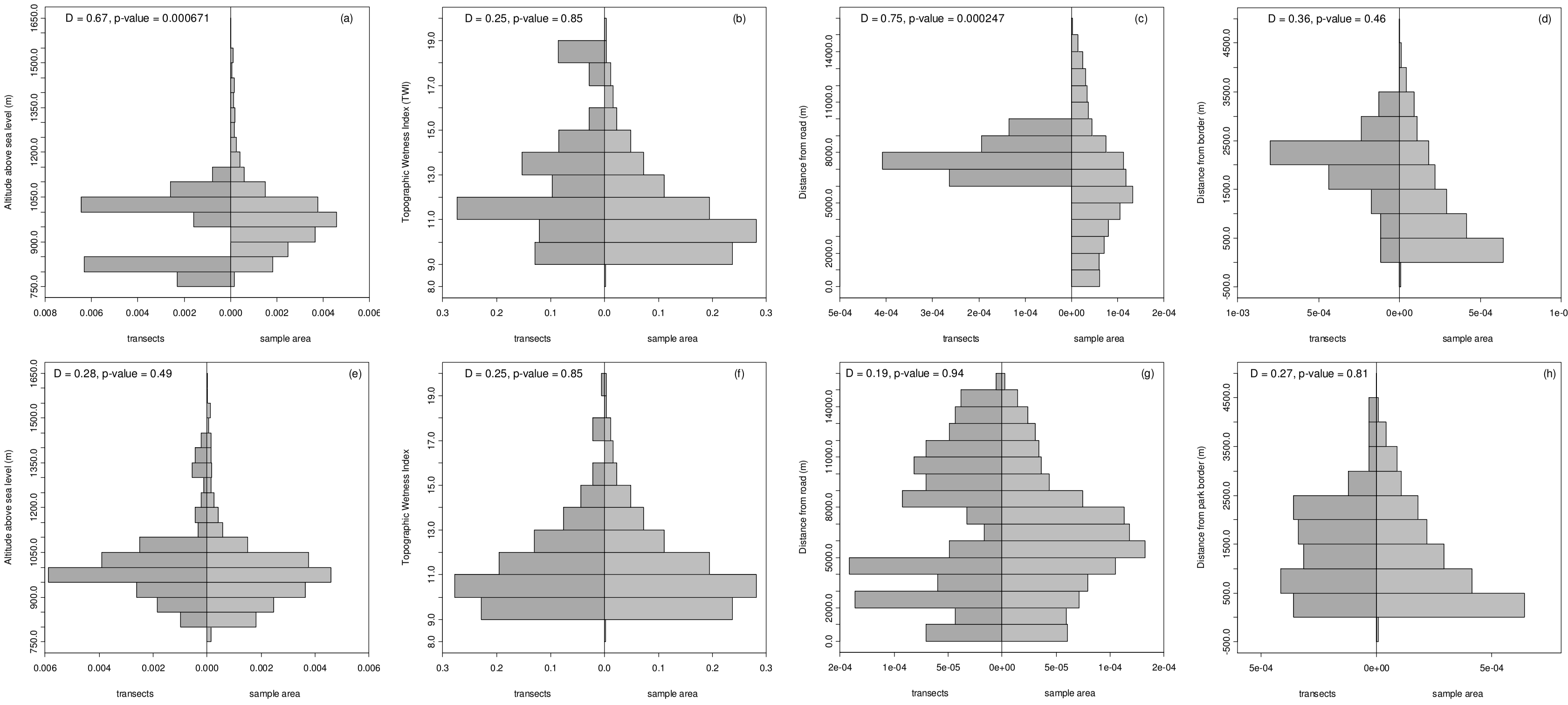
Additional Supporting Information may be found in the online version of this article:

Appendix S1. Sampling representativeness.
Appendix S2. Principal Components.
Appendix S3. Habitat Suitability.
Appendix S4. Generation of pseudo-absences.
Appendix S5. Regression – Kriging.
Appendix S6. Literature Review.

Supporting material

Appendix S1 Sampling representativeness

To evaluate how well our survey effort encompassed the environmental gradients in the study area (Núcleo Santa Virgínia) we compared the distribution of four of our environmental predictors within the study area. The non-parametric Kolmogorov-Smirnov test was used to compare the probability distribution of predictors within the study area with the area covered by i) our overall line-transect survey effort (figures (a) to (d)) and ii) the trails monitored by park guards (figures (e) to (h)).



Appendix S2 Principal Components

Principal component analysis (PCA) was used to derive linear predictors for modeling the spatial distribution of *Tayassu pecari*. As our PCA was derived from both quantitative and categorical variables we applied a function ("dudi.mix" from the ade4 package) that implements a generalization of the method proposed by Hill and Smith (1976). The principal components were obtained from a scaled and centred data matrix of our 7 environmental predictors, and axes derived from either i) the squared correlation coefficients with quantitative variables or ii) squared multiple correlation coefficients with polynoms correlation ratios with factors.

Importance of components

Based on the Kaiser-Guttman criterion (Legendre & Legendre 2003) only the first 4 principal components (with eigenvalues > 1) should be interpreted (Table S2.1).

