UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

DEFAUNAÇÃO E FRAGMENTAÇÃO FLORESTAL NA MATA ATLÂNTICA SUBTROPICAL E SUAS CONSEQUÊNCIAS PARA A REGENERAÇÃO DE *Araucaria angustifolia*

CARLOS RODRIGO BROCARDO

Junho - 2017

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CARLOS RODRIGO BROCARDO

Orientador: Mauro Galetti Rodrigues

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 - Zoologia

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Rio Claro, 13 de junho de 2017

Dedico a Amarildo, Diana e Daiane

O que os homens do Paraná executaram pelas derrubadas e queimadas do mato não pode ser descrito. Em nenhum outro país o mato é tão absurdamente destruído como aqui (1931)... Em pouco tempo as primitivas regiões de matas estarão completamente destruídas no Estado do Paraná. As últimas reservas de matas virgens talvez resistirão ainda durante uma geração (1968).

Reinhard Maack (1857-1969)

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RESUMO GERAL

A ação humana tem levado ao declínio nas áreas cobertas por habitats naturais em todo mundo, levando consigo a perda de espécies e de interações ecológicas. Nesse contexto, com um mundo dominado pela presença humana, torna-se fundamental compreender como as espécies respondem a essas alterações, quais mecanismos permitem sua persistência, e como as suas interações ecológicas são afetadas. Nessa tese, com dados coletados entre 2013 e 2017, abordei dois temas, o primeiro busca compreender como fragmentação florestal atua na extinção e persistência de mastofauna (Capítulo II: Large forest remnants and connectivity explain mammal resilience in a landscape dominated by commodity croplands), e segundo busca avaliar como as interações com a árvore dominante (*Araucaria angustifolia*) no ecossistema de estudo são afetadas pela redução de habitat (Capítulo III: Forest fragmentation and selective logging affect the seed survival and recruitment of a relictual conifer). Os dados do Capítulo II foram coletados com armadilhamento fotográfico que somou mais de 8.236 câmeras-trap/dia, e os resultados indicaram o tamanho dos remanescentes como principal responsável pela manutenção da riqueza e biomassa de mamíferos de médio e grande porte. Os dados do Capítulo III foram coletados com uma série de experimentos de remoção de sementes e amostragem de regeneração de *A. angustifolia*, com resultados indicando o tamanho do fragmento e abundância de *A. angustifolia* como principais variáveis explanatórias em explicar as taxas de remoção de sementes, bem como a regeneração dessa espécie.

Palavras-chave: Floresta vazia, caça, Floresta Ombrófila Mista, interação animal-planta, *Dasyprocta azarae*

ABSTRACT

Humans have been occupying almost all ecosystems in the world, directly causing loss of species and ecological interactions. In this context, with a world dominated by humans, it is fundamental understanding how species respond to this changes, what mechanisms allow their persistence and how ecological interactions are affected. In this thesis, with data collected between 2013 and 2017, I addressed two themes, in the first one I investigated the effects of forest fragmentation on extinction and persistence of mammals (Chapter II: Large forest remnants and connectivity explain mammal resilience in a landscape dominated by commodity croplands), and in second theme, I evaluated how interactions with the dominant tree (*Araucaria angustifolia*) are affected by habitat reduction (Chapter III: Forest fragmentation and selective logging affect seed survival and recruitment of relictual conifer). The data of Chapter II were collected with camera trap sampling that added more than 8,236 camera-traps / day, and the results indicated the size of the remnants as the main predictor of richness and biomass of large and medium-sized mammals. The data of Chapter III were collected with seed removal experiments and sampling of *A. angustifolia* regeneration. The results indicated the fragment size and *A. angustifolia* abundance as main explanatory variables for explaining the rates of seed removal, as well as the regeneration of this species.

Key-words: Empty forest, poaching, *Araucaria* moist forest, animal-plant interaction, *Dasyprocta azarae*

INTRODUÇÃO GERAL

Ecossistemas de todo mundo têm sido convertidos em áreas dominadas por atividades humanas, como agricultura, pastagens para gado e áreas urbanas. Estima-se que 83% de terras livres de gelo no planeta sofram influência direta da presença humana (Sanderson et al. 2002), e a perda de florestas chegue perto de 200 mil km² por ano (Hansen et al. 2013). O saldo desse avanço é a substancial redução de habitats naturais, e a consequente fragmentação e degradação dos ambientes remanescentes (Haddad et al. 2015). De fato, a ação humana tem sido tão impactante na superfície do planeta que foi proposto que vivemos sob uma nova época geológica, o Antropoceno, onde uma espécie (*Homo sapiens*) tem conduzido alterações que vão desde grandes impactos locais, como conversão do uso do solo em agricultura intensiva de larga escala, a influências planetárias, como o aquecimento global, devido à emissão de carbono emitido por atividades industriais (Johnson et al. 2017; Smith & Zeder 2013; Steffen et al. 2011).

Uma das facetas do Antropoceno é a perda de espécies, que vem ocorrendo de forma tão acelerada que é comparável às extinções em massa ocorridas no passado do planeta (Barnosky et al. 2011; Dirzo et al. 2014). Estima-se que a atual taxa de extinção (número de espécies extintas / milhares de anos) seja até 1000 vezes superior que as taxas de extinção tenham sido no passado (Pimm et al. 2014). Sendo a redução de habitat, causada diretamente pelo avanço das atividades humanas, uma das principais responsáveis por essa crise de biodiversidade (Ceballos & Ehrlich 2002; Galetti & Dirzo 2013; Pimm et al. 2014; Young et al. 2016). Para clados como vertebrados, a redução de habitat tem sido particularmente danosa, levando a contrações na distribuição de diversos grupos (Gaston et al. 2003; Hoffmann et al. 2010). Faunas intactas de mamíferos terrestres de maior porte (>20 kg), por exemplo, só podem ser

encontradas em menos de 21% da superfície do planeta, e na maioria dos casos se restringem a habitats remotos (Morrison et al. 2007).

Embora outros fatores atuem em sinergismo com a redução de habitat, como a sobre-exploração das espécies, que no caso de animais terrestres está, sobretudo, ligada à caça (Dirzo et al. 2014; Galetti & Dirzo 2013; Peres & Palacios 2007; Wilkie et al. 2011; Young et al. 2016) (Figura 1). A caça de subsistência, e principalmente a comercial, tem levado a declínios de até 90% na abundância de mamíferos e de até 76% na abundância de aves em ambientes tropicais (Benítez-López et al. 2017). Essa atividade se torna substancialmente favorecida pela fragmentação de habitas (Cullen et al. 2001; Peres 2001), embora cause danos mesmo a populações silvestres em habitats naturais pouco modificados (Antunes et al. 2016; Galetti et al. 2016; Galetti & Dirzo 2013; Peres & Palacios 2007). De fato o termo "floresta vazia" expressa bem esse fenômeno, a perda de animais em ambientes relativamente prístinos (Redford 1992; Wilkie et al. 2011). Diferente de perdas de cobertura de vegetação natural, que podem ser facilmente perceptível, mesmo por meios remotos, a perda de espécies animais dentro de ambientes naturais é mais difícil de ser percebida e mensurada, e se desdobra para consequências diversas no ambiente, sendo uma das peculiaridades da "defaunação contemporânea" (Galetti & Dirzo 2013; Peres & Palacios 2007). A defaunação contemporânea foi pela primeira vez abordada em 1988, durante o Simpósio Internacional de interação animal-planta, realizado na Universidade Estadual de Campinas (Galetti & Dirzo 2013), e posteriormente debatida em dois trabalhos (Dirzo & Miranda 1990; Dirzo & Miranda 1991). Desde então estudos vem reforçando as consequências da defaunação sobre processos ecológicos, e mesmo evolutivos, nos quais os animais estão envolvidos (Figura 1) (Dirzo et al. 2014; Estes et al. 2011; Galetti et al. 2013; Young et al. 2016).

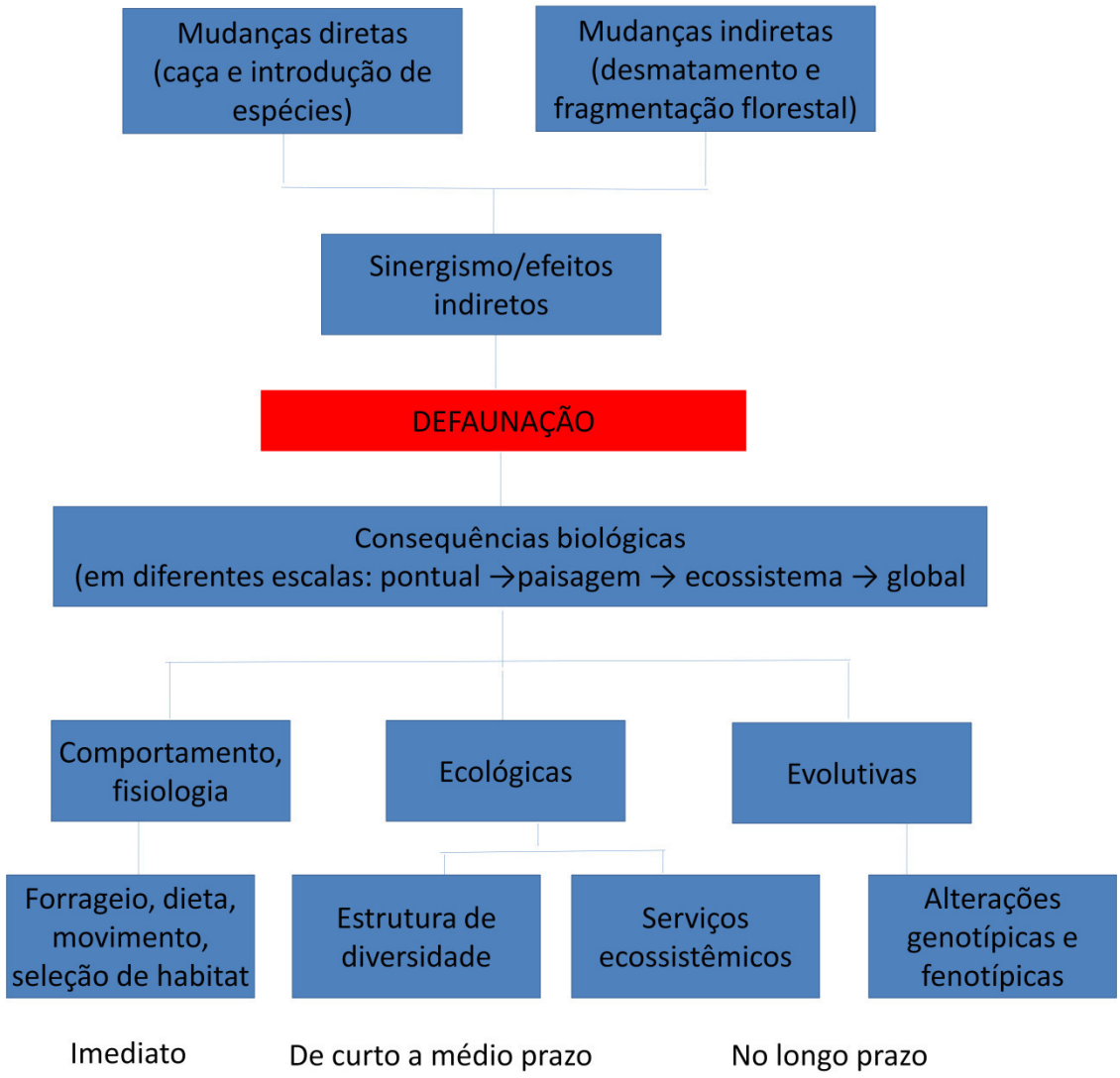


Figura 1. Diagrama conceptual das causas e consequências da defaunação imediatamente, em curto e médio prazo e no longo prazo. Adaptado de Galetti & Dirzo (2013).

A perda de predadores de topo de cadeia pode levar ao crescimento descontrolado de herbívoros, o que prejudica o recrutamento vegetal, além de indiretamente afetar populações de outros animais (Côté et al. 2004; Estes et al. 2011). Já a baixa presença de herbívoros, como ungulados, diminui a pressão sobre a vegetação (Brocardo et al. 2013; Estes et al. 2011; Silman et al. 2003), e ainda pode influenciar no aumento da população de espécies de menor porte, como roedores, devido ao relaxamento competitivo (Figura 2) (Galetti et al. 2015b; Young et al. 2015). Para processos como a

dispersão e predação de sementes, a defaunação atua de forma antagônica, diminuindo por um lado as taxas de dispersão dos propágulos (Galetti et al. 2006; Nuñez-Iturri et al. 2008; Terborgh et al. 2008; Wright et al. 2007; Wright et al. 2000), ao mesmo tempo que por outro lado aumenta a incidência de predação sobre as sementes, devido ao crescimento da população de pequenos roedores, principais granívoros, que além de não serem espécies preferenciais de caçadores, tendem a ser favorecidas pela ausência das espécies maiores (Figura 2) (Galetti et al. 2015a; Galetti et al. 2015b; Wright et al. 2000).

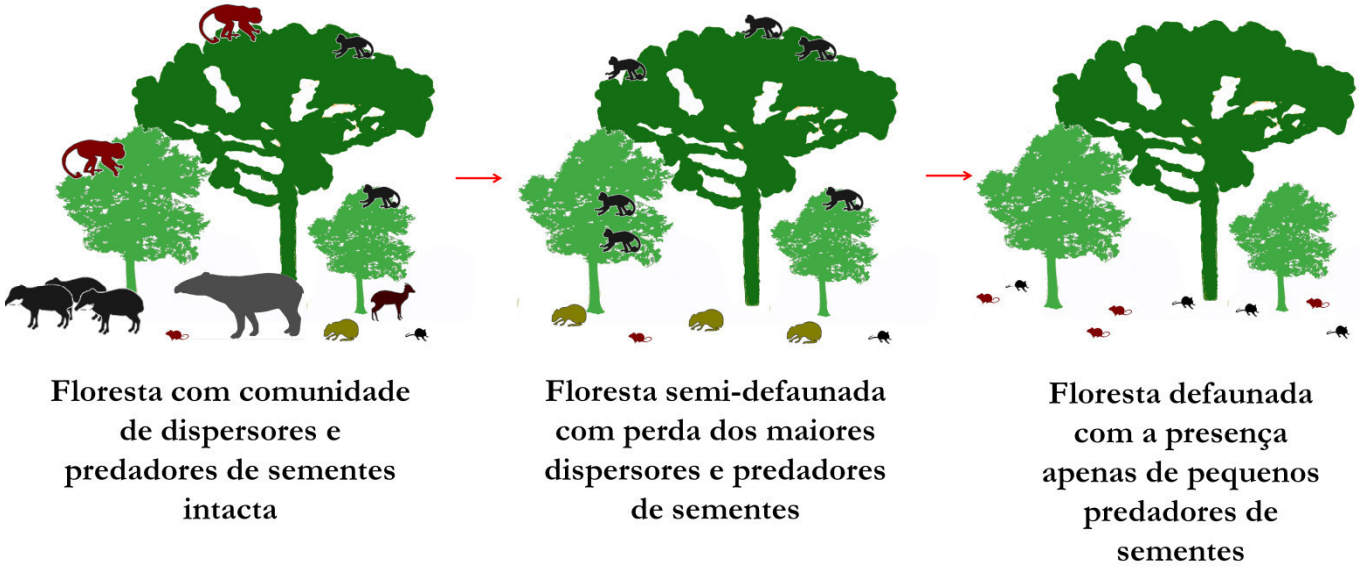


Figura 2. Mudança na comunidade de mamíferos frugívoros e predadores de sementes em diferentes níveis de defaunação, com a gradual perda de dispersores de maior porte e crescimento na abundância de pequenos predadores de sementes.

Além dos danosos efeitos que a quebra de interações têm nos ecossistemas, em última instância a defaunação afeta os serviços ecossistêmicos providos às sociedades humanas (Bello et al. 2015; Galetti et al. 2015b; Young et al. 2016). Por exemplo, animais de maior porte dispersam sementes maiores, que pertencem às espécies de árvores com madeira mais dura, ou seja, que têm maior potencial de sequestro de carbono, desse modo, com a perda de grandes dispersores a floresta passa a reter menos carbono (Bello

et al. 2015). Assim ampliar a proteção sobre as espécies e os ecossistemas tem implicações não só na conservação da biodiversidade, mas também importância vital para nossa própria existência no planeta (Crist et al. 2017; Johnson et al. 2017). Para esse propósito é fundamental compreender quais mecanismos permitem a persistência das espécies, e como suas interações ecológicas são afetadas em um mundo antrópico. Da mesma forma é um grande desafio indicar como podemos atuar para minimizar os impactos das ações humanas, e como reverter esses processos.

No capítulo I desse trabalho apresento uma descrição do ambiente de estudo e as ameaças à sua conservação. Nos capítulos subsequentes apresento resultados de minha pesquisa em campo. No capítulo II (Large forest remnants and connectivity explain mammal resilience in a landscape dominated by commodity croplands) avaliei a resiliência, riqueza, abundância e biomassa de mamíferos de médio e grande porte na Mata Atlântica subtropical, sobretudo na Floresta Ombrófila Mista em relação aos efeitos do tamanho do habitat remanescente e a conectividade. Em um segundo experimento (Capítulo III: Forest fragmentation and selective logging affect the seed survival and recruitment of a relictual conifer) medi os efeitos combinados da fragmentação florestal e da alteração na comunidade de granívoros sobre a predação e regeneração da árvore dominante nesse ecossistema, *Araucaria angustifolia*, testando as hipóteses apresentadas na Figura 3.

Os resultados obtidos nessa tese preenchem uma lacuna de conhecimento sobre uma importante região do Bioma Mata Atlântica, bem como direcionam medidas que poderão mitigar os efeitos antrópicos sobre esse e outros ecossistemas.