Table S2.1 – Importance of components.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Eigenvalue	2.54	1.98	1.72	1.02	0.94	0.76	0.48	0.33	0.21
Proportion of variance	0.25	0.20	0.17	0.10	0.09	0.08	0.05	0.03	0.02
Cumulative proportion	0.25	0.45	0.63	0.73	0.82	0.90	0.94	0.98	1.00

Interpretation of PCA components

We used component loadings (Table S2.2) and visual inspection of maps (Fig. S2) to identify the environmental characteristics represented by our PCA axes. The four axes with eigenvalues >1 (PC1, PC2, PC3, and PC4) generally represented primary forest cover, slope and altitude, topographic wetness and forest cover, and classes of vegetation cover respectively, and PC5 represents distance from asphalt road and park border, but it was not possible to identify any obvious interpretation for the remaining axes

Table S2.2 – Contribution of environmental variables to the principal components.

Variable	Description	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
distBord	Distance from park border	-0.44	0.21	-0.11	0.16	0.37	-0.11	0.56	-0.45	0.24
distRoad	Distance from asphalt road	-0.23	0.43	0.28	-0.14	0.15	0.34	-0.61	-0.27	0.26
Slope	Topographic morphometry	-0.14	-0.52	0.34	-0.08	-0.12	0.29	0.05	-0.55	-0.44
DEM	Digital elevation model – altitude above sea level	-0.33	0.45	0.30	0.05	0.03	0.14	0.21	0.41	-0.60
Veg5	Vegetation cover – 5 categories									
	cat1	0.39	0.58	0.34	-0.47	-0.91	-0.13	0.48	-0.35	0.21
	cat2	2.03	0.30	-3.88	-0.73	1.20	7.69	2.10	0.76	0.20
	cat3	0.34	0.34	0.13	6.04	-1.53	0.88	-0.83	-0.58	0.09
	cat4	0.43	-0.36	0.45	0.14	1.37	-0.21	-0.19	0.20	-0.17
	cat5	-0.61	-0.21	-0.42	-0.08	-0.15	-0.04	-0.24	0.14	-0.05
Veg2	Vegetation cover - 2 categories: forest and non-forest									
	cat1	0.43	0.15	0.30	0.06	0.11	0.03	0.17	-0.10	0.04
	cat2	-0.61	-0.21	-0.42	-0.08	-0.15	-0.04	-0.24	0.14	-0.05
TWI	Topographic wetness index	0.26	0.34	-0.49	-0.03	0.10	-0.23	-0.23	-0.41	-0.54

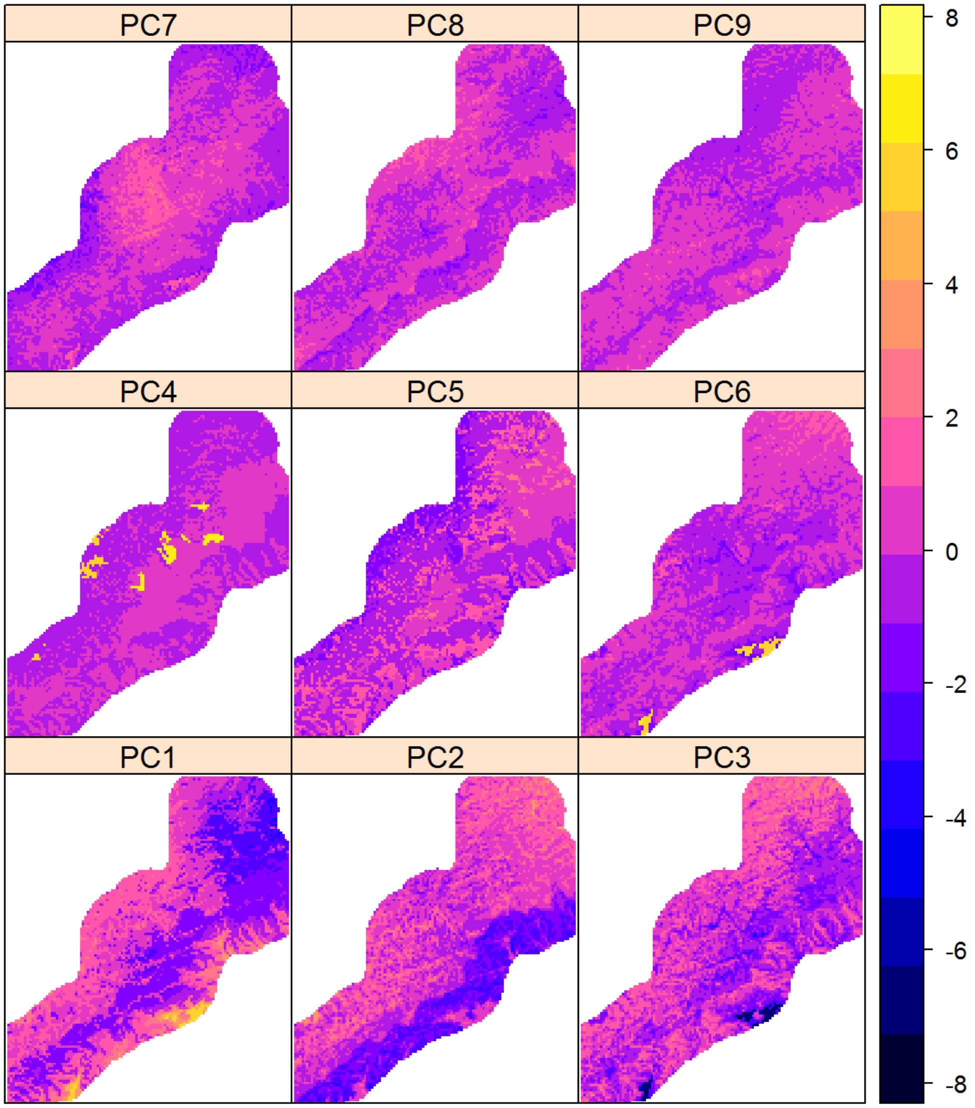


Fig. S2 - Visualization of principal component axes values mapped onto geographic space.

Appendix S3
Habitat Suitability

As the maximum-entropy and ENFA models scale habitat-suitability values differently when constructing maps we derived a standardized habitat suitability index (based on ranked values with a range of 0-100 that were centered at 50 around the median value from the original HSI values) to compare results between the 2 algorithms. Despite contrasting modelling approaches and algorithms there was a strong relationship between HSI maps from ENFA and MAXENT (Pearson correlation, r = 0.68, Fig. S3.1a). A scatterplot (Fig. S3.1b) revealed a much stronger positive correlation between values of MAXENT and ENFA suitability indexes above 50.

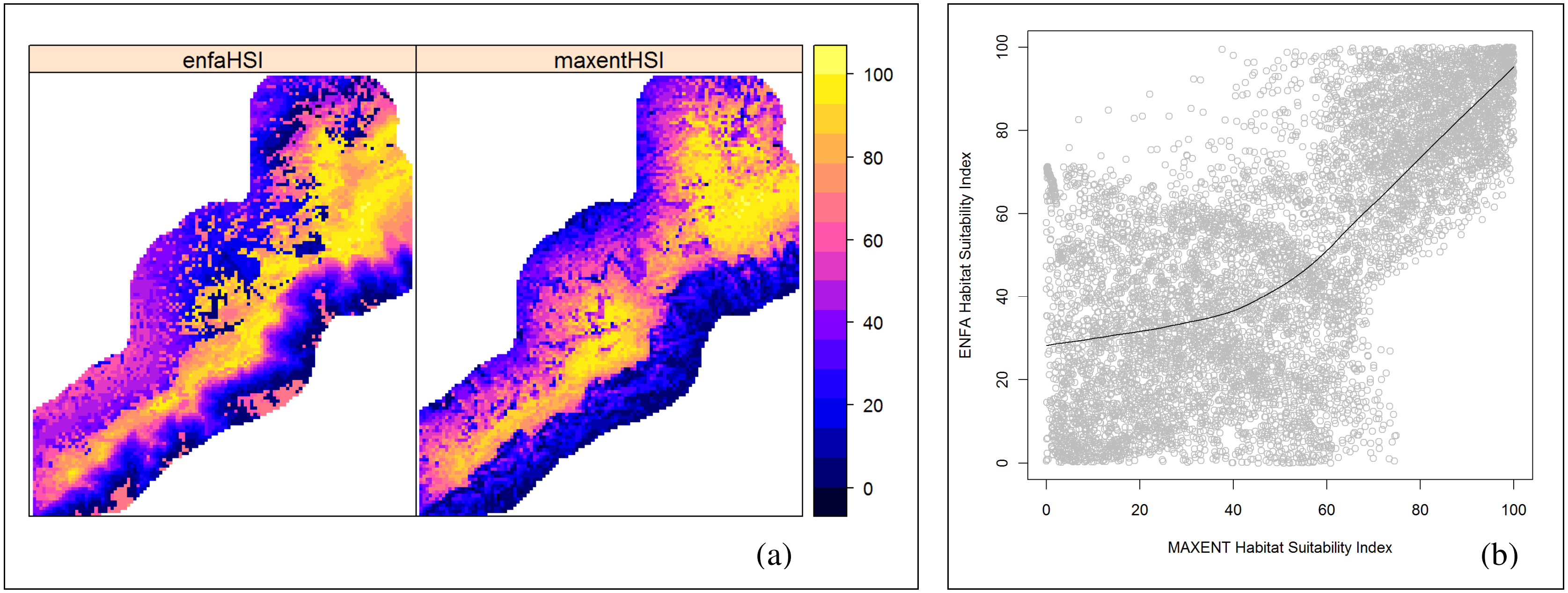


Fig. S3.1 Comparison of habitat suitability maps derived from 45 *T.pecari* locations using ENFA and MAXENT. (a) Visualization of the ranked HSI values in geographic space. (b) Correlation plot of ranked HSI values.

Pseudo-absence probability distribution weights

The weight maps derived from ENFA and MAXENT habitat suitability maps were also strongly correlated (Pearson correlation, r = 0.78; Fig. S4.2). Finding an increased correlation was expected as weight maps are calculated from i) habitat suitability maps and ii) a map of distances from the occurrences of *T.pecari*. The spatial similarity (Fig. S3.2a) and correlation between probability weights (Fig. S3.2b) suggests that there will be little difference between pseudo-absences derived from ENFA or MAXENT.