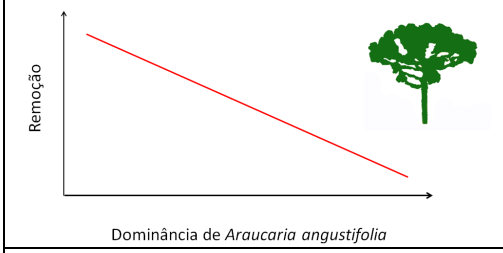
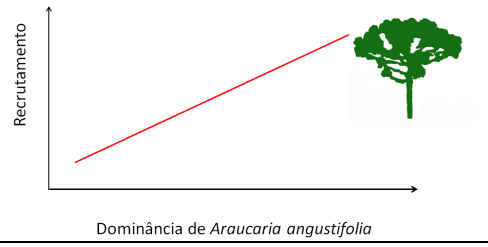
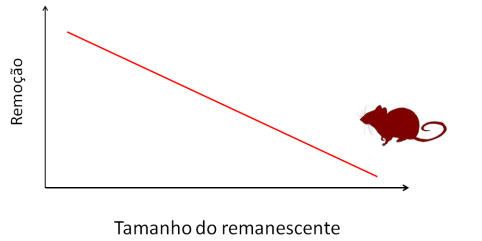
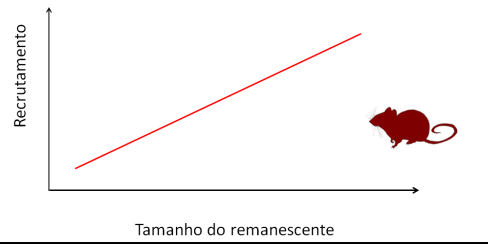
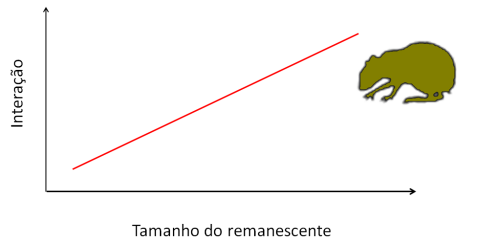
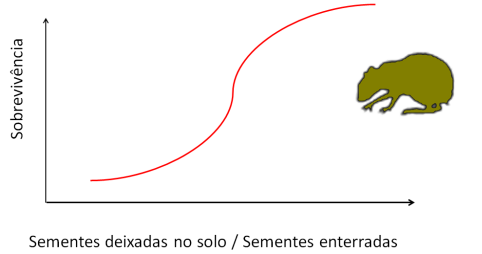
Hipótese	Reposta esperada
Hipótese I: A remoção de sementes de *Araucaria angustifolia* será negativamente relacionada à dominância dessa espécie, e em sentido oposto, a regeneração será positivamente relacionada à dominância.	 
Hipótese II: A remoção de sementes de *Araucaria angustifolia* será negativamente relacionada ao tamanho do remanescente florestal, devido, sobretudo ao crescimento nas interações com pequenos roedores. A regeneração seguirá sentido oposto, sendo positivamente relacionada ao tamanho do remanescente.	 
Hipótese III: A interação com cutias (*Dasyprocta azarae*), maior dispersor de *A. angustifolia,* será negativamente relacionada ao tamanho da área remanescente.	
Hipótese IV: Sementes enterradas (estocadas no solo) terão maior probabilidade de sobreviver do que sementes deixadas acima do solo, independentemente da distância de *A. angustifolia* produtivas.	

Figura 3. Hipóteses testadas no capítulo III.

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Capítulo I. Caracterização do ecossistema de estudo

Floresta Ombrófila Mista

A Floresta Ombrófila Mista (FOM), também conhecida como Mata dos Pinhais ou Floresta com Araucária, constitui uma formação florestal do bioma Mata Atlântica, e é considerada uma das ecorregiões globais (Dinerstein et al. 1995; Ribeiro et al. 2009). A distribuição original dessa floresta abrangia uma área de mais de 238 mil km², com um núcleo principal que se estendia desde o sudeste do estado de São Paulo indo até noroeste da província de Misiones na Argentina, incluindo a maior parte dos estados do Paraná e Santa Catarina e porção norte do Rio Grande do Sul (Figura 1). Núcleos menores ocorriam de forma disjunta ao longo da Serra do Mar (São Paulo), Serra de Paranapiacaba (São Paulo), Serra da Mantiqueira (São Paulo, Minas Gerais e Rio de Janeiro) e em pontos isolados de Minas Gerais, São Paulo e Rio Grande do Sul (Backes 2009; Hueck 1953; Tortorelli 2009). A ocorrência da FOM está relacionada ao clima subtropical, com invernos sujeitos a geadas, e precipitação pluviométrica bem distribuída ao longo do ano (Backes 2009), sendo que sua a expansão até os limites atuais teve início por volta de 3.000 anos atrás, com o estabelecimento de um clima mais úmido (Behling 2002).

A Floresta com Araucária tem como característica principal a presença e dominância de *Araucaria angustifolia* (Backes 2009) (Figura 2), que em ambientes conservados pode apresentar densidades de 30 a 60 indivíduos adultos por hectare (Brocardo et al. 2017; Mantovani et al. 2004; Paludo et al. 2009). Espécie popularmente conhecida como pinheiro-brasileiro, pinheiro-do-paraná ou simplesmente pinheiro (Backes 2009; Mattos 2011), se distingue da maioria das espécies da família Araucariaceae por ser em regra dióica, com a produção de estróbilos femininos (pinhas) e masculinos em indivíduos distintos (Figura 2) (Farjon 2010; Mattos 2011). O ciclo de reprodutivo dura entre 20 e 24 meses, ocorrendo em uma primeira etapa a formação dos estróbilos femininos e

masculinos, com a posterior a polinização pelo vento (cerca de seis meses após o aparecimento dos estróbilos), e na fase final um crescimento das pinhas até a maturação, com a queda das sementes (pinhões) no período entre o outono e inverno (Mantovani et al. 2004) (Figura 2). A produção anual de pinhões em florestas nativas varia de acordo com número de indivíduos adultos, podendo atingir de 117 kg/ha a 222,4 kg/ha, o que equivale de 17 mil a 31 mil sementes por hectare, respectivamente (Figueiredo-Filho et al. 2011; Mantovani et al. 2004), com oscilações na produtividade ao longo dos anos (Mantovani et al. 2004; Souza et al. 2010).

Figura 1. Distribuição principal da Floresta Ombrófila Mista (verde escuro) e núcleos menores com populações de pinheiros (triângulos em verde escuro) no contexto da Mata Atlântica original (verde claro) na América do Sul.

Devido à alta produção de sementes nutritivas (um pinhão médio de 7 g = 14,8 kcal) e o intenso consumo destas por animais, o pinheiro tem sido considerado uma planta chave no fornecimento de recursos para a fauna (Brocardo et al. 2017; Ferracioli 2014; Iob &

Vieira 2008; Mantovani et al. 2004; Pagno et al. 2015; Vieira & Iob 2009). Ainda que a dominância e alta densidade de *A. angustifolia* possam descaracterizá-la como espécie chave (sensu Peres 2000; Power et al. 1996), a oferta substancial de recursos propiciada em uma época de escassez de frutos (Liebsch & Mikich 2009; Paise & Vieira 2005), o alto número de espécies que usam esse recurso (consumida por 84% dos mamíferos de médio e grande porte da FOM que incluem frutos na sua dieta, Brocardo et al. 2017; Vieira & Iob 2009) e previsibilidade anual de produção de sementes (Mantovani et al. 2004; Souza et al. 2010) possam ser usadas para justificar seu status de planta chave para vertebrados frugívoros (sensu Galetti & Aleixo 1998; Stevenson 2005).

Além de ser importante para a fauna, o pinheiro tem papel nucleador de vegetação durante o processo de regeneração florestal, sendo considerada uma espécie berçário por favorecer o recrutamento de outras árvores abaixo de sua copa (Duarte et al. 2006). O grande porte dos pinheiros, que podem superar os 50 m de altura e 3,5 m diâmetro, (mais comumente entre 20-35 m, Figura 2) destaca sua presença na mata (Farjon 2010; Mattos 2011), sendo a existência de dois estratos arbóreos distintos uma das características da FOM (Figura 3). O estrato arbóreo inferior é formado principalmente por espécies como a erva-mate (*Ilex paraguariensis*), o jerivá (*Syagrus romanzoffiana*), o pinheiro-bravo (*Podocarpus lambertii*), mirtáceas como a guabiroba (*Campomanesia xanthocarpa*), pitanga (*Eugenia uniflora*), uvaia (*Eugenia pyriformis*) e jabuticaba (*Plinia peruviana*), e lauráceas, com diversas espécies dos gêneros *Ocotea* e *Nectandra* (Cordeiro & Rodrigues 2007; Jarenkow & Budke 2009; Klein 1960; Maack 2012).

Figura 2. A) Pinheiro com altura estimada superior a 30 m no Parque Nacional do Iguaçu; B) pinheiro com copa típica em forma de taça; C) estróbilos masculinos maduros; D) estróbilos femininos imaturos, e; E) sementes maduras (Fotos: CR Brocardo).

Embora tanto a dominância de pinheiros como a composição da vegetação mude de acordo com o clima, degradação antrópica, solo e influência de outras vegetações com a qual mantém contato, como as Florestas Estacionais Semidecidual e Decidual, a Floresta Ombrófila Densa e os campos de altitude (Jarenkow & Budke 2009; Maack 2012). Abaixo do estrato arbóreo, o sub-bosque pode ser composto por uma camada

regenerante das espécies do dossel, coberto por taquarais (*Merostachys spp* e *Chusquea gaudichaudii*), samambaias rasteiras, xaxins (*Dickisonia sellowiana* e *Alsophila setosa*) ou apresentar uma mistura desses componentes (Maack 2012; Sanquetta et al. 2009) (Figura 3).

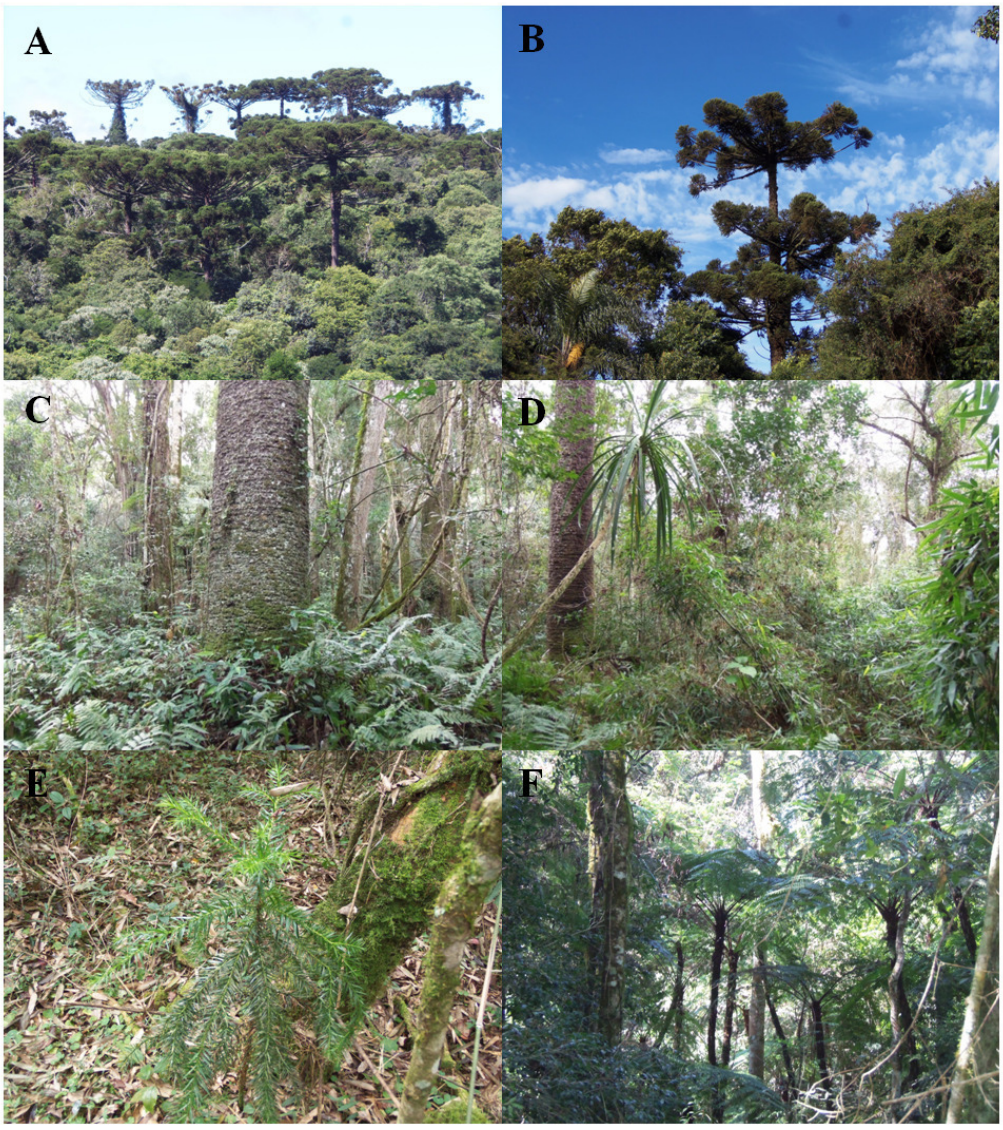

Figura 3. Características da Floresta Ombrófila Mista - Padrão florestal com dois estratos arbóreos distintos (A - Parque Nacional do Iguaçu, B – Parque Municipal Danilo Galafassi). Sub-bosque: dominado por samambaiais rasteiras (C); dominado por taquaral (D); "limpo", com destaque para indivíduo juvenil de *Araucaria angustifolia* (E); e dominado por samambaiaçu *Alsophila setosa* (F) (Fotos: CR Brocardo).

A fauna da FOM de forma geral, devido à característica sazonal do clima subtropical, possui riqueza de espécies um pouco inferior a formações tropicais da Mata Atlântica, não havendo, por exemplo, nenhuma espécie endêmica de ave, mamífero ou borboleta (Silva & Casteleti 2005). Embora existam espécies endêmicas de anfíbios (Conte 2010), e algumas aves, apesar de terem distribuição marginalmente ultrapassando os limites da FOM, têm forte ligação com *A. angustifolia*, como é o caso do papagaio-charão (*Amazona pretrei*) e do grimpeiro (*Leptasthenura setaria*) (grimpas são as folhas dos pinheiros) (Straube & Di Giácomo 2007). A FOM também mantém a maior parte dos mamíferos encontrados em outras formações da Mata Atlântica (Tabela 1) (Brocardo & Cândido-Jr 2012; Brocardo & Galetti 2017; Marques et al. 2011), com espécies ameaçadas e de distribuição restrita (exemplo, veado-poca *Mazama nana*), o que a coloca entre as 13 ecorregiões com maior prioridade para conservação de mamíferos no Brasil, dentro um total de 48 analisadas (Alves & Brito 2013).

Tabela 1. Número de espécies de mamíferos nativos não voadores identificados em algumas áreas de FOM, Floresta Ombrófila Densa (FOD) e Floresta Estacional Semidecidual (FES)

Grupos de mamíferos	FOM[1]	FOD[2]	FES[3]
Pequenos roedores (< 1 kg)	9 a 14	12 a 17	6
Marsupiais	7 a 8	9	9
Primatas	1 a 2	4 a 5	3
Médios e grandes (> 1 kg)[4]	27 a 28	28 a 29	27

[1] Região do Parque Nacional do Iguaçu (Brocardo & Cândido-Jr 2012; Brocardo & Galetti 2017; Ferracioli 2014) e Planalto Gaúcho (Marques et al. 2011); [2] Parque Estadual Carlos Botelho (Brocardo et al. 2012; Galetti et al. 2016) e Parque Estadual da Serra do Mar (Rocha-Mendes et al. 2015); [3] Parque Estadual Morro do Diabo; [4] excluindo marsupiais e primatas.

Degradação, ameaças e conservação da Floresta Ombrófila Mista

A perda de FOM teve início com a exploração madeireira local e em pequena escala promovida pela necessidade de matéria prima para construção civil durante o processo colonizatório, contudo a exploração em maior volume só foi iniciada no período compreendido entre o final do século XIX e início século XX, com a concessão de terras públicas a grandes empresas e a construção de ferrovias, o que viabilizou o escoamento da madeira extraída até os portos marítimos (de Carvalho & Nodari 2008). Com o aumento da demanda por madeira no exterior, em decorrência da impossibilidade da madeira europeia ser explorada e exportada devido às duas guerras mundiais (1914-1919, 1939-1945), o pinheiro-brasileiro passa a ser a principal fonte de madeira leve no mercado externo, o que multiplicou o número de serrarias em quase toda a extensão da FOM (de Carvalho & Nodari 2008; Lavelle 1981). Nessa época as exportações brasileiras de madeira de *A. angustifolia* dão um salto gigantesco, sendo um dos principais produtos de exportação do país (Lavelle 1981). E mesmo depois da queda na exportação de madeira para o mercado europeu (após 1950), a perda de floresta cresce dentro da FOM, tendo seu ápice na década de 1960 impulsionado pelo aumento na demanda nacional e de países vizinhos por madeira (Argentina e Uruguai), abertura de terras para agricultura, e avanços tecnológicos que aceleraram o processo de exploração florestal (Brocardo 2013; de Carvalho & Nodari 2008; Gubert Filho 2010) (Figura 4).

Figura 4. Degradação da Floresta Ombrófila Mista entre as décadas de 1950 e 1970 na cidade de Cascavel - Paraná. A) Derrubada de mata e queima para plantio de roça de subsistência; B) pinheiro derrubado com uso de serrote; C) com o advento do motosserra e do trator de esteira a devastação sobre a floresta foi acelerada; D) serraria com mata devastada ao fundo e torras de pinheiros centenários no pátio E) Madeira de *Araucaria angustifolia* serrada em pranchas para exportação para a Argentina; F) Redução da mata nativa frente à urbanização - o fragmento da foto corresponde ao atual Parque Ambiental Danilo Galafassi (Fonte das imagens: Museu da Imagem e Som de Cascavel, http://www.cascavel.pr.gov.br/servicos/museu/index.php, reprodução autorizada para autor).

Como saldo, tal como as demais formações do Bioma Mata Atlântica, a FOM sofreu grande perda da cobertura da original, restando apenas 12% (Ribeiro et al. 2009), embora dados para o estado do Paraná indiquem que menos de 1% corresponda a florestas em estágio sucessional avançado (Castella & Britez 2004). Soma-se como agravante que maioria dos remanescentes (90%) de FOM tem área inferior a 100 ha (Ribeiro et al. 2009), e na maioria dos casos sem ou com baixa abundância de pinheiros devido ao corte seletivo sobre a espécie, descaracterizando essa formação florestal (Castella & Britez 2004). Devido a essa redução substancial de cobertura, a FOM é considerada uma das ecorregiões mais ameaçadas na América Latina (Dinerstein et al. 1995), e o pinheiro-do-paraná está Criticamente em Perigo de extinção em nível global (Thomas 2013).

Obviamente a perda de habitat, associada com a caça de subsistência e "esportiva" (Figura 5), levou a extinções locais de espécies da fauna, sendo particularmente incomum nos remanescentes de FOM a presença de espécies de grande porte, como o queixada (*Tayassu pecari*), a anta (*Tapirus terrestris*), o veado-mateiro (*Mazama americana*) e a onça-pintada (*Panthera onca*) (Bogoni et al. 2016; Brocardo & Cândido-Jr 2012; Brocardo et al. 2017; Marques et al. 2011). Embora, em um contexto geral os efeitos das atividades antrópicas sobre a defaunação da FOM são menos conhecidos que em outras áreas da Mata Atlântica e mesmo da Amazônia (exemplo Beca et al. 2017; Canale et al. 2012; Cullen et al. 2000; Galetti et al. 2016; Peres 2001).

Figura 5. Fotos de atividades cinegéticas no município de Cascavel - Paraná entre as décadas de 1950 e 1970. A) crianças em retrato com onça-pintada abatida em área que corresponde hoje às proximidades do centro município; B) anta criada provavelmente após o abate da progenitora - detalhe para arma e cães empregados em atividades cinegéticas; C) veado caçado em área aberta para roça de subsistência; D) abate de seis queixadas por grupo de caçadores (Fonte das imagens: Museu da Imagem e Som de Cascavel, http://www.cascavel.pr.gov.br/servicos/museu/index.php, reprodução autorizada para autor).