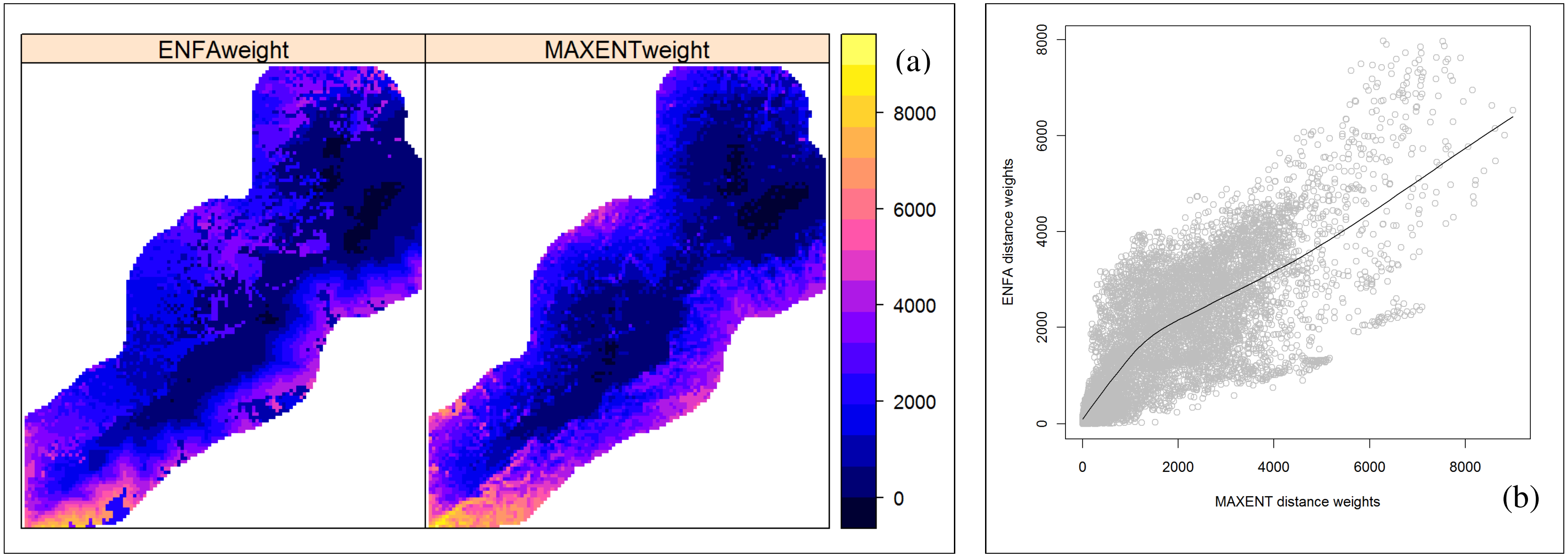


Fig. S3.2 Comparison of environmental distance weight maps derived from habitat suitability maps using ENFA and MAXENT. (a) Visualization of the weights in geographic space. (b) Correlation plot of weights derived from MAXENT and ENFA.

Appendix S4
Generation of pseudo-absences

As our objective was to generate "realized" distributions, expert validation was used to ensure the distribution of pseudo-absences reflected not only environmental suitability (i.e. species potential distribution) but also took into consideration anthropogenic and historical events that may preclude the presence of *T.pecari* in *a priori* environmentally suitable places. Collectively our 3 experts have > 30 years of conservation and ecological research in the Atlantic Forest of Sao Paulo state and >15 years of research experience in the study area. Experts evaluated a set of 45 pseudo-absences and should one point be considered invalid a new set of 45 pseudo-absences was generated. The validity of points was assessed taking into consideration the scale of analysis (774 km^2 modelling area and our 300 m resolution grids). It is therefore possible that some absence locations are not indeed true absences. However, the known benefits of using pseudo-absences e.g. reducing prediction errors (Chefaoui and Lobo, 2008) outweigh the potential for errors caused by absence generation. As such, we do not consider the use of pseudo-absence locations a limitation to the usefulness or applicability of the models and maps generated.

Appendix S5 Regression – Kriging

Pseudo-absences were generated and then presence–pseudo-absence locations are modelled with regression-kriging [a hybrid technique that uses kriging to make spatially explicit predictions from regression models and the residual variogram (Hengl, 2009)] to predict: i) species occupancy (with presences and pseudo-absences) and ii) density distributions (with Kernel smoothed densities and pseudo-absences). Readers are referred to the freely available Hengl (2009) for extensive and detailed demonstrations of the application of geostatistics, with pages 27–40 introducing regression-kriging.

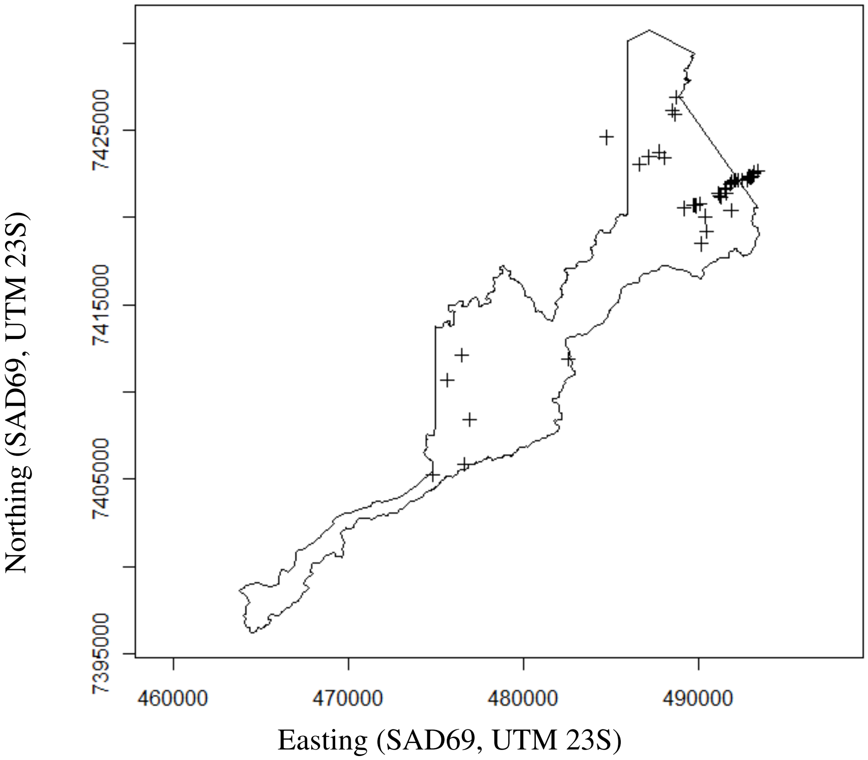


Fig S5.1 Spatial locations of 45 *T.pecari* occurence points (crosses) within our Atlantic forest study area (Núcleo Santa Virgínia – solid line).

We adopted a regression-kriging approach as although our 45 *T.pecari* locations were distributed throughout the study area there was distinct clustering with locations having a median nearest neighbour distance of 214 m (Fig. S5.2a) and spatial autocorrelation (Fig. S5.2b). We believe the approach we apply (adapted from Hengl *et al.* 2009) enables us to fit a useful model to the data, generating predictions with data that has been traditionally considered unsuitable for modeling. The data in our case being spatially autocorrelated which is a reflection of the species not a sampling bias. As our objective is to predict the occurrence and density distribution from 45 autocorrelated locations it therefore seems appropriate to account for spatial dependence within the modelling framework.

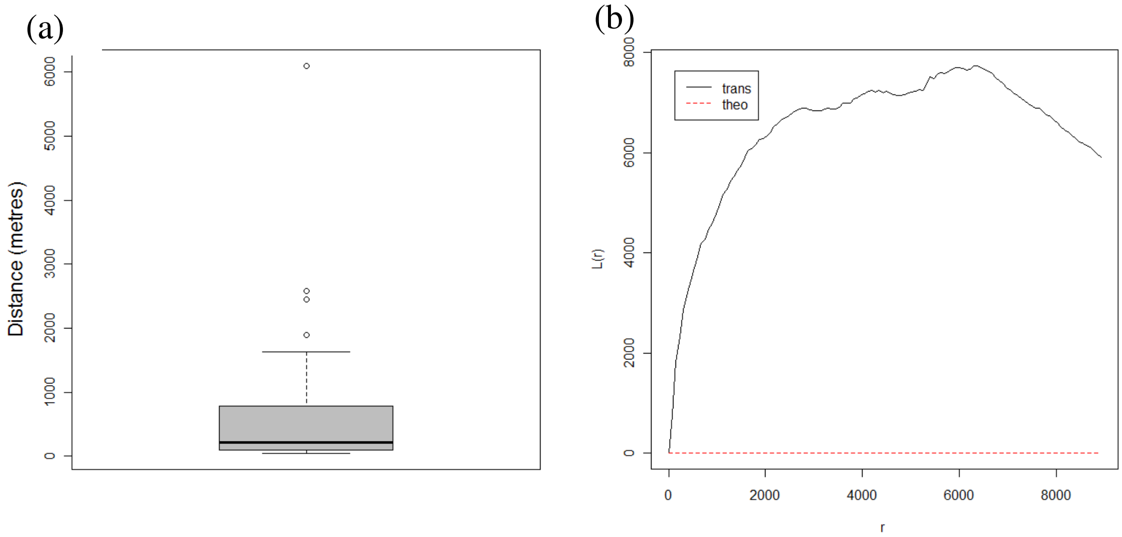


Fig S5.2 Spatial relations between *T.pecari* locations. (a) nearest neighbour distances and (b) spatial autocorrelation (L function derived from Ripleys K).

Kernel density estimates

The key parameter for kernel smoothing is the bandwidth i.e. the smoothing parameter, which can be connected with the choice of variogram in geostatistics (Hengl, 2009). The output of kernel smoothing is a map showing spatial pattern of clustering of the response. To determine the kernel smoothing parameter (bandwidth) objectively we followed Berman & Diggle (1989), obtaining a value of 305 meters, although based on the Mean Squared Error (MSE) of the Kernel density any value above 305 seems suitable (Fig S5.3).