Outra ameaça muito forte sobre os remanescentes de FOM é a coleta descontrolada de pinhões para consumo humano ou de animais domésticos, apontada com uma das causas do baixo recrutamento de *A. angustifolia* (Paludo et al. 2009; Paludo et al. 2011; Souza 2007; Souza et al. 2010). A única regulamentação sobre o extrativismo dessas sementes reza sobre o período de início de coleta, que deveria ocorrer após o dia 15 de abril de cada ano, contudo sem fazer qualquer menção à quantidade que pode ser retirada da mata (Portaria Normativa nº 20 IBDF 1976). Dados oficiais do Instituto Brasileiro de Geografia e Estatística (IBGE, disponível em www.sidra.ibge.gov.br)

indicam uma coleta média anual de 5.442,5 toneladas para todo o Brasil (entre 1986-2015), o que corresponde a quase 800 milhões de sementes (Figura 6).

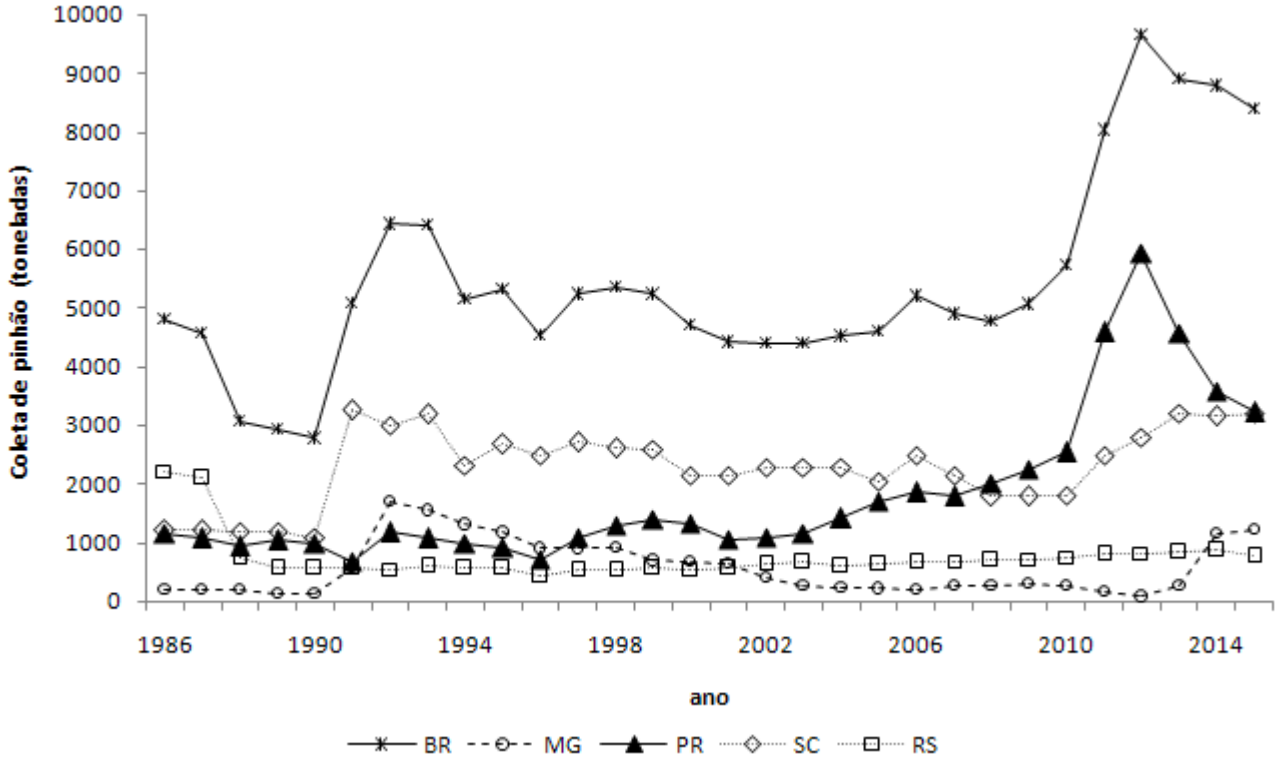

Figura 6. Quantidade de pinhão oficialmente comercializado (em toneladas) entre os anos de 1986 e 2015 para o Brasil (BR), e valores parciais para os estados com maior contribuição: Minas Gerais (MG), Paraná (PR), Santa Catarina (SC) e Rio Grande do Sul (RS).

A maior safra registrada ocorreu em 2012 com quase 10 mil toneladas contabilizadas, seguindo uma ascensão a partir de 2006, fato que pode estar ligado à proibição do corte da espécie em 2001 (Resolução nº 278 COMAM 2001), o que provavelmente tenha levado a um aumento na inclusão de indivíduos reprodutivos nas populações pela primeira vez desde que os dados vêm sendo coletados, principalmente nos estados do Paraná e Santa Catarina (Figura 6). Nesses estados a atuação de madeireiras explorando *A. angustifolia* nativa sempre se manteve intensa, o Paraná, por exemplo, foi o estado que mais perdeu Mata Atlântica nos últimos 30 anos (1985-2014), somando mais de 450 mil ha de devastação (Fundação SOS Mata Atlântica & Instituto Nacional de

Pesquisas Espaciais 2015). E apesar de que a taxa de desmatamento anual vinha caindo desde 2005, houve nova retomada após 2011, principalmente dentro da FOM (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais 2015), possivelmente em resposta às alterações no Código Florestal, que anistiaram desmatamentos anteriores a 2008, assim na falta de punição, houve estimulo a novas infrações ambientais, na esperança de que futuras anistias beneficiem novamente quem desmatar.

Esse crescimento no desmatamento dentro da FOM é preocupante, já que apenas 3,1% da cobertura florestal remanescente está protegida dentro de Unidades de Conservação (UCs), o que corresponde somente a 0,39% da área original (Ribeiro et al. 2009). Áreas protegidas (parques nacionais e estaduais, florestas públicas e Estações Ecológicas) que incluem FOM no seu interior somam 51 mil ha no Rio Grande do Sul, em Santa Catarina 172 mil ha, no Paraná 303 mil ha, em São Paulo 203 mil ha, no Rio de Janeiro 132 mil ha e em Minas Gerais 23 mil ha, embora a presença real de área de FOM dentro do conjunto de unidades de cada estado seja bem inferior, pois a maioria delas inclui outras formações florestais, áreas de campos ou mesmo silvicultura no seu interior (Indrusiak & Monteiro 2009).

Ampliar a proteção sobre os remanescentes de FOM é fundamental para perpetuação dessa floresta e da biodiversidade contida nela, visto que áreas protegidas são reconhecidamente a maneira mais eficaz de conter a perda de cobertura vegetal nativa e de biodiversidade (Bruner et al. 2001). Num contexto futuro, a ampliação de proteção ganha ainda mais importância, uma vez que o aquecimento global esperado para as próximas décadas é apontado como uma ameaça à existência dessa floresta (Wrege et al. 2016; Wrege et al. 2007). Se o cenário mais pessimista para elevação de temperatura no planeta se concretizar (RPC 8.5, elevação entre 2,6 e 4,8 °C), as condições climáticas para ocorrência de *A. angustifolia* em 2100 serão reduzidas a menos de 0,50% da atual

distribuição da FOM, restringindo como favoráveis apenas porções das Serras Catarinense e Gaúcha (Wrege et al. 2016). Contudo, como *A. angustifolia* tem ciclo de vida secular (Mattos 2011), manter populações preservadas dentro de UCs, que serviriam de "refúgios", pode garantir novas expansões se as condições ambientais se tornarem novamente favoráveis, da mesma forma que a FOM se expandiu no passado (Behling 2002).

Região principal de estudo

A maior parte dos dados coletados para essa tese ocorreu na FOM da região oeste do estado Paraná, Brasil (outras duas áreas são descritas no capítulo III). Nessa região a Floresta Ombrófila Mista recebe influência da Floresta Estacional Semidecidual (FES), com a qual mantém contato, formando um ecótono (Castella & Britez 2004) (Figura 7). O clima segundo a classificação de Köppen é Cfa, com temperaturas anuais médias de 19 °C e precipitação anual de 1.800 mm, sem estação seca (Alvares et al. 2013; Castella & Britez 2004). O solo deriva do basalto do derrame de Trapp ocorrido no limite Triássico-Cretáceo da formação da Serra Geral, com predomínio de Latossolos roxos e associação de solos Litólicos Eutróficos e Terra roxa estruturada, em revelo ondulado a fortemente ondulado, sob uma altitude que varia de 550 a 850 metros do nível do mar (Castella & Britez 2004).

O extrativismo florestal nessa região teve início entre o fim do século XIX e começo do século XX, com a concessão de terras a empresas argentinas e inglesas, que exploravam erva-mate e madeiras de lei num sistema conhecido como *obrages*, ciclo que perdurou até meados da década de 1930, quando o sistema de *obrages* entra em declínio e a colonização da região por população brasileira é incentivada pelo governo federal

(Brocardo 2013; Wachowicz 1987; Westphalen 1987). O impulso maior, contudo se deu a partir da década de 1950, motivado pelo crescimento da população agrícola de outras regiões do país que buscavam terra, e pela diminuição dos pinhais nativos em Santa Catarina, Rio Grande do Sul e Centro-sul do Paraná (Brocardo 2013; Gubert Filho 2010; Lavelle 1981). Como toda região era praticamente inexplorada até essa década (Gubert Filho 2010; Maack 2012), a grande reserva de pinheiros propiciou um ciclo extrativista que perdurou até a metade de 1970 (Brocardo 2013; Lavelle 1981).

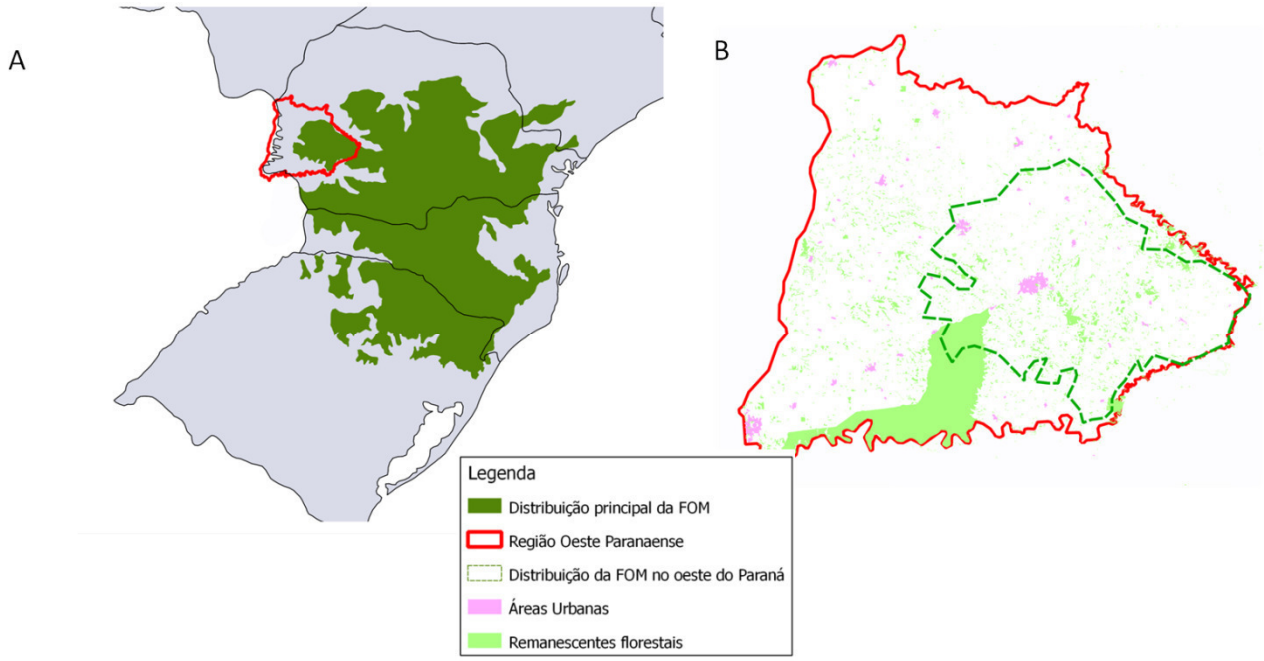

Figura 7. A) Localização da região Oeste do Paraná na área de distribuição principal da Floresta Ombrófila Mista (FOM); B) remanescentes florestais atuais presentes na região de estudo. A linha tracejada em verde escuro delimita a FOM, sendo o restante da região composto por Floresta Estacional Semidecidual.

Devido ao revelo favorável e ao solo fértil, a maior parte das terras foi convertida para agricultura mecanizada, com predomínio de plantio de grãos (soja, milho e trigo; Figura 8), e menores proporções para pastagem (principalmente em áreas de relevo mais acidentado) e reflorestamento, sendo em pequena escala e em declínio, o feito com

espécies nativas (*A. angustifolia* e *I. paraguariensis*), e em maior escala e em expansão, o feito com espécies exóticas (*Pinus* spp e *Eucalyptus* spp).

Figura 8. A) Um dos poucos fragmentos da região que mantém grande quantidade de *A. angustifolia,* área que deveria ser transformada em Unidade Conservação; B) situação mais comum, com fragmento degradado e com baixa presença de pinheiros; C) pinheiros nativos isolados em lavoura, infelizmente a legislação é mais permissiva para liberação do corte nessa situação; D) pinheiros derrubados para duplicação de rodovia; E) abertura de via e loteamento, com a supressão de mata nativa em terreno com alta declividade e próximo a manancial de abastecimento humano; F) desmatamento em três hectares cortando fragmento florestal ao meio, com objetivo de lotear a área com chácaras de lazer.

Em toda região oeste do Paraná a cobertura florestal nativa remanescente soma perto de 14%, e em grande parte é concentrada na FES do Parque Nacional do Iguaçu, UC criada em 1939 (Figura 7). Atualmente não há grandes desmatamentos, porém ainda é comum a liberação dada para derrubada de pinheiros nativos isolados, corte de indivíduos secos no interior de fragmentos (causando grande prejuízo ao estrato regenerante), supressão de vegetação para fins de loteamento urbano e rural, e obras de interesse público (Figura 8). Também são comuns, pequenos desmatamentos irregulares, principalmente nas bordas de lavouras, favorecidos principalmente pela deficiência de pessoal nos órgãos de fiscalização.

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Capítulo II. Large forest remnants and connectivity explain mammal resilience in a landscape dominated by commodity croplands

Large forest remnants and connectivity explain mammal resilience in a landscape dominated by commodity croplands

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Abstract

Replacement of forests by commodity croplands is one of the largest threats to biodiversity, leading to directly and indirectly the loss of species. However, the effects of rapid transformation of forest landscape on biodiversity remains poorly studied. Here we investigated mammal resilience and extinction in forest patches immersed in commodity croplands in subtropical Atlantic Forest of South America. We compare species richness, abundance and biomass of mid and large mammals in 17 forest patches (ranging from 4.6 to 180,000 ha). Our results showed that decreasing of forest patch size leads to loss of species (27 to 98% of species) and biomass (reduced from 1.7-fold to 66-fold), with a strong relationship to forest patch size, reinforcing the negative impacts of forest fragmentation on biodiversity. However, despite species loss in each fragment, the fragmented landscape presented almost all mammal species found in control site (93% of species), including top predators and large ungulates. Correct application of Forest Brazilian Bill may increase connectivity among forests remnants helping the process of species recolonization. In addition, the most urgent action to allow mammal population recovery and is the augment of protection against illegal hunting.

Key-words: soybean plantations, defaunation, *Araucaria* moist forest, landscape management, hunting

1. Introduction

Expansion of commodity croplands (sugar cane, soybean, corn, coffee and palm oil) is directly responsible for the loss of natural vegetation cover worldwide (Foley et al. 2011; Gibbs et al. 2010; Grau et al. 2005; Meyfroidt et al. 2014; Morton et al. 2006). In early years of the twenty first century, global deforestation exceed two million square kilometers for the first time (Hansen et al. 2013), and the pressure from continuing human population growth may result in the conversion of additional natural habitats into agricultural lands, which could mean the loss of approximately 1 billion ha of forests by 2050 (Foley et al. 2005; Tilman et al. 2001; Vitousek et al. 1997). Due to this intense, anthropogenically induced cover land change, most the world's remaining forests have become a myriad of degraded fragments, 70% of which are forest patches in human-dominated landscapes that are less than 1 km from forest edges (Haddad et al. 2015).

Habitat loss and fragmentation profoundly impacts biodiversity and ecosystem functionality (Butchart et al. 2010; Fahrig 2003; Haddad et al. 2015; Schipper et al. 2008), and the size of habitat patches limits the species richness as well as the population of diverse organisms (Fahrig 2003; Turner 1996). Edge effects lead to modification of the characteristics of a forest up to varying distance, causing the replacement of forest-specialist species by open-habitat or generalist species (Beca et al. 2017; Gascon et al. 1999; Tabarelli et al. 2010a). Consequently, ecological processes, such as seed dispersal and predation, can be affected by forest edges, defaunation and habitat patch size, which can lead to changes in forest composition (Brocardo et al. 2017a; Fleury & Galetti 2006; Galetti et al. 2006). The matrix may also limit the movements of animals among suitable habitats, thus preventing the recolonization of patches and restricting gene flow (Gascon et al. 1999).

Large and medium-sized mammals are particularly affected by anthropogenic land-cover change (Cardillo et al. 2005; Ceballos et al. 2005; Schipper et al. 2008) to the extent that world's ecosystems might lose most of their large mammals in next century, if currently threatened species become extinct (Barnosky et al. 2011; Dirzo et al. 2014). This situation is extremely worrying because mammals are key ecosystem elements (Dirzo et al. 2014; Estes et al. 2011; Galetti & Dirzo 2013; Young et al. 2016). Some species act as unique seed dispersers for many trees (Bueno et al. 2013; Donatti et al. 2009); carnivores control the populations of their prey (Ripple & Beschta 2012); and ungulates and seed predators influence plant recruitment and the size of populations of small species via top-down cascading effects (Brocardo et al. 2013; Galetti et al. 2015; Silman et al. 2003).

Although the creation of protected areas has been relatively successful at preventing the degradation of natural habitats (Bruner et al. 2001), such designations alone may not guarantee the conservation of mammals over the long term (Brito et al. 2008; Craigie et al. 2010; De Angelo et al. 2013); this will require increased protection and management of entire landscapes (Ceballos et al. 2005; Gurd et al. 2001). Thus, expanding our knowledge of how different species are affected by disturbances and their capacity for persistence in remnant habitat patches in anthropogenic landscapes may be important for guiding conservation efforts (Beca et al. 2017; Bengtsson et al. 2003; Gardner et al. 2009; Peres et al. 2010; Tscharntke et al. 2012). Here, we evaluated mammal resilience in an intensive agricultural landscape, where we specifically investigated 1) capacity of medium-sized and large mammals to persist in study landscape; 2) the effects of forest patch size and connectivity on species richness, abundance and biomass; 3) defaunation scenarios for these landscapes; and 4) conservation value of these sites.

2. Materials and Methods

2.1 *Study region*

Our study landscape was western Paraná State, Brazil (Figure 1), a landscape that includes two ecoregions of the Atlantic Forest Biome global biodiversity hotspot (Myers et al. 2000): the subtropical semideciduous Atlantic forest and the *Araucaria* moist forest. Both are characterized by a subtropical climate (Cfa in the Köppen classification) with an annual mean temperature of 19 °C and 1,800 mm of rainfall per year without a dry season (Alvares et al. 2013; Castella & Britez 2004).