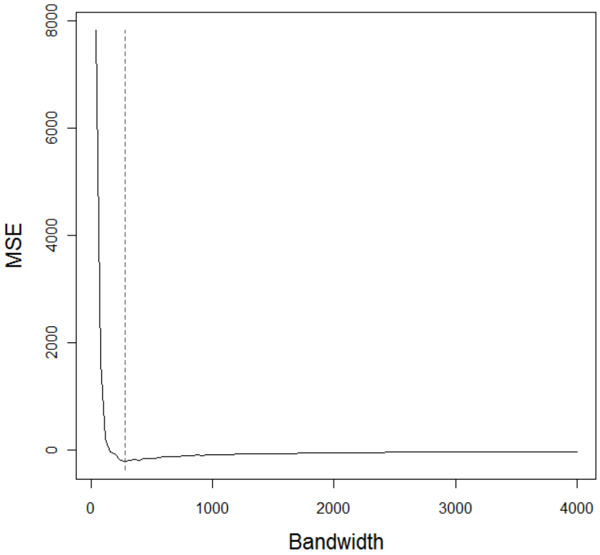


Fig S5.3 Selection of the optimal bandwidth using the method of Berman and Diggle (1989)

Variogram modeling

We used a generalised linear model (GLM, family=binomial, link="logit") to predict the occurrence of *T.pecari* (presence–pseudo-absences), which is a separate process to the estimation of the log transformed Kernel density (family=gaussian, link="identity") obtained via point-pattern analysis. Although the response variables are derived independently they are modeled within the same framework i.e. regression, then variogram of residuals, and finally regression-kriging. The outputs from this process are i) an occupancy model that reveals areas where *T.pecari* are likely to occur and ii) a realised density distribution that provides additional information as to how dense the population will be. Although we are unable to estimate population levels for *T.pecari*, the density distribution also represents a relative intensity of use. The ability to map areas of relative use is important for the management and conservation of Neotropical forests as *T.pecari* are recognised as ecosystem engineers: directly influencing the structure, composition and dynamics of forest areas through seed predation, trampling and herbivory (Beck, 2006; Beck, Thebpanya, & Filiaggi, 2010).

The spatial autocorrelation in the regression analysis is modeled via a variogram of the resiudals (Fig S5.4). Although"noisy" the variograms show clear autocorrelation up to distances of 5000 m, which is similar to the results from Ripleys K (Fig. S5.2b). Modelling the spatial relationship of the residuals is therefore necessary to generate reliable predictions.

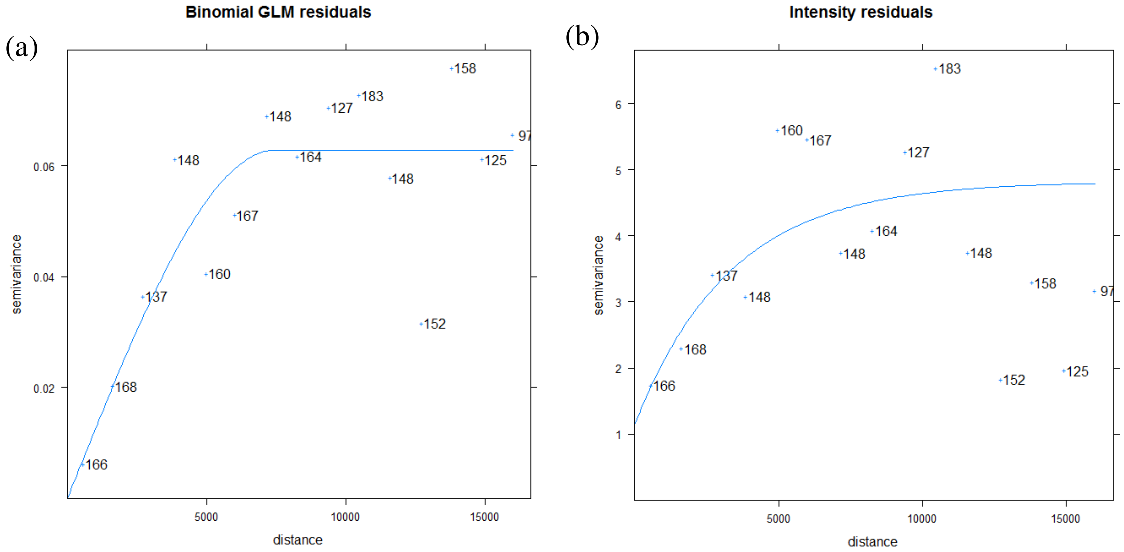


Fig S5.4 Variogram models for residuals fitted using occurrence–pseudo-absence locations: (a) probability values (b) density values (logits).

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Appendix S6 Literature Review

We used Web of Science (http://www.isiwebofknowledge.com/) to search for publications that present density estimates of terrestrial mammals. Our initial search criteria (search conducted on 8 October 2010) were as follows:

Topic=(densit* or abundanc*) AND Topic=(mamma*)
Refined by: Publication Years=(2008 OR 2009 OR 2006 OR 2007 OR 2010 OR 2005) AND Source Titles=(CONSERVATION BIOLOGY OR ANIMAL CONSERVATION OR BIODIVERSITY AND CONSERVATION OR BIOLOGICAL CONSERVATION OR ORYX)
Timespan=All Years.

This search returned a total of 226 publications which were then read and filtered to ensure we considered only those that present densities i.e. express results as number of individuals or sign such as nests or tracks per unit area. We excluded studies that only presented relative abundances i.e. encounter/capture rates as we were interested in the application of spatially explicit techniques to inform / derive / refine density estimates. From a total of 226 potential reports we obtained 24 that met these criteria (Table S6).

Each of the 24 articles was checked to see if they considered spatial dependencies in the data. We define “considered” as testing for spatial relationships / dependencies for example via correlograms, variograms, mantel test and / or explicitly including spatial relationships in final predictions. We did not include cases where spatial independence was “assumed” and or autocorrelation was “reduced” or otherwise “accounted for” but not empirically tested. We did however consider kernel based home range estimates from telemetry studies as incorporating spatial relationships.

We recognised four classes of techniques: Distance (Distance based sampling methodologies), Mark-recapture, Home-range (density estimates from individual home-range estimates, commonly obtained via telemetry studies), Other (includes total counts, surveys of indirect sign etc).

Table S6 – References used to evaluate whether spatial dependencies are considered when deriving density estimates.

Technique	Consider spatial	Authors	Year	Title	Journal	Vol	Pages
Other	no	Agoramoorthy, G;Sha, C M;Hsu, M J	2006	Population, diet and conservation of malayan flying lemurs in altered and fragmented habitats in singapore	Biodiversity and Conservation	15	2177-2185
Distance	no	Clark, C J;Poulsen, J R;Malonga, R;Elkan, P W	2009	Logging Concessions Can Extend the Conservation Estate for Central African Tropical Forests	Conservation Biology	23	1281-1293
Other	no	Cousins, J A;Compton, S G	2005	The Tongan flying fox Pteropus tonganus: status, public attitudes and conservation in the Cook Islands	Oryx	39	196-203
Mark-recapture	no	Firth, R S C;Brook, B W;Woinarski, J C Z;Fordham, D A	2010	Decline and likely extinction of a northern Australian native rodent, the Brush-tailed Rabbit-rat Conilurus penicillatus	Biological Conservation	143	1193-1201
Mark-recapture	no	Hawkins, C E;Racey, P A	2005	Low population density of a tropical forest carnivore, Cryptoprocta ferox: implications for protected area management	Oryx	39	35-43
Home-range	no	Hawkins, C E;Racey, P A	2005	Low population density of a tropical forest carnivore, Cryptoprocta ferox: implications for protected area management	Oryx	39	35-43
Distance	no	Inogwabini, B I;Matungila, B;Mbende, L;Abokome, M;Tshimanga, T W	2007	Great apes in the Lake Tumba landscape, Democratic Republic of Congo: newly described populations	Oryx	41	532-538
Other	yes	Jepsen J U; Madsen A B; Karlsson M; Groth D	2005	Predicting distribution and density of European badger (Meles meles) setts in Denmark	Biodiversity and Conservation	14	
Home-range	yes	Jhala, Y V;Mukherjee, S;Shah, N;Chauhan, K S;Dave, C V;Meena, V;Banerjee, K	2009	Home range and habitat preference of female lions (Panthera leo persica) in Gir forests, India	Biodiversity and Conservation	18	3383-3394
Mark-recapture	no	Johnson, A;Vongkhamheng, C;Hedemark, M;Saithongdam, T	2006	Effects of human-carnivore conflict on tiger (Panthera tigris) and prey populations in Lao PDR	Animal Conservation	9	421-430
Distance	no	Jorge, M L S P	2008	Effects of forest fragmentation on two sister genera of Amazonian rodents (Myoprocta acouchy and Dasyprocta leporina)	Biological Conservation	141	617-623

Distance	no	Kiffner, C;Meyer, B;Muhlenberg, M;Waltert, M	2009	Plenty of prey, few predators: what limits lions Panthera leo in Katavi National Park, western Tanzania?	Oryx	43	52-59
Other	no	Kindberg, J;Ericsson, G;Swenson, J E	2009	Monitoring rare or elusive large mammals using effort-corrected voluntary observers	Biological Conservation	142	159-165
Mark-recapture	no	Kolowski, J M;Alonso, A	2010	Density and activity patterns of ocelots (Leopardus pardalis) in northern Peru and the impact of oil exploration activities	Biological Conservation	143	917-925
Distance	yes	Kuehl, H S;Nzeingui, C;Yeno, S L D;Huijbregts, B;Boesch, C;Walsh, P D	2009	Discriminating between village and commercial hunting of apes	Biological Conservation	142	1500-1506
Other	no	Lynam, A J;Laidlaw, R;Noordin, W S W;Elagupillay, S;Bennett, E L	2007	Assessing the conservation status of the tiger Panthera tigris at priority sites in Peninsular Malaysia	Oryx	41	454-462
Mark-recapture	no	Manor, R;Saltz, D	2008	Conservation implications of competition between generalist and specialist rodents in Mediterranean afforested landscape	Biodiversity and Conservation	17	2513-2523
Distance	no	Naranjo, E J;Bodmer, R E	2007	Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico	Biological Conservation	138	412-420
Distance	no	Parry, L;Barlow, J;Peres, C A	2009	Hunting for Sustainability in Tropical Secondary Forests	Conservation Biology	23	1270-1280
Home-range	no	Sepulveda, M A;Bartheld, J L;Monsalve, R;Gomez, V;Medina-Vogel, G	2007	Habitat use and spatial behaviour of the endangered Southern river otter (Lontra provocax) in riparian habitats of Chile: Conservation implications	Biological Conservation	140	329-338
Home-range	yes	Simcharoen, S;Barlow, A C D;Simcharoen, A;Smith, J L D	2008	Home range size and daytime habitat selection of leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand	Biological Conservation	141	2242-2250
Mark-recapture	no	Simcharoen, S;Pattanavibool, A;Karanth, K U;Nichols, J D;Kumar, N S	2007	How many tigers Panthera tigris are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture-recapture sampling	Oryx	41	447-453
Other	no	Stephens, P A;Zaumyslova, O Y;Miquelle, D G;Myslenkov, A I;Hayward, G D	2006	Estimating population density from indirect sign: track counts and the Formozov-Malyshev-Pereleshin formula	Animal Conservation	9	339-348
Mark-	no	Trolle, M;Noss, A J;Lima, E	2007	Camera-trap studies of maned wolf density in the	Biodiversity	16	1197-