The forest cover of this region was mainly lost between 1950 and 1975, initially due to the logging of Paraná-pine (*Araucaria angustifolia*) and other timber species followed by open of forests for agricultural use (Brocardo 2013; Gubert Filho 2010). Today, most of the region is dominated by grain croplands (soybean, corn, bean, wheat and oat) and, to a minor extent, by cattle pastures, reforestation with exotic (*Pinus* and *Eucalyptus*) and native trees (*Araucaria angustifolia* and *Ilex paraguariensis*), and urban areas; only 14% of the remaining native forest cover remains and it is distributed in several forest patches within a human-dominated landscape. However, this region holds the largest protected area of Atlantic Forest in the interior of Brazil, the Iguaçu National Park (created in 1939), that encompass more than 180,000 ha and together with protected and unprotected forests in Argentina forms a continuous forest block of approximately 1 million ha.

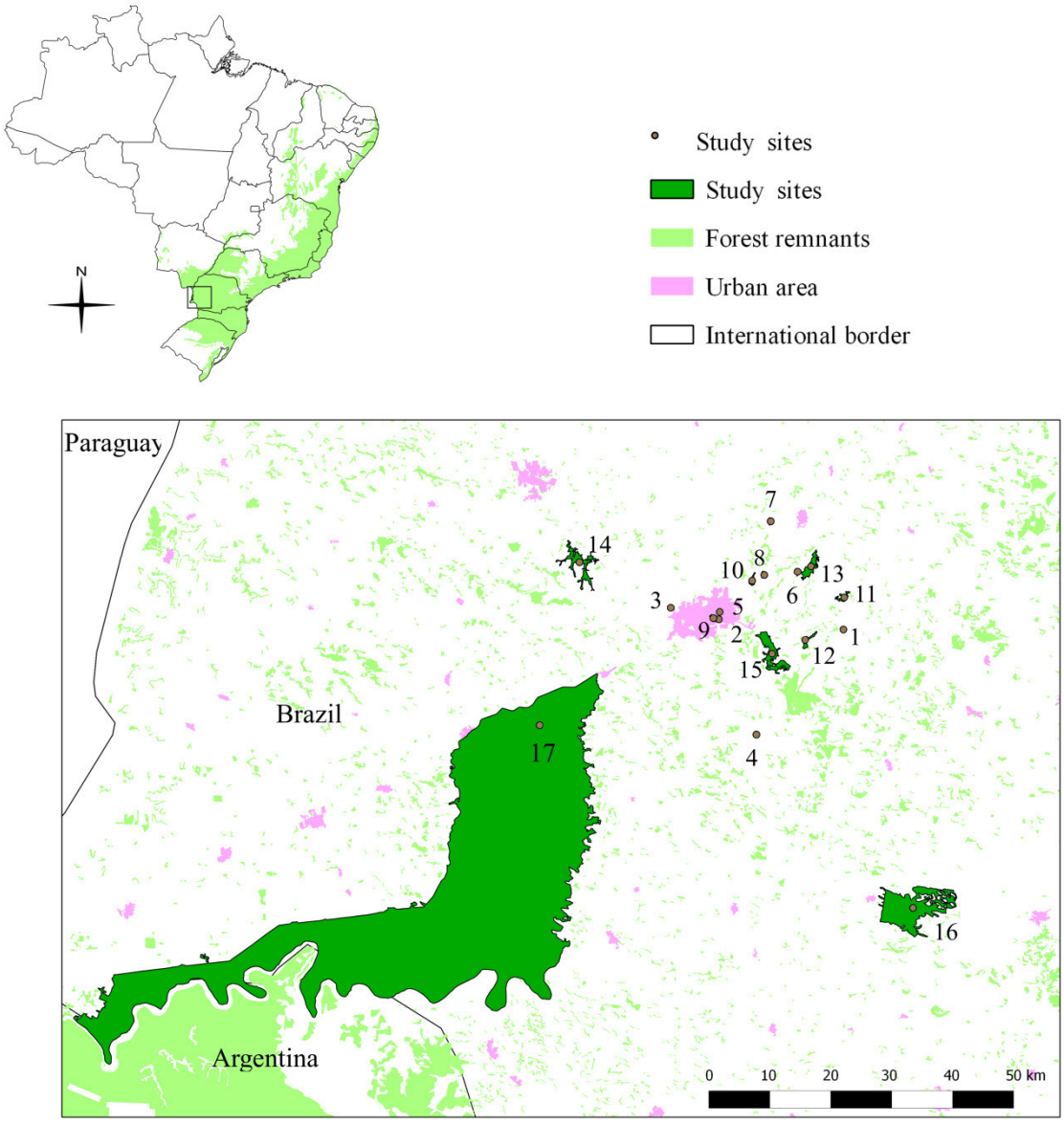

Figure 1. Study region located in original Brazilian Atlantic Forest (high-left). Study sites are represent by dots and dark green (names and characteristic see Table 1).

2.2 *Survey*

Between 2013 and 2017, we surveyed large and medium-sized mammals in 17 forest patches, which included, one large control site (Iguaçu National Park: 181,588 ha) and 16 forest fragments (ranging from 4.6 – 6,244 ha) (Table 1), using camera traps (models Ecotone [triggered function with 3 photos with a delay of 1 s; 15% of our effort] and

Bushnell HDView [video function for 10 s with delay=1 s; 85% of our effort]) combined with indirect records (tracks, carcasses, burrows and feces) and occasional sightings because the combination of these methods can better sample the large mammal assemblage (Brocardo et al. 2012; Silveira et al. 2003). Each camera was installed 30 cm above the soil in tree trunks and away from roads or humans trails, where we observed animal trails. In IGU we established 63 sampling stations (but only 59 were effectively sampled due to the theft of camera traps and equipment problems) following the TEAM approach with a camera for every 2 km² (TEAM Network 2011); in the fragments, due to their small size, we reduced the number of sampling stations (2 to 28) with each camera placed a minimum of 100 m apart from each other. Our total effort summed to 8,236 camera days (Table 1).

Table 1. Characteristics of study sites and effort sampling (Ara = *Araucaria* moist Forest, Sd= Semideciduous Atlantic Forest). Direct connection: 1= presence of forest riparian corridor; 0 = absence of riparian corridor.

Site name	Forest patch size (ha)	Direct connection	Forest type	Matrix	Effort (camera trap- day)	Camera trap stations
1. São João (Sjo)	4.6	0	Ara	Agriculture	24	2
2. Teatro Barracão (Tba)	7.9	0	Ara	Urban	80	5
3. FAG (Fag)	17.1	0	Ara	Agriculture/urban	117	6
4. Santa Lourdes (Slo)	19.9	1	Ara	Agriculture	144	4
5. Danilo Galafassi Municipallity Park (Dag)	20.1	0	Ara	Urban	84	12
6. Recanto do Lago (Rla)	63.7	1	Ara	Agriculture	102	3
7. Rio Melissa (Mel)	71.3	1	Ara	Agriculture/reforestment	475	20
8. Barreiro (Bar)	78.4	0	Ara	Agriculture	240	17
9. Paulo Gorski Ecological Park (Pgo)	95.1	0	Ara	Urban	281	21
10. Alto Alegre (Aal)	105.2	1	Ara	Agriculture	409	20
11. Rio Piquirizinho (Piq)	167.5	1	Ara	Agriculture/reforestment	336	12
12. Cascavel Environmental Park (Pac)	192.8	1	Ara	Agriculture	314	18
13. Rio Sapucaí (Sap)	610.5	1	Ara	Agriculture	544	13
14. Rio São Francisco Verdadeiro (Rsf)	1,216.5	1	Ara	Agriculture	498	14
15. Rio São José (Rsj)	1,421.2	1	Ara	Agriculture	635	25
16. Rio Guarani State Park (Gua)	6,244.5	1	Sd/Ara	Agriculture	1,312	27
17. Iguaçu National Park (Igu)	181,588.2	1	Sd/Ara	Agriculture	2,618	59

We only considered native species larger than 1 kg in our analysis, except for the Brazilian squirrel (*Guerlinguetus brasiliensis*), which is easily detectable and typically recognized in surveys for larger mammals (Brocardo et al. 2012; Galetti et al. 2016).

2.3 *Measures of mammal assemblage integrity*

2.3.1 *Species richness and beta diversity*

We tested whether the sampling effort was sufficient to represent the native mammal assemblage in each site using a first order Jacknnife estimator with the camera trap data (effort was expressed as camera trap days) using the *vegan* package (Oksanen et al. 2007) in R program (R Development Core Team 2016).

Beta diversity was calculated using the Sørensen dissimilarly index and its decomposition, species spatial turnover (Simpson dissimilarly index - β_{sim}) and species nestedness (nestedness index - β_{nes}) (Baselga 2010) using the *betapart* package in R (Baselga & Orme 2012). We also performed a pair-wise site comparison by β-diversity values as a function of the difference among the forest patches in terms of size and distance between them using linear regression (Galetti et al. 2016; Wen et al. 2016).

2.3.2 *Mammal abundance*

We measure mammal abundance using the capture rate (*Cr*) by the camera traps (Srbek-Araujo & Chiarello 2005), since capture rate may be used to estimate density (O'Brien et al. 2003), as follows:

$$Cr = \frac{Ic}{Ef} \cdot 100$$

We considered an independent capture (*Ic*) to be an observation of a species recorded a minimum of 30 minutes after the previous record for the same species (following O'Brien et al. 2003); for social species, we counted all individuals in each independent capture to calculate abundance. The total effort (*Ef*) corresponded to the sum of the days sampled by all camera traps in each site. By multiplying the capture rate by the mean body mass (kg) of each species (Table S3), we calculated the biomass in each site.

2.3.2 *Defaunation*

We calculated the level of defaunation at the study sites using the defaunation index (D) proposed by Giacomini and Galetti (2013):

$$D_{(r,f)} = \frac{\sum_{k-1}^{S} \omega_k \left(N_{k,r} - N_{k,f}\right)}{\sum_{k-1}^{S} \omega_k \left(N_{k,r} + N_{k,f}\right)}$$

where:

f = the focal mammal assemblage

r = a reference mammal assemblage used to estimate defaunation in other sites

S = the total number of species composing the mammal assemblage of all sites

k = identification of species

$N_{k,f}$ = abundance (capture rate) or presence of species k in focal assemblage *f*

$N_{k,r}$= abundance (capture rate) or presence of species k in reference assemblage *r*

ω_k= importance of species *k* to defaunation

$D_{(r,f)}$= defaunation of focal assemblage *f* compared to reference assemblage *r*

We calculated defaunation in two ways: one using capture rates (abundance) and using only presence-absence because some species were not recorded by camera trap sampling in all sites despite being present. In both cases, we raised the body size of each mammal species (kg; Table S3) by ¾ power to indicate its importance value (ω) because the ecology and life history of mammals can be inferred from body size (Giacomini & Galetti 2013). To determine D with abundance data, we used IGU as the reference assemblage *r*, and we used an assemblage of 34 species historically present in the study region for the presence-absence approach (Table S3).

2.3.4 *Conservation value*

We calculated the conservation value of the mammals at each site following the species specific Conservation index created by Galetti et al. (2009):

$$Ci = \sum_{k}^{s} \log(W_k) \cdot U_{k,i} \cdot q_{k,i}$$

This index is particularly interesting as an indication of the conservation value of a site since it accounts for species richness, body mass of a species (W_k, in gram), the conservation status of a species ($U_{k,i}$, a ranked value calculated by assigning weights to the IUCN threat category), and the relative abundance of a species (we used capture rate) at site in relation to all analyzed sites ($q_{k,i}$).

We adopted the red list of Paraná State (see Table S3) to define conservation status of a species ($U_{k,i}$), because regional threats are typically greater than global threats and are

more important for conservation planning (Galetti et al. 2009). We followed the ranking adopted by Galetti and colleagues (2009): Not threatened = 1; Near threatened or Deficient data = 2; Vulnerable = 3; Endangered = 4; Critically endangered = 5.

We used the camera-trap capture rate to calculate species relative abundance ($q_{k,i}$).

With the C_i values we calculated the mammalian priority conservation index (MP_i) of each site using the function:

$$MP_i = C_i \cdot \mathrm{A}^{0.25}$$

where A corresponds to forest patch size (in km²) elevated by an exponent (0.25) due to the implications of size for species conservation (Galetti et al. 2009). We classified the sites following Galetti et al. (2009), with $MP_i > 50$ indicating higher-priority sites, values between 15 and 50 being medium-priority sites, and $MP_i < 15$ for lower-priority sites.

2.4 *Analyses and environmental variables*

We used two landscape metrics that may influence mammalian persistence as explanatory variables: forest patch size (Chiarello 1999; Cullen et al. 2000) and direct connection to other forest patches via forest corridors (Pardini et al. 2005). We calculated the forest patch size for each site using the program QuantumGis (version 2.12) based on the shapefile of Atlantic forest remnants from *SOS Mata Atlântica* (https://www.sosma.org.br) together with open-source Google Earth resources to correct the sizes of the patches in shapefile, which do not include more recent forest regeneration as well as some areas dominated by bamboo. Direct connection was determined from the presence of a forest corridor (observed in the field and through

Google Earth images) between the target site and other forest patches; these corridors are primarily composed of riparian forests.

To verify the relationship of the response variables to the explanatory environmental variables, we performed a generalized linear model analysis using the lme4 package (Bates et al. 2007) in program R (R Development Core Team 2016), and an analysis of the distribution of the residuals indicated that Gaussian distribution best fit the data. We used the AIC value corrected for small sample sizes to test the model against a null model (Burhnam & Anderson 2002).

3. Results

3.1 *Species richness and beta diversity*

We analyzed more than 26,000 archives (images and videos) from camera traps, which combined with visual and indirect records, resulted in the identification of 32 native species and five exotic species. The recorded exotic species were: domestic dog (*Canis lupus familiaris*) (present in all sites), domestic cat (*Felis catus domesticus*) (two sites), wild boar (*Sus scrofa*) (just one site) and European hare (*Lepus europaeus*) (four sites).

Native mammal richness varied from just one species in a small fragment (TBA = 7.9 ha), which was represented by the omnipresent white-eared opossum (*Didelphis albiventris*), to 31 species at the control site (IGU, more than 180,000 ha) (Table 3 and Table S1). In most sites the first-order jackknife estimator indicated that the number of species we recorded approximated the expected value (Table S2). Forest size and direct connection explained 90% of the species richness with forest size alone explaining 86%

(*t*-value = 7.35, $p < 0.001$) and direct connection only 4% (*t*-value = 2.16, $p = 0.04$) (Figure 2, Table 2).

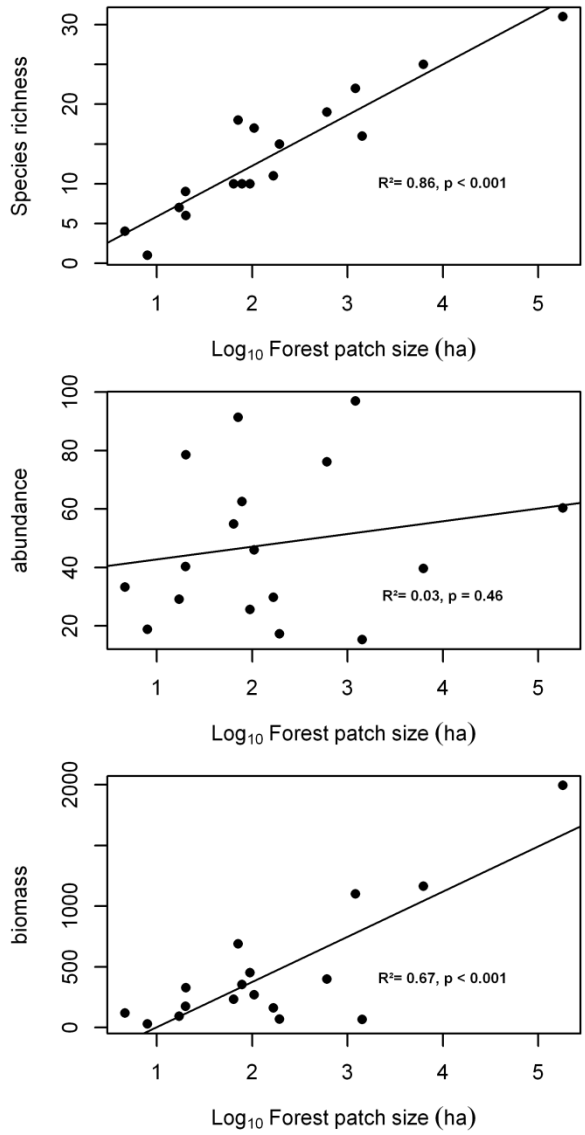

Figure 2. Relationship between Forest patch size (Log_{10}) and species richness, abundance (ind/ 100 cam.day) and biomass (kg/ 100 cam.day).

Table 2. Results of Generenalized Linear Model analysis. Significant explanatory variables are indicated in **bold**.

Variable response	Explanatory model	Model weight	ΔAICc
	Null model	0	33.07
Species richness	**Forest size (Log10)** + **direct connection**	1	0
	Forest size (Log10) + direct connection	0.05	6.35
Abundance	Null model	0.94	0
	Null model	0.001	14.35
Biomass	**Forest size (Log10)** + direct connection	0.999	0

The more common species were represented by generalist and species with low habitat specificity, such as *D. albiventris*, which was present in all sites, followed by the crab-eating fox (*Cerdocyon thous*) and the nine-banded armadillo (*Dasypus novemcinctus*) (in 94% of sites). The rare species were predators and large ungulates, and two species were exclusive to the largest patches, jaguar (*Panthera onca*) and red brocket deer (*Mazama americana*). Puma (*Puma concolor*), white-lipped peccary (*Tayassu pecari*) and tapir (*Tapirus terrestris*) were detected in 17% of the site, while ocelot (*Leopardus pardalis*) and collared-peccary (*Pecari tajacu*) were in 23%.

The results of the β-diversity analysis reflected the processes of species loss and species replacement with nestedness-related dissimilarity responsible for 44.4% (β_{nes}=0.35) and species turnover responsible for 55.6% (β_{sim}= 0.44) of the total variation in β-diversity (β_{sor} = 0.79). Pair-wise sites comparisons showed that total β-diversity was related to difference among the size of sites (β_{sor} R^2 = 0.12, $p < 0.001$; β_{nes} R^2= 0.27, $p < 0.001$; β_{sim} R^2 = - 0.23, $p < 0.001$), whereas the distances among the sites did not explain patterns of β-diversity (Figure S1). These results indicate that the difference in β-

diversity between the larger and smaller sites is driven by species loss while those among smaller sites are mainly due to species turnover.

3.2 *Mammal abundance*

Capture rate (individuals/100 cam.day) varied from 18.7 ind/100 cam.day (TBA) to 96.9 ind/100 cam.day (RSF), and the captured biomass (kg/100 cam.day) varied from 30 kg/ 100 cam.day (TBA) to 1,993 kg/ 100 cam.day (IGU).

Capture rate was not explained by forest patch size, while captured biomass did (R^2 = 0.67, $p < 0.001$) (Figure 2, Table 2). Forest fragments presented increased captures of mesopredators, armadillos and opossums, but this did not compensate for the loss of biomass (Figure 3).

3.3 *Defaunation*

The defaunation index (D) based on mammal abundance (capture rate) varied from 0.10 (RSF) to 0.92 (TBA); values near zero represent less defaunated sites relative to the abundance of the reference mammal assemblage, and those near 1 indicate more defaunated sites (Giacomini & Galetti 2013). When only presence-absence data were used, D varied from 0.02 at the control site (IGU), where only three species were absent, to 0.99 in TBA, where just one species was recorded. In both analyses, the low abundance or absence of the largest species provided more weight to the defaunation status (Giacomini & Galetti 2013) (Table 3).

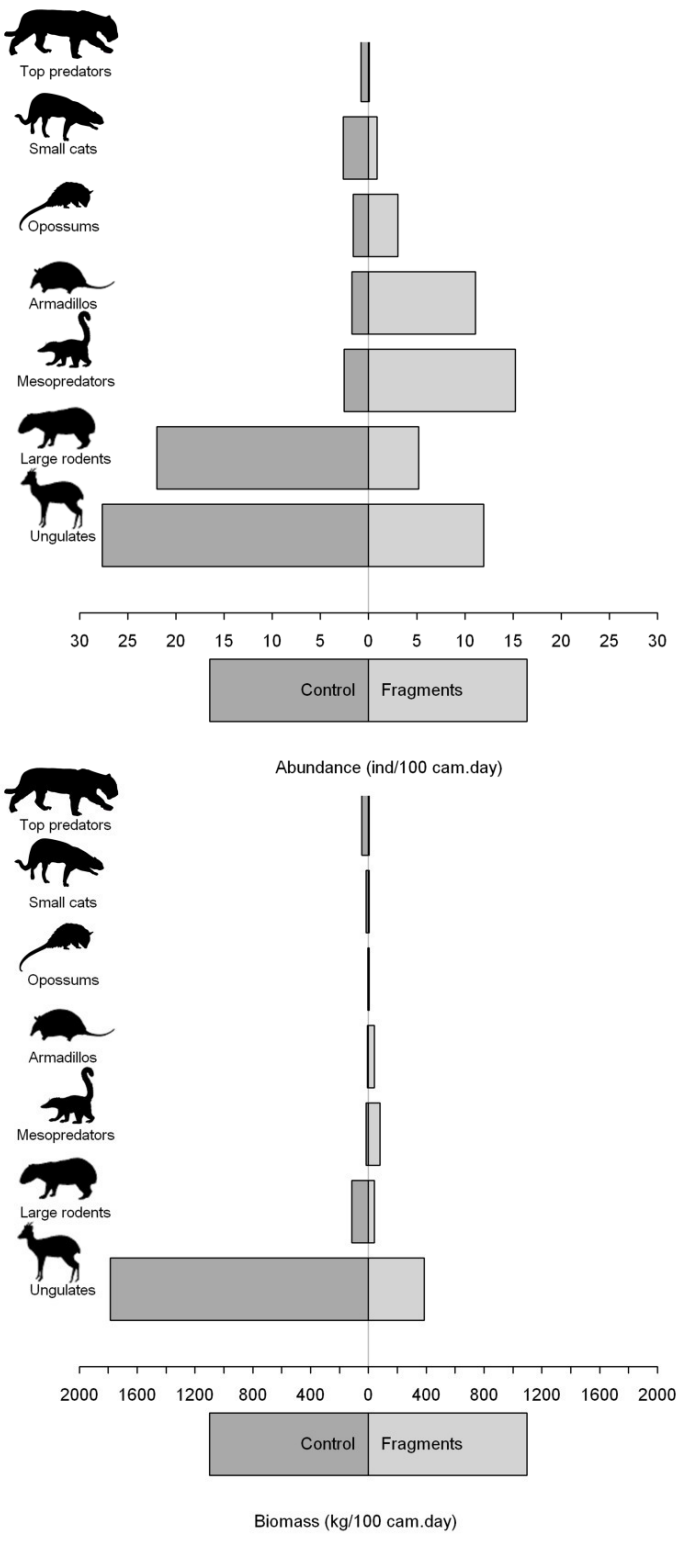

Figure 3. Abundance and biomass of mammal groups in control site and fragments. **Top predator**: *P. onca* and *P. concolor*; **Mesopredators**: *C. thous*, *E. barbara*, *N. nasua* and *P. cancrivorus*; **Small cats**: *L. guttulus*, *L. pardalis*, *L. wiedii* and *P. yaguoaroundi*; **Opossums**: *D. albiventris* and *D. aurita*; **Large rodents**: *C. paca*, *D. azarae* and *H. hydrochoerus*; **Armadillos**: *C. tatouay*, *D. novemcintus* and *E. sexcinctus*; **Ungulates:** *M. americana*, *M. nana*, *P. tajacu*, *T. pecari* and *T. terrestris*.

Most sites presented larger D index values with the abundance analysis than species presence analysis. This means that species may remain in fragments, but their abundances are generally lower than in the control site.

Table 3. Defaunation based in abundance data (ab) and in presence-absence data (p). Conservation index (Ci) values and Mammalian priority conservation sites (Mpi). Medium and higher priority conservation sites are in **bold**.

Sites	Defanaution (ab)	Defanaution (p*)	Ci	Mpi
SJO	0.77	0.90	0.9	0.4
TBA	0.92	0.99	0.7	0.4
FAG	0.81	0.88	7.0	4.5
SLO	0.70	0.82	1.2	0.8
DGA	0.53	0.80	3.4	2.2
RLA	0.57	0.76	10.1	9.0
MEL	0.27	0.57	17.1	**15.7**
BAR	0.51	0.77	8.8	8.3
PGO	0.56	0.71	4.9	4.8
AAL	0.60	0.40	8.7	8.8
PIQ	0.74	0.67	2.9	3.3
PAC	0.85	0.69	3.1	3.6
SAP	0.46	0.46	17.9	**28.1**
RSF	0.11	0.42	33.8	**63.1**
RSJ	0.87	0.58	2.3	4.4
GUA	0.20	0.07	36.0	**101.2**
IGU	Reference	0.02	110.0	**718.6**

* Based in a mammalian assemblage of 34 species historically present in this region; see Table S3.

3.4 *Conservation importance value*

The highest conservation importance value was found for the control site (*Ci* = 110.09) followed by two large fragments (GUA and RSF) with *Ci* values higher than 30. Together, these three sites corresponded to more than 60% of the total *Ci* value and presented higher mammalian priority index values ($MP_i > 50$). Two other sites presented medium priority index values (SAP and MEL), and the remainder presented lower values (Table 3). Because *Ci* is based on abundance, the defaunated sites presented low conservation values (Table 3).

When we calculated a combined C_i value for all fragments *versus* the control site, the fragments together presented a relatively high mammal conservation value in the studied landscape (fragments C_i = 92.9, MPi = 296.32; control site C_i = 199.9, MP_i = 1305.5), which corresponded to 18.5% of the mammal conservation priority value.

4. Discussion

Our results showed that fragmented landscape retained most of the mammal assemblage found in the control site (29 out of 31 species), and all forest patches (control and fragments) maintained 94% of the expected mammal richness, indicating a relatively low species extinction rate in this intensive agriculture-dominated landscape. The overall integrity of the large mammal community compared to other fragmented landscapes of the Atlantic Forest (Beca et al. 2017; Bogoni et al. 2016; Canale et al. 2012; da Silva & Pontes 2008) may be related to more recent deforestation (mainly after 1960). Additionally, the presence of a large remnant, Iguaçu National Park, which together with Argentinean forests totaled nearly 1 million ha, may provide a constant source of emigration for fragments after forest fragmentation has occurred, highlighting the importance of large protected sites to the maintenance of biodiversity (Bruner et al. 2001).

We found that species richness was strongly related to patch size following the species-area relationship observed for large mammals (Ahumada et al. 2011; Chiarello 1999; Michalski & Peres 2007). Large forest remnants maintain high habitat diversity and so can retain higher species richness (Laurance 2008), while smaller forest patch sizes cannot include the characteristics necessary to accommodate some species (Bierregaard

Jr et al. 1992). Thus our results also support the negative impacts of forest fragmentation on mammal diversity (Ahumada et al. 2011; Beca et al. 2017; Chiarello 1999; Cullen et al. 2000; Michalski & Peres 2007) since species loss occurred in all sampled sites.

The observed loss of species richness with a decrease in forest patch size was responsible for large portion of the total β-diversity (44.4 %), above all on a pair-wise comparison of larger sites against smaller ones. The limited size of the fragments, which also limited their capacity to provide resources to mammal species (Chiarello 1999, 2000; Prugh et al. 2008), may explain the other part of β-diversity, the species turnover (55.6%), due to the increase in competition among species. For example, no fragment contained all of the four smaller cats (ocelot *Leopardus pardalis*, margay cat *L. wiedii*, Southern tiger cat *L. guttulus* and jaguarondi *Puma yagouaroundi*), which was likely a response to an increase in territory size and diet overlap (Silva-Pereira et al. 2011).

The low availability of resources in fragments may reduce the density of some species (Chiarello 2000), and the defaunation analyses generally indicated that sites were more defaunated in terms of mammal abundance than species richness (presence-absence analysis). Furthermore, forest fragments increase the susceptibility of animals to poaching, which strongly impacts mammal persistence and abundance (Cullen et al. 2001; Cullen et al. 2000; Peres 2001). We recorded signs of hunting in most sites (Table S5), and the absence or low abundance of large game species, mainly in some of the large fragments, may be related to historic and current hunting pressure. The rarest species in fragments are those preferred by hunter colonists (ungulates, Galetti et al. 2016; Redford 1992) or persecuted for potential economic damages to livestock (predators, Conforti & Azevedo 2003).

In fact the less defaunated sites were those where large ungulates, species known to be responsible for most of the biomass in Neotropical forests, were present (Cullen et al. 2001; Galetti et al. 2016; Peres 2000). We found a positive relationship between forest size and biomass, but mammal abundance was not associated with forest size. For instance, the difference in biomass between the control site and the most defaunated site was 66-fold, while the difference in abundance between them was only a factor of 3. This result was related to species density-compensation, a common phenomenon in tropical forests (Galetti et al. 2016; Peres 2000; Peres & Dolman 2000). With the loss of larger species and predators, smaller species tend to increase in abundance, but this does not compensate for the lost biomass (Galetti et al. 2016; Terborgh et al. 2001). Fragmentation has increased the abundance of smaller and matrix-tolerant species, such as white-eared opossums, coatis, crab-eating foxes and nine banded-armadillos.

The loss of mammal biomass had a great impact on the conservation priority of sites. The most important sites for conservation were precisely those that have maintained more biomass, primarily due to the presence of large and threatened species. The control site (IGU) stands out for its importance to mammal conservation in the study region, and it is probably important in the context of the whole Atlantic Forest (Galetti et al. 2009) since it presents greater mammal richness and abundance than several sites located in the *Serra do Mar* forest continuous (Galetti et al. 2016).

However, despite the loss of species and biomass, some fragments were also important to mammal conservation, presenting medium and higher mammalian priority conservation values, and all fragments together accounted for nearly 20% of the overall priority value. These results reinforce the importance of fragments to mammal conservation in human-dominated landscapes (Beca et al. 2017; Magioli et al. 2016; Sampaio et al. 2010) as they have maintained range-restricted and globally threatened

species, such as the Brazilian dwarf brocket deer (*Mazama nana*) and the southern tiger cat (de Oliveira et al. 2016; Duarte et al. 2015). The persistence of endangered species in a landscape may permit population recovery and gene flow, if threats can be reduced (Schipper et al. 2008), and thus promote the occupation to new sites (Turner & Corlett 1996). For example, the white-lipped peccary was absent from IGU for 20 years, and its return may be associated with recolonization from extant populations in forest fragments (Brocardo et al. 2017b). The jaguar, which is also extremely threatened in Atlantic Forest (Galetti et al. 2013; Paviolo et al. 2016), has not been previous reported for GUA (Jorge et al. 2013; Paviolo et al. 2016), indicating the capacity of this species to reoccupy habitats within human-dominated landscapes (Casanova & Bernardo 2017). Expanding jaguar occupation in subtropical Atlantic Forest fragments is key to the conservation of jaguars in the Atlantic Forest because these forest remnants connect the Jaguar Conservation Unit (JCU) of *Iguaçu-Misiones* to the *Serra do Mar* and to the *Alto-Paraná* JCUs (Rabinowitz & Zeller 2010).

5. Conclusion and conservation measures

Our results showed the loss of species and biomass from forest fragments, and they highlight the negative impacts of habitat fragmentation on biodiversity (Ferraz et al. 2003; Turner 1996). Fragments do not compensate for the value of primary forest in maintaining intact faunal assemblages, therefore, the maintenance of large and primarly ecosystems is surely the best approach to biodiversity conservation (Gibson et al. 2011). Realistically, however, the Atlantic forest has lost nearly 90% of its original area (Ribeiro et al. 2009), and protected and large forest remnants are primarily located at high elevation and in areas with low potential to agricultural use (Tabarelli et al. 2010b).

Efforts to conserve mammals in fragmented habitats, which will require intensive landscape management and protection against human pressures, may substantially increase our conservation capacity (Ceballos et al. 2005).

However, deforestation in the Atlantic Forest, above all in the subtropical *Araucaria* moist forest, has been increasing in recent years (Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais 2015), probably in response to changes to the Brazilian Forest Bill (Soares-Filho et al. 2014). Therefore, it is essential that this pressure be deterred otherwise the situation of mammals will be worsened. The creation of new protected areas, mainly in sites with higher and medium conservation priority values (Galetti et al. 2009), may facilitate forest protection as well as contribute to obtaining financial resources for ecosystem management. Several states in Brazil (including Paraná) pay municipalities to maintain protected areas (Ring 2008), and some of these resources may be used to promote forest restoration, mostly along rivers, which require strict protection according the Brazilian Forest Bill (Beca et al. 2017). Reversing forest loss and increasing the connectivity among fragmented patches may benefit species richness (Beca et al. 2017) and also amplify the value of fragments as stepping-stones for large mammals (Galetti et al. 2009). It is urgent that hunting pressure be reduced as this human activity is responsible for both types of defaunation in Neotropical forests: reduced species richness and decaying mammal biomass (Antunes et al. 2016; Galetti et al. 2016; Peres & Palacios 2007). In our study region, the hunting is widely practiced for "sport" or to obtain "exotic meat" (for self consumption or sale) since people do not need protein from wildlife. Therefore, enhancing the intelligence programs of environmental law enforcement and field monitoring can stop these criminal groups.

The future of mammals in the Atlantic Forest depends on true landscape management, effective protection, continuous research, and of course, involvement of the entire society in the cause of conservation. Diverse studies have been showing negative human impacts on the biodiversity of the Atlantic Forest (Beca et al. 2017; Chiarello 2000; Galetti et al. 2016; Magioli et al. 2016; Tabarelli et al. 2010b), but the same studies have indicated feasible measures to mitigate and reverse species loss and thus increase our conservation power.

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Supplemental Material

Table S1. Species recorded in each site

	Sites																
Species	Sjo	Tba	Fag	Slo	Dga	Rla	Mel	Bar	Pgo	Aal	Piq	Pac	Sap	Rsf	Rsj	Gua	Igua
*Bos taurus**														X			
Mazama americana																X	X
Mazama nana						X	X	X	X	X	X	X	X	X	X	X	X
*Sus scrofa**														X			
Pecari tajacu													X	X		X	X
Tayassu pecari														X		X	X
*Canis lupus familiaris**	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cerdocyon thous	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
*Felis catus domesticus**						X			X								
Leopardus guttulus			X			X	X	X		X			X		X	X	X
Leopardus pardalis										X				X		X	X
Leopardus wiedii							X	X			X	X	X	X	X	X	X
Panthera onca																X	X
Puma concolor													X			X	X
Puma yagouaroundi			X				X			X			X	X			X
Galictis cuja									X	X					X		X
Eira barbara				X		X	X				X	X	X	X	X	X	X
Lontra longicaudis				X			X				X		X	X	X	X	X
Nasua nasua	X		X	X		X	X	X		X	X	X	X	X	X	X	X
Procyon cancrivorus								X		X		X		X	X	X	X
Cabassous tatouay							X			X		X	X	X			X
Dasypus novemcinctus	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Euphractus sexcinctus							X										
Didelphis albiventris	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Didelphis aurita													X	X		X	X
*Lepus europaeus**				X			X					X			X		
Sylvilagus brasiliensis																	X
Tapirus terrestris										X						X	X
Myrmecophaga tridactyla																	X
Tamandua tetradactyla						X				X				X	X	X	X
Sapajus nigritus					X	X	X	X	X	X	X	X	X	X	X	X	X
Hydrochoerus hydrochaeris					X		X		X		X		X	X	X	X	X
Cuniculus paca							X			X		X	X	X		X	X
Dasyprocta azarae				X	X	X	X	X	X	X		X	X	X	X	X	X
Coendou spinosus				X			X		X			X		X	X	X	X
Myocastor coypus									X			X					X
Guerlinguetus brasiliensis			X	X			X			X	X	X	X	X	X	X	X

*exotic species

Table S2. Results of First order Jackknife analysis

site	Native species recorded through camera traps	Total native species	Expected species	±s.e.
Sjo	3	4	4.92	1.36
Tba	1	1	1	na
Fag	6	7	7.98	1.4
Slo	5	9	6.98	1.4
Dga	4	6	4.98	0.98
Rla	8	10	9.98	1.98
Mel	15	18	19.98	2.23
Bar	10	10	12.98	1.72
Pgo	7	10	8.99	1.4
Aal	14	17	20.98	2.63
Piq	9	11	11.99	1.72
Pac	7	15	8.99	1.4
Sap	15	19	17.99	1.72
Rsf	19	22	22.99	1.99
Rsj	12	17	18.98	2.64
Gua	23	25	28.99	2.44
Igu	26	31	26.99	0.99

Table S3. Historically mammal species present in study region. Species taxonomy, mean body's mass and conservation status (according red lists of IUCN, Brazil and Paraná state)

Order	Family	Species	Body mass (kg)	Conservation status		
				IUCN	Brazil	Paraná state
Artiodactyla	Cervidae	*Mazama americana*	36	DD	DD	VU
		Mazama nana	17.5	VU	VU	VU
	Tayassuidae	*Pecari tajacu*	26	LC	LC	VU
		Tayassu pecari	35	VU	VU	CR
Carnivora	Canidae	*Cerdocyon thous*	6.5	LC	LC	LC
		Speothos venaticus	6	NT	VU	VU
	Felidae	*Leopardus guttulus*	2.25	VU	VU	VU
		Leopardus pardalis	9.5	LC	VU	VU
		Leopardus wiedii	6	NT	VU	VU
		Panthera onca	109.5	NT	VU	CR
		Puma concolor	46	LC	VU	VU
		Puma yagouaroundi	4.5	LC	LC	DD
	Mustelidae	*Eira barbara*	7	LC	LC	LC
		Galictis cuja	2	LC	LC	LC
		Lontra longicaudis	6	NT	LC	NT
	Procyonidae	*Nasua nasua*	5.1	LC	LC	LC
		Procyon cancrivorus	5.4	LC	LC	LC
Cingulata	Dasypodidae	*Cabassous tatouay*	5.35	LC	LC	DD
		Dasypus novemcinctus	3.65	LC	LC	LC
		Euphractes sexcinctus	5.4	LC	LC	LC
Didelphiphormia	Didelphidae	*Didelphis albiventris*	1.6	LC	LC	LC
		Didelphis aurita	1.2	LC	LC	LC
Lagomorpha	Leporidae	*Sylvilagus brasiliensis*	1.2	LC	LC	VU
Perissodactyla	Tapiridae	*Tapirus terrestris*	260	VU	LC	EN
Pilosa	Myrmecophagidae	*Myrmecophaga tridactyla*	30.5	VU	VU	CR
		Tamandua tetradactyla	5.2	LC	LC	LC
Primates	Atelidae	*Alouatta guariba*	5.6	LC	LC	NT
	Cebidae	*Sapajus nigritus*	3.5	NT	LC	DD
Rodentia	Caviidae	*Hydrochoerus hydrochaeris*	50	LC	LC	LC
	Cuniculidae	*Cuniculus paca*	9.3	LC	LC	EN
	Dasyproctidae	*Dasyprocta azarae*	2.9	DD	LC	LC
	Erethizontidae	*Coendou spinosus*	1.8	LC	LC	LC
	Myocastoridae	*Myocastor coypus*	1	LC	LC	LC
	Sciuridae	*Guerlinguetus brasiliensis*	0.17	LC	LC	LC

Taxonomy and mean body mass were based in Paglia et al. (2012), except for *L. guttulus* (Trigo et al. 2013) and *G. brasiliensis* (Patton et al. 2015). Conservation status: IUCN red list (IUCN 2016), Brazilian (Chiarello et al. 2008) and Paraná state red list (Estado do Paraná Decreto nº 7264 2010)

Table S4. Mammal richness, proportion of species, abundance and biomass.