recapture		D S;Dalponte, J C		Cerrado and the Pantanal of Brazil	and Conservation		1204
Other	no	Wegge, P;Odden, M;Pokharel, C P;Storaas, T	2009	Predator-prey relationships and responses of ungulates and their predators to the establishment of protected areas: A case study of tigers, leopards and their prey in Bardia National Park, Nepal	Biological Conservation	142	189-202

6 CONCLUSÕES FINAIS

Neste trabalho demonstrou-se como variáveis ambientais e antrópicas influenciam grandes mamíferos em remanescentes contínuos de Mata Atlântica Brasileira. Especificamente, como é necessário avaliar aspectos antrópicos e ambientais para entender os padrões de distribuição e abundância de mamíferos de médio e grande porte em remanescentes maiores que 10 000 ha. Este resultado apoia e amplia as pesquisas recentes que demonstraram como "aging human-modified landscapes" estão levantando novos desafios para a conservação da biodiversidade (Galetti *et al.* 2009, Metzger *et al.* 2009, Pardini *et al.* 2009, Tabarelli *et al.* 2010, Aronson *et al.* 2011, Carlson *et al.* 2011).

Remanescentes contínuos da Mata Atlântica apresentam um ambiente altamente heterogêneo, resultado dos fatores ambientais e dos impactos antrópicos (Capítulos 2, 3 e 4). Mas para algumas espécies de mamíferos de médio e grande porte a heterogeneidade induzida por aspectos antrópicos reduz a adequação do hábitat dentro dos remanescentes contínuos restantes (Capítulos 2, 3 e 4), gerando "ilhas" de hábitat adequado para espécies de mamíferos dentro de áreas protegidas (Capítulos 3 e 4). Este resultado sugere que para a manutenção da biodiversidade nos remanescentes da Mata Atlântica contínua é necessário adotar e aplicar conceitos e ações que são tipicamente propostas para pesquisas sobre efeitos de perda e fragmentação de hábitats. Os resultados do Capítulo 2 mostraram que padrões na distribuição da diversidade e riqueza variam tanto dentro quanto entre áreas protegidas e como as relações espaciais da diversidade e riqueza devem fazer parte da gestão dos parques. Além disso, os capítulos 3 e 4 mostraram que para as espécies mais sensíveis e/ou ameaçadas de extinção é necessária uma gestão "ativa" dentro de um quadro de meta-população.

Os resultados apresentados nos 4 capítulos dessa tese destacam que, embora a Mata Atlântica seja o bioma mais intensamente estudado para mamíferos no Brasil (Brito *et al.* 2009), ainda não se atingiu o conhecimento necessário para a conservação e gestão eficaz desta classe na Mata Atlântica. Estudos futuros enfocando na ecologia das espécies, preferências de hábitat e densidades populacionais são obrigatórios para informar e dar suporte às atividades de gerenciamento dentro das áreas protegidas. Estes estudos são particularmente necessários em áreas maiores, as quais poderiam servir como fontes para atividades de restauração futuros (Fonseca *et al.* 2009, Metzger 2009, Aronson *et al.* 2011, Carlson *et al.* 2011). Apesar da riqueza e diversidade de espécies ser um critério para estabelecimento do valor de conservação de zonas dentro dos parques (Instituto Florestal

2008), p. 257), ainda não existem dados que definem um mapa de distribuição das espécies espacialmente explícito para qualquer grupo da flora ou fauna dentro das áreas protegendo os maiores remanescentes da Mata Atlântica Brasileira (Serra do Mar massif (Ribeiro *et al.* 2009)). Estudos adicionais são necessários para permitir a definição de zonas dentro das áreas protegidas como definido pela legislação brasileira (Lei: 9.985/2000 (SNUC)). Este zoneamento é necessário para a realização dos objetivos múltiplos das áreas protegidas (incluindo a manutenção da biodiversidade e o fornecimento dos serviços dos ecossistemas) dentro do contexto sócio-econômico em um escala regional e nacional (Wells & Brandon 1993, Halpin 1997).

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