Sites	Richness	Proportion of species*	Abundance (ind/ 100 cam.day)	Biomass (kg/ 100 cam.day)
Sjo	4	0.11	33.3	120.2
Tba	1	0.02	18.7	30
Fag	7	0.20	29.0	94.1
Slo	9	0.26	40.3	176.0
Dga	6	0.17	78.6	328.6
Rla	10	0.29	54.9	233.8
Mel	18	0.52	91.3	688.0
Bar	10	0.29	62.5	354.9
Pgo	10	0.29	25.6	450.7
Aal	17	0.50	45.9	270.6
Piq	11	0.32	29.7	161.6
Pac	15	0.44	17.2	69.4
Sap	19	0.55	76.1	398.7
Rsf	22	0.64	96.9	1099.7
Rsj	16	0.47	15.3	66.5
Gua	25	0.73	39.6	1164.7
Igu	31	0.91	60.3	1993.2

* In relation to a Mammalian assemblage of 34 species, see Table S3.

Table S5. Hunting signs found in study sites (recorded: 1; non-recorded: 0)

	hunting signal						
Site	Human trail	*jirau* and *ceva*[1]	Shot	Camping	People detained for hunting	Hound[2]	Camera trap stolen
Sjo	0	0	0	0	0	0	0
Tba	0	0	0	0	0	0	0
Fag	0	0	0	0	0	0	0
Slo	0	0	0	0	0	0	0
Dga	0	0	0	0	0	0	0
Rla	0	0	0	0	0	0	0
Mel	1	0	0	0	0	1	0
Bar	1	1	0	0	0	0	0
Pgo	1	0	0	0	1	0	0
Aal	1	1	1	0	0	1	0
Piq	1	0	0	0	0	1	0
Pac	0	0	0	0	0	0	0
Sap	1	1	0	0	0	1	1
Rsf	1	1	0	0	0	0	1
Rsj	1	1	0	1	0	1	0
Gua	1	1	0	0	0	1	0
Igu	1	1	0	1	1	1	1

[1] *jirau* = platform on trees used to wait animal to shoot them, *ceva*: food (corn or fruits) and salt used to attract mammals. [2] Considering only direct visualization or camera trap caught of breed dogs used to hunting.

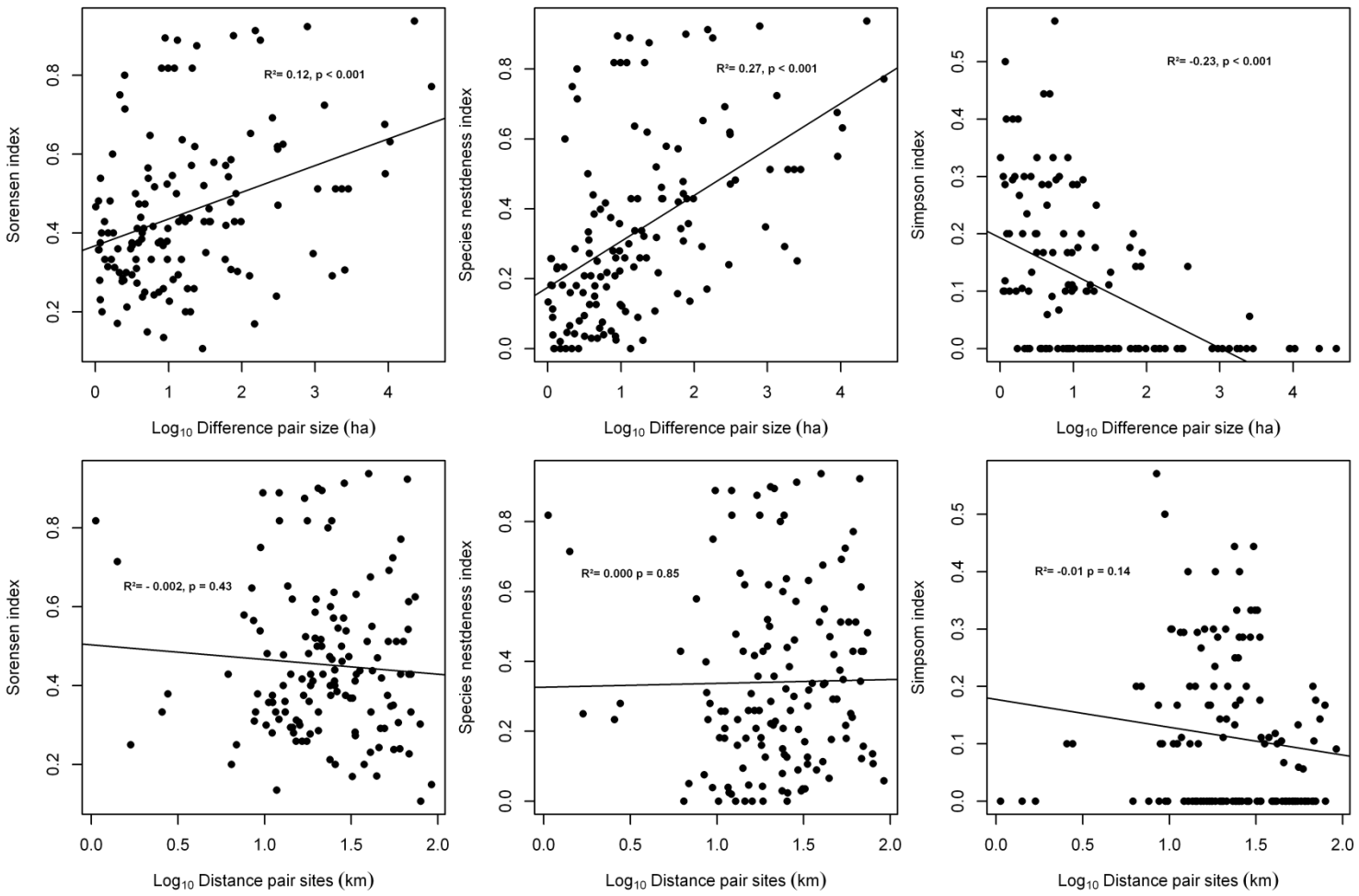

Figure S1. Pair-wise site comparison by β-diversity values as a function of the difference among the forest patches in terms of size and distance between them.

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Capítulo III. Forest fragmentation and selective logging affect the seed survival and recruitment of a relictual conifer

Forest fragmentation and selective logging affect the seed survival and recruitment of a relictual conifer

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Abstract

Defaunation, invasive species and forest fragmentation are considered to be the major drivers for the disruption of key ecological processes, particularly those related to plant animal-interactions such as seed dispersal and predation. The disruption of critical phases in the plant life cycle may ultimately have negative impacts on plant recruitment and the survival of plant populations. Here, we compared the seed removal and recruitment of *Araucaria angustifolia*, a critically endangered and relictual gymnosperm species, in continuous and fragmented forest areas in the Brazilian Atlantic subtropical forest. We found that seed survival and recruitment were related to the density of adults *A. angustifolia*. Therefore the formation of large and dense groves, a characteristic of pristine *Araucaria* moist forests which are endangered by forest fragmentation and selective logging, may be an attempt to satiate seed predator communities. Additionally, forest fragmentation and the introduction of wild boar decreased seed survival to very low rates at some sites, and forest fragmentation decreased recruitment by four-fold on average. The increased protection and recuperation of *Araucaria* moist forests and the eradication of the invasive wild boar where possible are necessary measures for increasing seed survival rates and the recruitment of this relictual conifer.

Key-words: scatter-hoarding, Araucariaceae, *Dasyprocta azarae*, *Cyanocorax chrysops*, *Sus scrofa*, Neotropics

1. Introduction

Seed survival and seedling recruitment represent a bottleneck in the life cycle of most vascular plants in which seed dispersal is an important process. Therefore, for zoochoric species, the presence of dispersers is indispensable to their success (Galetti et al. 2013; Nathan & Muller-Landau 2000; Neuschulz et al. 2016; Schupp et al. 2010). In fact, both seed dispersal and seed predation have been suggested to regulate plant dominance and thereby maintain forest diversity (Connell 1978; Janzen 1971). As a result these ecological interactions play major roles in determining the composition of forests (Kurten et al. 2015).

However, ecosystems suffer globally with human interference altering biological communities and consequently leading to breaks and changes in ecological processes (Butchart et al. 2010; Dirzo et al. 2014; Estes et al. 2011; Galetti & Dirzo 2013; Sanderson et al. 2002; Tylianakis et al. 2008; Young et al. 2016). Forest fragmentation (Cordeiro et al. 2009; Galetti et al. 2006), the loss of seed dispersal (Galetti et al. 2006; Wright et al. 2000), and changes in the seed predator community (Galetti et al. 2015a; Tella et al. 2016b) are among the Anthropocene's effects that may negatively affect plant populations and recruitment dynamics, posing real risks to the future survival of some plant species (Pérez-Méndez et al. 2016). Understanding these impacts on plant recruitment is fundamental to guiding conservation efforts (Kurten 2013).

In this study, we aimed to investigate the effects of forest fragmentation, selective logging and changes in the animal community on seed predation and the recruitment of Paraná-pine (*Araucaria angustifolia*), a relictual conifer from a genus originating in the Jurasic period (Kershaw & Wagstaff 2001). The use of this species as a model is interesting because its presence characterizes a global ecoregion, the *Araucaria* moist

forest. In its absence, this ecosystem becomes uncharacterized, a rare case, where the loss of a single species may completely change the ecosystem. *Araucaria* moist forests have experienced strong fragmentation and timber exploitation (Castella & Britez 2004; Ribeiro et al. 2009). As result of these activities, Paraná-pine is Critically Endangered (Thomas 2013) and has shown recruitment failures in forest fragments (Paludo et al. 2016; Souza 2007).

Since Paraná-pine seeds rely on animals for dispersal and encounter high rates of seed predation (Brum et al. 2010; Iob & Vieira 2008; Vieira et al. 2011), we tested the hypotheses that: I) seed removal will be negatively related to Paraná-pine dominance and higher rates of seed survival (i.e., seeds are not removed) and recruitment will be observed in dense groves as a result of high seed abundances (satiation hypothesis) (Beck & Terborgh 2002; Vieira et al. 2011); II) fragmentation will increase seed removal and decrease seedling recruitment, and small rodents will dominate interactions in fragmented forests due to the release of competition with large mammals (DeMattia et al. 2004; Galetti et al. 2015a; Iob & Vieira 2008); III) interactions with the largest seed disperser (agouti) will be negatively affected by forest fragmentation (Galetti et al. 2015a; Galetti et al. 2006; Iob & Vieira 2008); and IV) buried seeds will have a greater chance of surviving than non-buried seeds, independent of their distance from adult tree (Brewer & Webb 2001), demonstrating the importance of scatter-hoarders for the recruitment of this plant.

2. Materials and Methods

2.1 Study species, ecosystem characteristics and threats

The Paraná-pine (*Araucaria angustifolia*) is a large (up to 50 m tall and 3.5 m in diameter at breast height) dioecious (rarely monoecious) wind-pollinated conifer (Farjon 2010; Mattos 2011) with long generation time (35 years) (Thomas 2013). The female-tree annually produce an average of 16 seed cones containing 87 recalcitrant seeds on average (each weighting 6.8 g on average), known in Portuguese as "pinhão" (plural: "pinhões") (Mantovani et al. 2004). Seed maturation occurs between March and August (the Autumn-Winter Austral period), when seed cones or separated seeds directly drop below mother-tree. Seed dispersal depends mainly on scatter-hoarders, such as plush-crested jays (*Cyanocorax chrysops*) (Uejima et al. 2012), agouties (*Dasyprocta azarae*) (Ribeiro & Vieira 2013) and squirrels (*Guerlinguetus brasiliensis*) (Bordignon & Monteiro-Filho 2000), although some seeds may occasionally be dispersed by parrots (Tella et al. 2016a) or by monkeys (Brocardo, C.R., pers. obs.), when these animals move from the mother tree carrying its seeds. Assemblage of Paraná-pine seed predators include all Neotropical seed predator groups, including invertebrates, rodents, primates, carnivores, birds, ungulates and even humans (Vieira & Iob 2009).

The presence, density and dominance of Paraná-pines characterize the *Araucaria* moist forest, an ecoregion of the Atlantic forest, which is a global biodiversity hotspot (Myers et al. 2000). The original distribution of Paraná-pine encompasses an area larger than 200,000 km² including great part of Southern Brazil, high altitude areas of Southeastern Brazil (mostly above 800 m, mainly in the Serra da Mantiqueira) and a small portion of Misiones Province in Argentina, overlapping high and regular annual precipitation

(annual rainfall range: 1,400-2,400 mm) and cool winters (temperatures can fall to -10 ºC) (Backes 2009; Hueck 1953).

Despite *A. angustifolia* having the largest distribution of any of the *Araucaria* species, the substantial timber exploitation and high conversion rates of its habitat into agricultural lands put it among the most threatened Araucariacae with this species considered to be Critically Endangered by IUCN (Thomas 2013). Today, only 12% of the Brazilian *Araucaria* moist forest remains, with most of the remaining forest being in patches (79% of remnants) smaller than 50 ha (Ribeiro et al. 2009), and in the great majority of cases, there is an extremely low abundance or even a total absence of Paraná-pine trees due to the heavily selective timber extraction of this species (Castella & Britez 2004). Additionally, seed harvesting and recruitment failure threaten this species (Paludo et al. 2016).

2.2 Study areas

To measure the effects of forest fragmentation and changes in the animal community on seed removal and the recruitment of *A. angustifolia* we studied ten forest fragments and three continuous areas (Figure 1). Study areas varied from 8 to 181,000 ha (more details about study sites see supplemental material). *Araucaria* moist forest fragments, in general, experienced timber extraction and reduction in seed predator and disperser communities (Brocardo & Cândido-Jr 2012), while two of our continuous areas represented more intact seed predator community (Iguaçu National Park and Campos do Jordão State Park) (Brocardo et al. 2017), and a third continuous area (Alto-Montana Reserve) exhibited an impoverished native fauna composition, with the presence of the exotic and invasive wild boar (*Sus scrofa*) (Pedrosa et al. 2015).

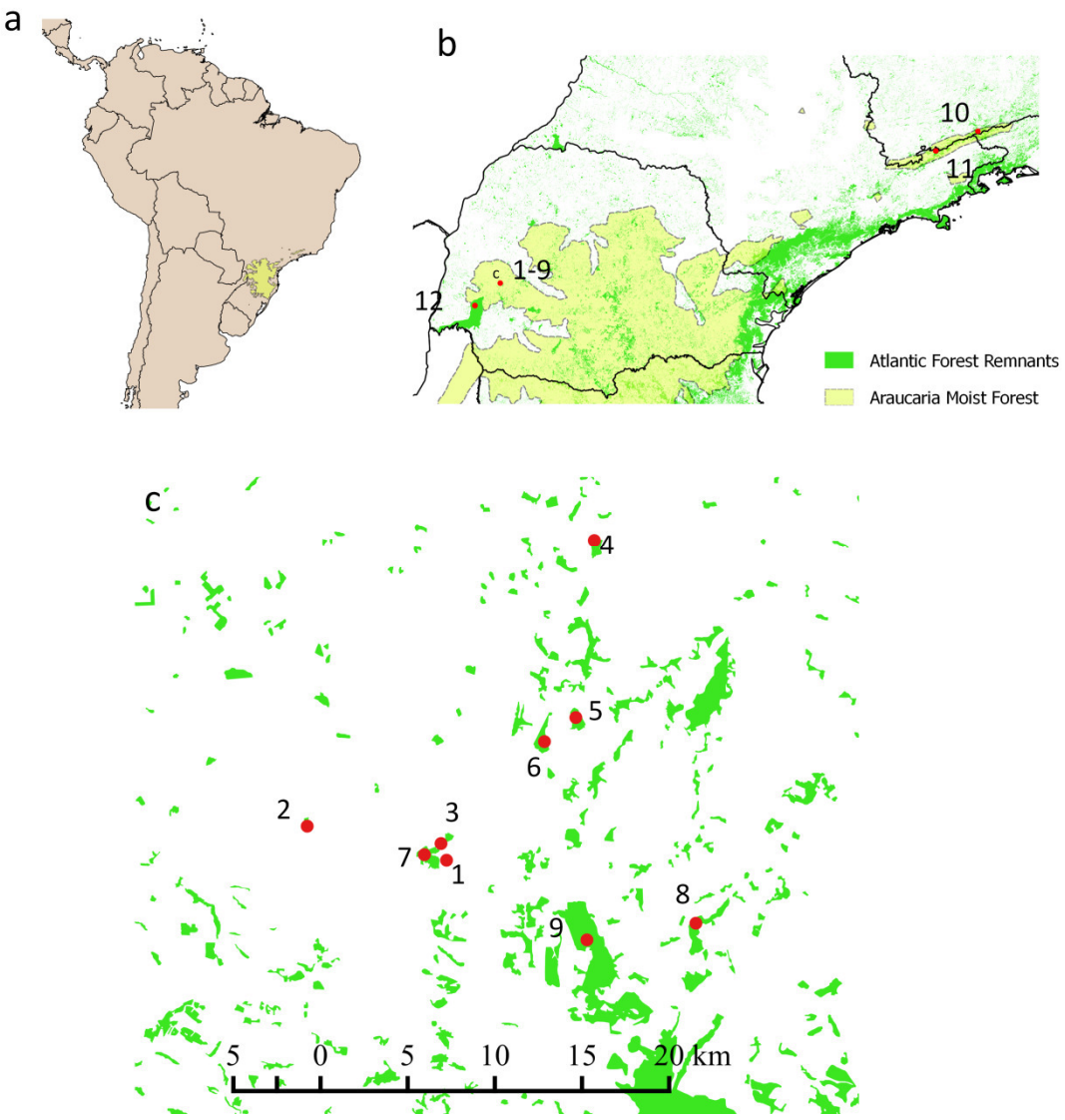

Figure 1. a) *Araucaria* moist forest in South America; b) Sampled sites, and; c) highlights for 1-9 sampled forest fragments (to site names see Table S1).

2.3 Experiments

1) Identifying and quantifying seed removers and interactions

We used camera-traps in video function (10s, with 1s delay, Bushnell HD Trophy) to identify and quantify animal species removing the seeds of *A. angustifolia*. The

camera-traps were set directly beneath adult Paraná-pine females during seed fall period (austral autumn-winter, March-August), where we set 60 seeds on average in front of the camera. We sampled 3 to 16 trees per site (11 sites, Table S1), according to forest size and our camera-trap availability. Each camera was placed at minimum 100 m from each other for cameras and let for a period of 17 days on average. In this experiment, we tested hypotheses I, II and III.

2) Effects of buried treatment and distance from parent tree to seed survival

We tested whether scatter-hoarding dispersal is necessary for the survival of *A. angustifolia* seeds because many seeds can be dispersed by barochory or occasionally be carried out by non-scatter hoarding frugivores, such as parrots (Tella et al. 2016a) or capuchin monkeys (Brocardo, C.R., pers. obs.). We used eight adult Paraná-pine female at six sites (Table S1), where we placed group of seeds every 5 meters along a line up to 30 m from each tree. At group of seeds, we placed five seeds above the soil surface separated 20 cm from each other and three buried seeds (at a depth 5 cm, mimicking scatter-hoarding) 20 cm from each other and 1 m away from the non-buried seeds. We returned to observe the fate of each group of seed after 15 days. We considered seeds that survived those that were not removed or preyed upon. In this experiment, we tested hypothesis IV.

3) Paraná-pine recruitment

With aim of verifying the effects of forest fragmentation and adult density on Paraná-pine recruitment, we established three vegetative plots (50 x 50 m) at 9 sites (Table S1). Each plot was placed at a minimum distance of 100 m from other plots. In these plots, we counted juvenile and adult Paraná-pines. Additionally, because factors other than

forest fragmentation and logging may interfere with the recruitment of gymnosperms, such as angiosperm trees (Bond 1989; Souza 2007), bamboos (Narukawa & Yamamoto 2002) and ferns (Coomes et al. 2005), we also measured the dominance of these components in the plots. For angiosperms, we measure the diameter of all trees with a d.b.h greater than 6.75 cm and for dominance of bamboo and ferns, we measured the total area (m^2) occupied by each in the plots.

In this experiment, we tested the hypotheses I and II.

2.4 Statistical analyses

The total seed removal monitored by camera-traps was analyzed using generalized linear mixed-effects models (family=binomial, link = "logit") using the lme4 package (Bates et al. 2007) in R program (R Development Core Team 2016). The random components of models were the sites and fixed components were the environmental variables (Paraná-pine predominance, distance from forest edge, forest patch size; see supplemental material). Non-significant variables were removed in subsequent models to produce as parsimonious model as possible. Afterwards, we separately analyzed the seed removal rate done by scatter-hoarder (agouties, squirrels and plush-crested-jays together) and seed predators (capuchin monkeys, small rodents and ungulates), and also separate models were used for agouties, plush-crested jays and small rodents (grouped together because reliable identification of mice species in the videos was not possible). In these analyses, because the seed removal by one group could interfere with that by another group, we also included proportion of seeds removed in the other groups' models as a fixed factor (Mendes et al. 2015). The best model was chosen according to the AIC with correction for small samples (AICc) (Burhnam & Anderson 2002).

The proportion of surviving seeds from the experiment with buried treatments was analyzed using a generalized linear mixed-effects model (family=binomial, link = "logit"), wherein sites and individual Paraná-pine within sites were combined as random factors in the models, and the distance of seeds from Paraná-pines, the treatment (buried vs. non-buried) and forest patch size were used as fixed factors.

For data about Paraná-pine recruitment, we used a generalized linear mixed-effects model (family=Poisson, link = "log"). We used the site as the random component, and fixed components were the number of female Paraná-pine in each plot, forest patch size (log-transformed), percentage of area occupied by angiosperm trees (the total area determined by the sum of areas determined from d.b.h), and the area dominated by ferns and bamboos (both in percentage). In subsequent analyzes, we removed non-significant variables with aim of reduce the explanatory variables and finding a more parsimonious model. The best model was chosen according to ΔAICc.

All models were confronted with null models, and analyses were preformatted in R program (R Development Core Team 2016).

3. Results

3.1 Identifying and quantifying seed removers and interactions

We found in average 83.5% of the seeds were removed (seeds removed or eaten in place), ranging from 28.5 % to 100% (Figure 2). When all the seeds were removed, the last seed was removed after 6.5 days on average (6.1 ± 1.0 days in forest fragments, and 7.6 ± 0.6 days in continuous sites).

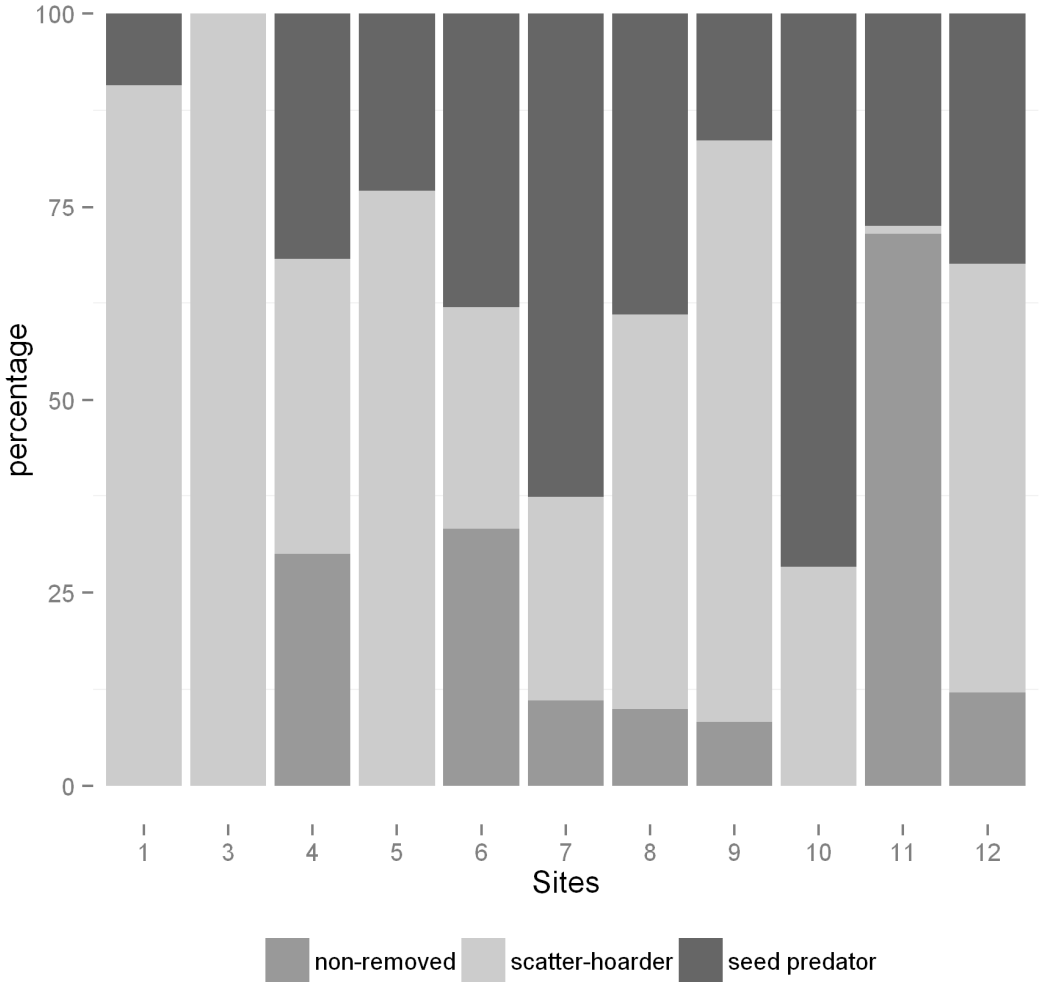

Figure 2. Percentage of *Araucaria angustifolia* seeds non-removed, removed by scatter-hoarders and removed by seed predators, monitorated through camera trap. Sites are ordered according to patch size. More details about sites see Table S1.

Most seeds were removed by scatter-hoarder species (50.1% of total available seeds, Figure 2). Plush-crested jays (*C. chrysops*) removed 28.4% of the seeds (ranging from 0% in some sites to 90%), while agouties (*D. azarae*) removed 18.5% (0 to 84%) and squirrels (*G. brasiliensis*) removed only 3.1% (0 to 28%) (Figure 3). Seed removal by species that act primarily as seed predators corresponded to 33.4%. Small rodents (Cricetidae) performed 13.9% of the removals (0 to 30%), followed by capuchin-monkeys (*Sapajus nigritus*) with 11.7% (0 to 36%) and by exotic and invasive feral pigs

(*Sus scrofa*), which consumed 4.5% of the total seeds, but preyed upon 59.7% of the seeds at a single site (Figure 3). Pacas (*Cuniculus paca*) and white-lipped peccaries (*Tayassu pecari*) rarely fed on the seeds (1 and 2% respectively of the total seeds).

Our analyses indicated that the total seed removal was negatively affected by forest patch size and Paraná-pine tree dominance**,** and was positively affected by the distance from forest edge (Table 1). Seeds have more chances to be removed in areas with low Paraná-pine dominance, in small fragments and in locations more distant from forest edges.

The proportion of seed removal performed by scatter-hoarder species was negatively affected by the seed removal performed by seed predators and forest patch size, and was positively affected by the distance to the forest edge. Seed removal by predators was negatively affected by scatter-hoarder seed removal and Paraná-pine dominance. Seed removal performed by agouties was negatively affected by the forest patch size and the seed removal performed by seed predators, and was positively affected by the distance to forest edge. Seed removal by plush-crested jays was negatively affected by the removal performed by both agouties and seed predators. Finally, the seed removal by nocturnal small rodents was positively affected by increasing distances from the forest edge and negatively affected by removal performed by scatter-hoarders (the value of the best model for each analysis is presented in Table 1, even though other models may have the same inference power $\Delta AICc \leq 2.0$, the significance of explanatory variables did not change; see Table S2).

Table 1. Results from GLMM analyses for *Araucaria angustifolia* seed removal. In bold significant responses (All models and value of ΔAICc are presented in Table S2).

Removal response	Explanatory variables present in chosen model	z-value	*p*
Total	Distance from forest edge (log m)	2.68	**<0.01**
	Paraná-pine dominance (%)	-2.76	**<0.01**
	Forest patch (log ha)	-2.35	**0.01**
All scatter-hoarders	Seed removal by seed predators	-4.4	**<0.01**
	Distance from forest edge (log m)	2.51	**0.01**
	Forest patch (log ha)	-2.22	**0.02**
All seed predators	Seed removal by scatter-hoarders	-2.4	**0.01**
	Paraná-pine dominance (%)	-2.74	**<0.01**
	Distance from forest edge (log m)	1.59	0.11
Agouties	Seed removal by plush-crested jays	-1.6	0.10
	Interaction with seed predators	-2.87	**<0.01**
	Distance from forest edge (log m)	1.95	**0.05**
	Forest patch (log ha)	-2.32	**0.02**
Plush-crested jays	Seed removal by agouties	-2.84	**<0.01**
	Seed removal by seed predators	-3.35	**<0.01**
	Distance from forest edge (log m)	1.68	0.09
	Forest patch (log ha)	-1.01	0.12
Small rodents	Seed removal by scatter-hoarders	-2.05	**0.03**
	Distance from forest edge (log m)	2.55	**0.01**
	Paraná-pine dominance (%)	-1.87	0.06

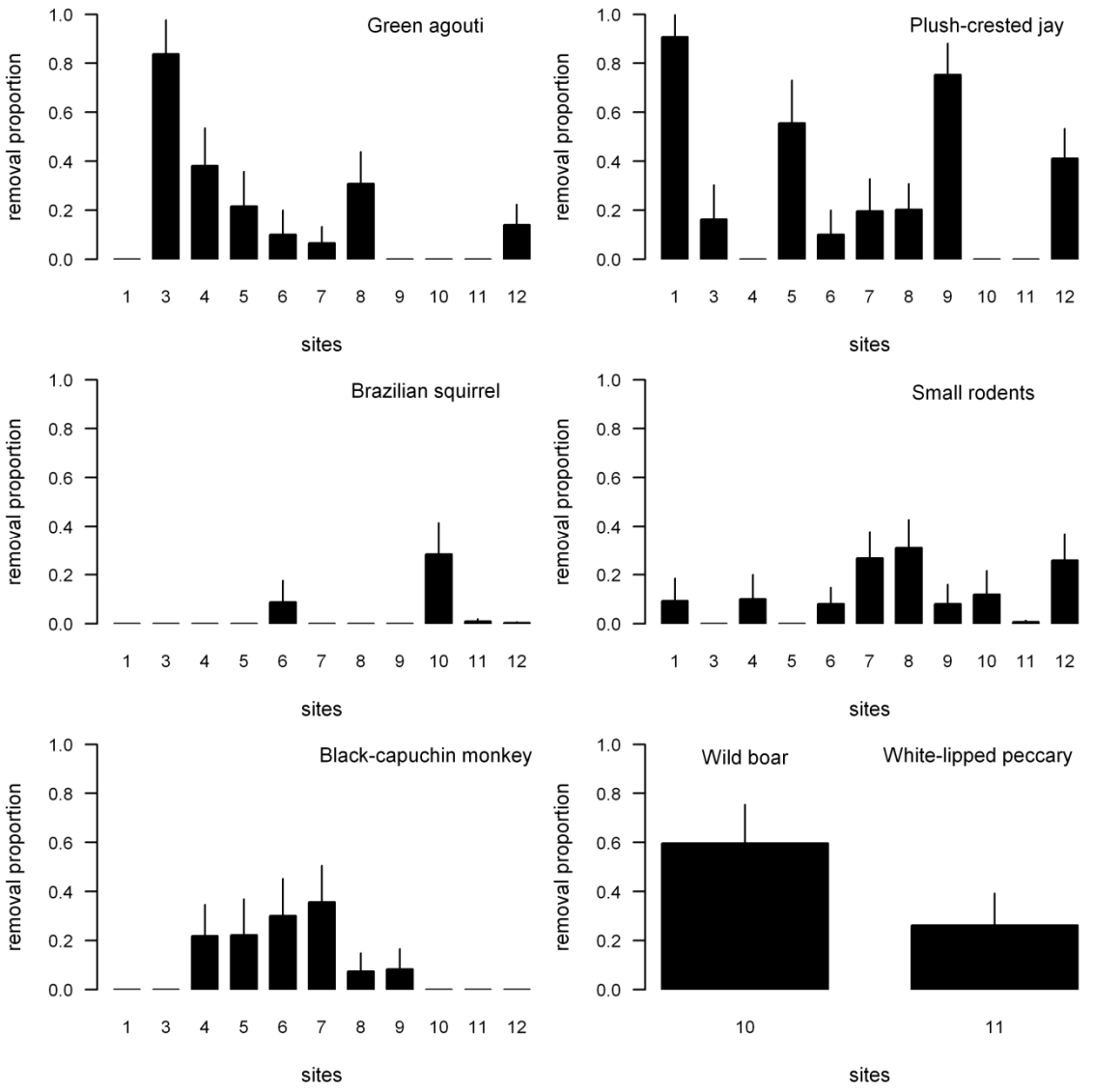

Figure 3. Proportion of *Araucaria angustifolia* seeds removed by green agouti (*Dasyprocta azarae*), plush-crested jay (*Cyanocorax chrysops*), Brazilian squirrel (*Guerlinguetus brasiliensis*), small rodents (family Cricetidae), black-capuchin monkeys (*Sapajus nigritus*), exotic feral pig (*Sus scrofa*) and white-lipped peccary (*Tayassu pecari*). Sites are presented in increasing patch size (See table S1).

3.2 Effects of buried treatment and distance from the parent tree on seed survival

Cached seeds had on average a 46% ± 2% (mean ± se) rate of survival, while only 1.8% ± 0.01% of seeds left on the surface of soil remained intact after 15 days of exposure. Our analysis found a significant impact of the burial treatment on of survival according to treatment (soil surface; z-value = -8.78, $p < 0.001$), whereas the distance of seeds

from fruiting-trees (z-value = 0.58, p = 0.56) and forest patch size (z-value = 1.54, p = 0.12) were not significant. Thus, the results showed that the buried treatment provided by scatter-hoarders increased seed survival 25-fold, independent of the distance from female-trees.

3.4 Paraná-pine recruitment

Our control site for the recruitment analysis (Iguaçu National Park – site number 12) exhibited the largest recruitment, with a mean of 382.6 ± 122.8 juveniles/ha (mean ± se), while forest fragments exhibited a mean recruitment that was 4-fold lower (86.5 ± 11.1, ranging from 6 to 125 juveniles/ha on average) (Figure 4). Paraná-pine adult density was also higher in the continuous site, with 52 ± 18 adults/ha, whereas forest fragments had a mean of 19.3 ± 2.9 adults/ha (ranging from 6.6 to 34.6 adults/ha on average) (Figure 4). Only Paraná-females numbers (z-value = 6.69, $p < 0.001$) and forest patch size (z-value = 2.36, $p = 0.01$) were significant explanatory variables, and both were positively related to the total number of juveniles in the plots (Table S2).

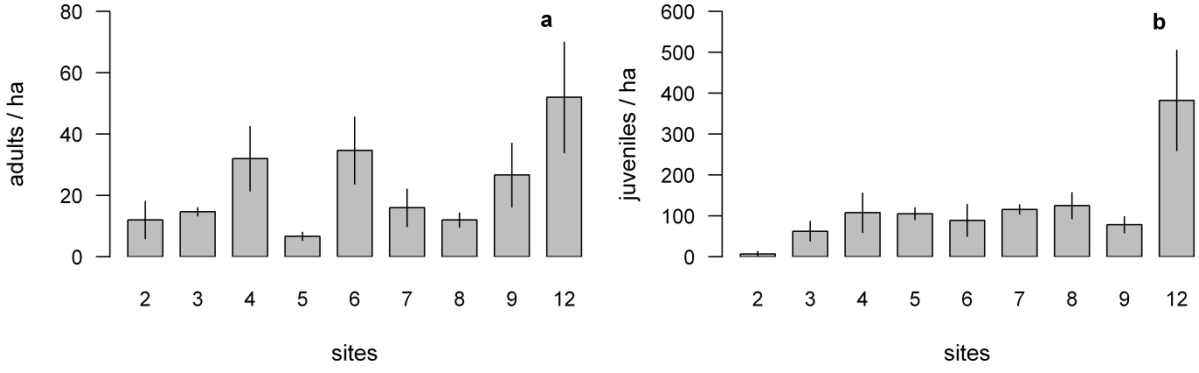

Figure 4. Adult and juveniles density of *Araucaria angustifolia* in nine sites where we measure recruitment. Sites are presented in size order (See table S1).

4. Discussion

Our results show that human interferences in *Araucaria* moist forest have had negative effects on the ecology of *A. angustifolia*, due to changes in the seed predator communities and the natural availability of seeds, which in turn diminish seed survival and recruitment, indicating that the seed stage may be the most critical phase in the Paraná-pine lifecycle.

In places with higher predominance of Paraná-pines, we observed increased chances for seeds to escape predation and higher rates of recruitment, as we had expected (hypothesis I). Thus, the formation of large and dense groves by this conifer, a characteristic of pristine *Araucaria* moist forests, probably represents an attempt to satiate its seed predators and dispersers. Therefore, forest fragments that had experienced harvesting of Paraná-pine trees tended to be more affected and present higher rates of seed removal. High seed abundance is a characteristic necessary for the success of scatter-hoarding seed dispersal (Forget 1990; Jansen et al. 2004; Theimer 2005; Vander Wall 2002). The high seed abundance in dense groves may sufficiently satiate dispersers, resulting in superior recruitment rates in these areas (Forget 1990, 1992; Jansen et al. 2004; Vieira et al. 2011). Our recruitment results related to female trees corroborate this view.

With regard to our second hypothesis (that forest fragmentation will increase seed removal and decrease recruitment), total seed removal was found to be related to patch size, and consequently, fragmentation increased the chances of seed removal, and decreased Paraná-pine recruitment. However, we did not find a significant response to fragmentation in the interaction between small rodents and Paraná-pine seeds, as we had expected. In fact, fragmentation appears to benefit the seed interaction with scatter-

hoarders, mainly agouties in some fragments, which led us to reject the third hypothesis (the negative effects of fragmentation in agouti interaction), contrary to other works in Atlantic forest (Brum et al. 2010; Galetti et al. 2015a; Galetti et al. 2006; Iob & Vieira 2008). Agouties may respond positively to forest fragmentation because of competitive and predator releases (Jorge 2008), even increasing seed caching in some defaunated sites, where they are not preferred game species (Kurten 2013). Constant interactions with scatter-hoarders, even in small forest fragments, might have a cascade effect on small rodent interactions, thus avoiding the predominance of the latter group in seed removal as observed in other studies in fragmented and defaunated sites of *Araucaria* moist forest (Brum et al. 2010; Iob & Vieira 2008). Indeed, competition may rule small rodent predation on seeds (Galetti et al. 2015a; Galetti et al. 2015b).

One advantage of maintaining a high level of interaction with scatter-hoarders is the functional service that they provide: seed dispersal via individual caching. Our study demonstrated that scatter-hoarders were important to *A. angustifolia* regeneration because the cached treatment was more important to seed survival than seed dispersal distance from its mother tree (hypothesis IV). The positive effect of scatter-hoarders on seed survival has been observed in diverse plant genera (Forget 1990; Gómez 2004; Jansen et al. 2004; Myczko et al. 2014), despite the fact that relatively few seeds can survive recovery by scatter-hoarders (Haugaasen et al. 2010; Jansen et al. 2004), a fact also observed for *A. angustifolia* (Ribeiro & Vieira 2016; Ribeiro & Vieira 2013). Because fragments provide limited resources, they may exhibit “island effects” (Fadini et al. 2009; Terborgh et al. 2001), with an increase in predation by agouties and plush-crested jays, which may diminish seedling recruitment (Fadini et al. 2009; Jorge & Howe 2009; Kurten 2013). In this situation, even though the seed dispersal mechanism is not lost, the conditional mutualism established between plants and their dispersers

may be affected, leading to most of the cached seeds being consumed and altering seed dispersal's effectiveness (Jorge & Howe 2009; Theimer 2005). Our results suggested this scenario, with Paraná-pine recruitment decreasing with reduction in forest size.

In addition to changing the efficiency of seed dispersal performed by scatter-hoarders, cascade effects caused by defaunation and resource limitation in forest fragments may lead other species to increase their impacts on seed predation. For example, black-capuchin monkeys, species that is not hunted in *Araucaria* moist forests, exhibited a higher impact on seed predation in forest fragments (17% on average considering only forest fragments) while they were not recorded removing seeds in continuous sites. Additionally, capuchin-monkeys may have a significant impact when directly feeding on seeds in female Paraná-pine trees, damaging more than half of all seeds produced in a year (Pagno et al. 2015).

Nevertheless, no seed predator (excluding scatter-hoarders) presented a seed removal as high as the exotic boar. This invasive species was responsible for killing 59.7% of the seeds at a single site (Alto Montana Reserve), the only continuous area where all seeds were removed. The high seed predation by the wild boar is extremely worrying, because similar native species, such as the white-lipped peccary and collared-peccary (*Pecari tajacu*), did not have the same impact. White-lipped peccaries were only recorded preying on seeds at one site, where they consumed 26.2% of the seeds, less than half of that consumed by wild boar. Currently, wild boar (and other forms of feral pigs) are established in most parts of *Araucaria* moist forest in Brazil and their population has increased and expanded to new areas (Figure S1) (da Rosa et al.; Pedrosa et al. 2015), which may affect *A. angustifolia* recruitment. In the Chilean and Argentinean *Araucaria-Nothofagus* temperate forests, the introduction of wild boar has caused a

considerable increase in seed predation and a reduction in the seedling recruitment of *A. araucana* (Sanguinetti & Kitzberger 2010; Tella et al. 2016b).

Seed dispersal and survival are critical stages in the plant life-cycle and will pose a challenge for the persistence of many animal-dispersed plants in the Anthropocene (Galetti et al. 2015a; Kurkjian et al.; Mendes et al. 2015; Pérez-Médez et al. 2016; Rosin & Poulsen 2016; Tella et al. 2016b). Our results highlight the effects of forest fragmentation, selective logging and animal community changes on seed predation and the recruitment of a relictual tree species. Today, most part of (90%) *Araucaria* moist forest is formed by fragments up to 100 ha (Ribeiro et al. 2009), indicating that few sites may be able to satiate their seed predators. In addition to animal pressure, Paraná-pine seeds are collected for human use, which may inhibit the regeneration of this species (Souza 2007). Controlling forest degradation, increasing the protection and recuperation of forest cover, and eradicating the invasive wild boar where possible, are all necessary measures for increasing seed survival rates and consequently recruitment of this relictual species.

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Supplemental material

Study sites description

The sampled fragments and Iguaçu National Park are located in western region of Paraná State Brazil (Figure 1). The mean altitude above sea level (a.s.l.) is 660 m, and the climate type is Cfa according to the Köppen classification system, with an average annual rainfall of 1,870 mm, no dry season, and an annual mean temperature of 19 °C (Alvares et al. 2013). In this region the *Araucaria* moist forest maintains contact with the Atlantic Semi-deciduous forest and remained forested until 1950, before the waves of settler emigration. Today most part of the landscape is occupied by grain monocultures and cattle pastures (Brocardo 2013; Castella & Britez 2004).

The other two areas, the Campos do Jordão State Park and Alto-montana Reserve, are located in Serra da Mantiqueira. Despite greater ancient forest exploitation and a greater European colonial presence (since 1700) (Rodrigues 2003) than the landscape of the Paraná sites, the Serra da Mantiqueira has maintained high forest cover due to their elevation and irregular topography, which forms a large continuous forest, and represent the most important refuge for *Araucaria* moist forests in Southeast Brazil, where this forest maintains contact with the Atlantic Rainforest, the Atlantic Semi-deciduous forest and natural grasslands (Meireles et al. 2008; Ribeiro et al. 2009).

Campos do Jordão State Park (São Paulo state, S22°41’58” W45°27’37”) is 1,600 m a.s.l., under a Cfb climate, with an annual rainfall of 1,860 mm (and a short dry season in the winter) and an average annual temperature of 14 °C. Alto-Montana Reserve (Minas Gerais state, S22°21’52” W44°48’03”) is approximately 1,500 m a.s.l., under a Cwb climate according to the Köppen classification scheme, with an annual rainfall of 1,600 mm (a dry season in the winter) and average annual temperature of 14 °C (Alvares et al. 2013).

Table S1. Study sites, patch size and protection status. Number of sampled points with camera traps in each site and information on the experiment carried in each site.

Site	Forest size (ha)	Sampled points with camera trap	Buried treatment experiment	Recruitment sampling
1. Teatro-Barracão	7.9	3	No	No
2. FAG	17.1	No	No	Yes
3. Danilo Galafassi Municipallity Park	20.5	6	Yes	Yes
4. Rio Melissa	71.3	10	No	Yes
5. Barreiro	78.4	9	Yes	Yes
6. Alto Alegre	105.2	10	No	Yes
7. Paulo Gorski Ecological Park	95.1	9	Yes	Yes
8. Cascavel Environmental Park	192.8	13	Yes	Yes
9. Rio São José	1,421	12	Yes	Yes
10. Alto Montana Reserve*	9,992	8	No	No
11. Campos do Jordão State Park*	20,903	8	No	No
12. Iguaçu National Park	181,588	16	Yes	Yes

*Corresponds to total patch size where site is inserted

Environmental variables used in analyses of seed removal

- Paraná-pine dominance. We used it as approach to seed production (crown densities may be used as proxy to seed production, Jansen et al. 2008). Paraná-pine cover dominance was estimated in a radius of 100 m around each sampled point through images from Google Earth in QuantumGis version 2.12.0 and using Open Layers Plugin Google maps. As Paraná-pine presents distinctive crown shapes easily identified in images, we were able to create polygons and thereby calculate the percentage occupied in each circle.
- Total area of forest cover. Forest patch size (in hectares log-transformed) of study sites calculated using shapefile of Atlantic forest remnants from *SOS Mata Atlântica* (https://www.sosma.org.br) together with open-source Google Earth resources to correct the sizes of the patches in shapefiles that do not include more recent forest regeneration as well as some areas dominated by bamboo.
- Distance from forest edge. Distance of sampled points in relation to forest edge (in meters, log transformed).

Table S2. Summary of GLMMs analyzed in seed removal and *Araucaria angustifolia* recruitment. Significant explanatory variables are in **bold**.

Response variable	Explanatory variables used in model	AICc	ΔAICc
Total seed removal	Null model	90.79	7.37
Total seed removal	**log10(dist_bord)** + **log10(size)** + **pin_cover**	83.41	0.00
Scatter hoarder removal	Null model	142.2	61.25
Scatter hoarder removal	**seed_pred** + **log(dist_bord)** + **log_size** + pin_cover	82	1.05
Scatter hoarder removal	**seed_pred** + **log(dist_bord)** + **log_size**	80.95	0
Seed predator removal	Null model	134.83	71.22
Seed predator removal	**Scatte**r**_hoard** + log10(dist_bord) + log10(size) + **pin_cover**	65.41	1.80
Seed predator removal	**Scatte**r**_hoard** + **pin_cover**	64.44	0.83
Seed predator removal	**Scatter_hoard** + log10(dist_bord) + **pin_cover**	63.61	0.00
Dasyprocta azarae removal	Null model	142.2	84.72
Dasyprocta azarae removal	**seed_pred**	85.64	28.16
Dasyprocta azarae removal	**seed_pred** + log10(size)	84.7	27.22
Dasyprocta azarae removal	**seed_pred** + log10(dist_bord) + **log10(size)**	84.37	26.89
Dasyprocta azarae removal	*C.chrysops* + **seed_pred** + **log10(dist_bord)** + **log10(size)** + pin_cover	59.25	1.77
Dasyprocta azarae removal	*C.chrysops* + **seed_pred** + **log10(dist_bord)** + **log10(size)**	57.48	0.00
Cyanocorax chrysops removal	Null model	116.77	47.46
Cyanocorax chrysops removal	***D.azarae*** + **seed_pred** + log10(dist_bord)+log10(size)+pin_cover	71.76	2.45
Cyanocorax chrysops removal	***D.azarae*** + **seed_pred** +log10(dist_bord)+log10(size)	69.47	0.16
Cyanocorax chrysops removal	***D.azarae*** + **seed_pred** + log10(dist_bord)	70.01	0.70
Cyanocorax chrysops removal	***D.azarae*** + **seed_pred**	69.31	0.00
Small rodent removal	Null model	82.75	25.15
Small rodent removal	**Scatter_hoard** + **log10(dist_bord)**	60.89	3.29
Small rodent removal	Scatter_hoard + log10(dist_bord) + **log10(size)** + **pin_cover**	59.81	2.21
Small rodent removal	**Scatter_hoard** + **log10(dist_bord)** + pin_cover	57.6	0.00
Araucaria angustifolia recruitment	Null model	358.87	47.41
Araucaria angustifolia recruitment	**Female_n** + **log10(size)** + ang%+ fern% + bamboo%	317.13	5.67
Araucaria angustifolia recruitment	**Female_n** + **log10(size)** + fern%	312.45	0.99
Araucaria angustifolia recruitment	**Female_n** + **log10(size)**	311.46	0.00

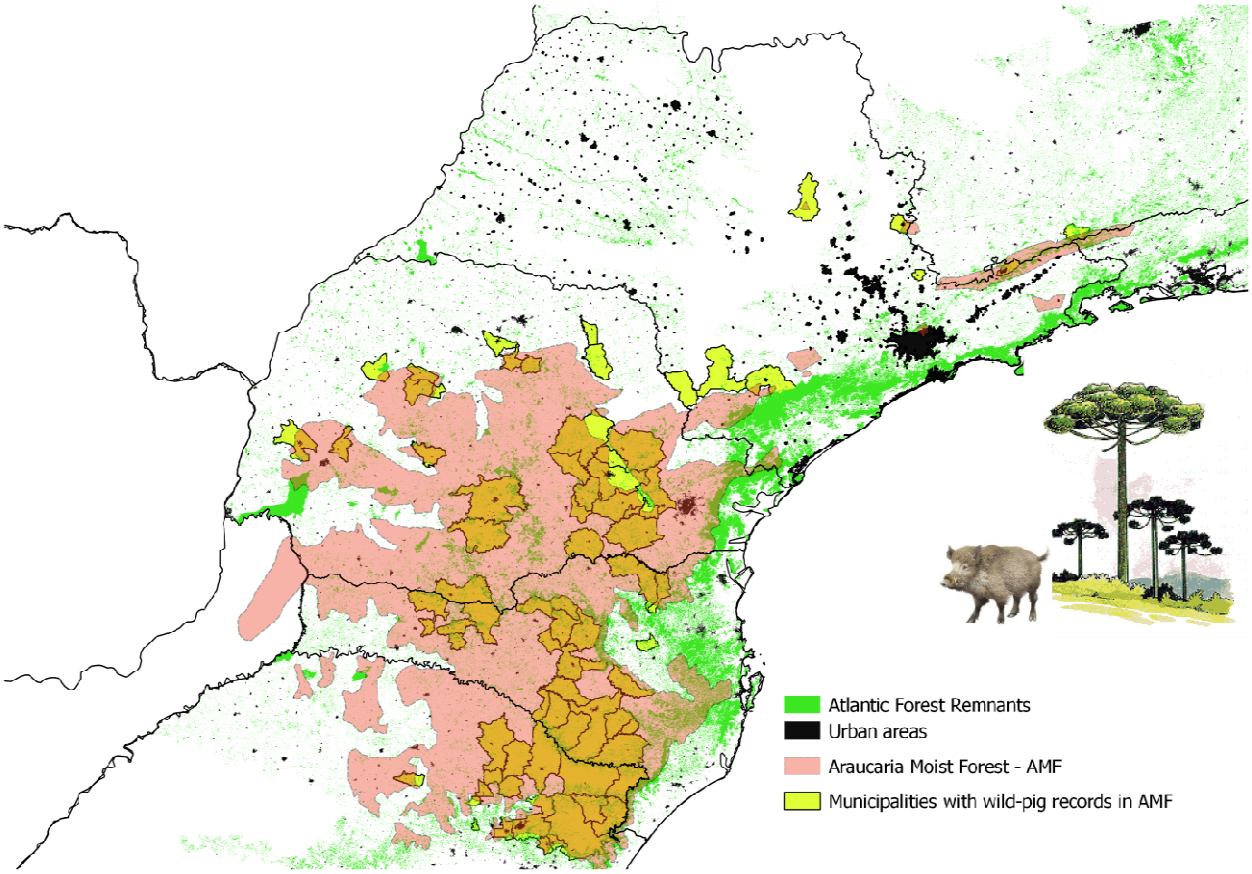

Figure S1. Southeastern and Southern Brazilian municipalities with presence of feral pigs (*Sus scrofa*) in *Araucaria* moist forest (green) based in (Pedrosa et al. 2015).

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CONSIDERAÇÕES FINAIS

A conversão de terras para agricultura e a caça constituem as principais ameaças a resilência de vertebrados nos mais diversos ecossistemas. A primeira atua na redução de ambientes disponíveis, e a segunda persiste mesmo nos habitats remanescentes. Como resultado ocorrem extinções locais, baixa na abundância de várias espécies e alteração na intensidade das interações ecológicas. Essa tese trouxe resultados inéditos para uma região de Mata Atlântica subtropical pouco explorada cientificamente que, contudo, já foi altamente convertida em uma paisagem dominada por atividades antrópicas.

No capítulo II fica evidente o efeito prejudicial da redução de habitat sobre a riqueza e biomassa de mamíferos de médio e grande porte. Assim a presença de grandes remanescentes florestais se mostrou fundamental para manutenção de riqueza de espécies e, sobretudo, em abrigar os maiores mamíferos. Aumentar a conectividade e, principalmente a proteção contra a caça, são medidas urgentes e necessárias para crescer as probabilidades de persistência dos mamíferos na paisagem de estudo. Nesse contexto, evitar desmatamentos, mesmo que de pequenos fragmentos ou parte de grandes áreas, é essencial para que os mamíferos possam aumentar suas populações e expandir suas ocupações. Oportunidades para recomposição de vegetação nativa também existem, por exemplo, na mata ciliar do rio Iguaçu, que conecta o Parque Nacional do Iguaçu e o Parque Estadual Rio Guarani, há um grande déficit de cobertura florestal nativa, situação que está em desacordo com o que legisla o Código Florestal. Essa recomposição poderia ser financiada por hidrelétricas (em funcionamento em construção) como medida de mitigação de impactos ambientais causados ao longo desse rio.

Os resultados do capítulo III demonstraram que a fragmentação florestal e alterações na comunidade de predadores de sementes levaram ao crescimento na remoção de sementes da árvore dominante (*Araucaria angustifolia*), o que somado a baixa abundância da espécie, devido ao corte seletivo no passado, reduz a regeneração em fragmentos florestais. Esse resultado destaca o efeito negativo do corte seletivo, medida de manejo proposta por setores madeireiros, e mesmo acadêmicos, como alternativa sustentável para conservação e uso da Floresta Ombrófila Mista. Como a presença e a dominância de *A. angustifolia* definem a Floresta Ombrófila Mista, o seu baixo recrutamento resultará em uma floresta ainda mais descaracterizada no futuro. Dado o baixo número de *A. angustifolia* em diversos fragmentos, a melhor medida de conservação seria o replantio ativo da espécie dentro dessas áreas, principalmente nas bordas florestais, o que poderia no futuro gerar maiores taxas de recrutamento dessa conífera globalmente ameaçada. Em áreas onde ainda ocorre a dominância da espécie, um controle rigoroso na coleta de sementes poderia resultar em maior saciação dos dispersores – que têm persistência mesmo nos menores fragmentos - aumentando assim as taxas de regeneração natural.

Em conclusão, embora a fragmentação florestal na Floresta Ombrófila Mista tenha causado perdas pontuais de espécies de mamíferos nos fragmentos e alterações na regeneração florestal, os resultados obtidos nessa tese demonstram que tanto a riqueza de mastofauna quanto o processo de recrutamento florestal, embora alterados, continuam resilientes dentro da paisagem amostrada. Um manejo integrado das Unidades de Conservação e de florestas particulares pode crescer substancialmente o nosso poder de conservação nessa situação, sendo fundamental, contudo, o engajamento da sociedade civil, cobrando e atuando junto com o poder público, para obtenção de melhores resultados e em menor espaço de tempo.