UNIVERSIDADE FEDERAL DE SANTA CATARINA
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CONTINGÊNCIA *VERSUS* DETERMINISMO: O PAPEL DOS PARADIGMAS NEUTROS E DE NICHO NOS PADRÕES DE DIVERSIDADE DE MAMÍFEROS NA MATA ATLÂNTICA SULAMERICANA

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Orientador: Prof.ª Dr. Nivaldo Peroni
Co-orientador: Dr. Maurício Eduardo Graipel

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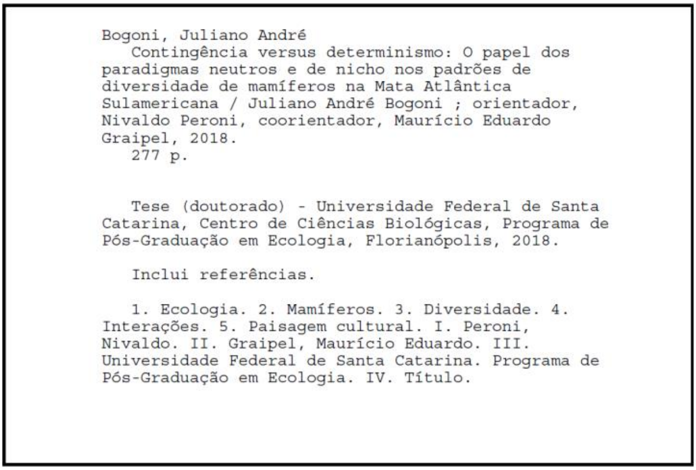

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“Contingência *Versus* Determinismo: O Papel dos Paradigmas Neutros e de Nicho nos Padrões de Diversidade de Mamíferos na Mata Atlântica Sulamericana”

Por

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Dedico à minha família.

"Truth is born into this world only with pangs and tribulations, and every fresh truth is received unwillingly"

Alfred Russel Wallace

"It is those who know little, and not those who know much, who so positively assert that this or that problem will never be solved by Science"

Charles Darwin

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Essa é uma tese sobre como o acaso e o determinismo influencia os elementos de maior porte da sobrevivente megafauna – os médios e grandes mamíferos, remanescentes de uma outrora mais majestosa biota – na floresta tropical com o maior gradiente latitudinal do mundo, mas esta seção é destinada às pessoas sem as quais nada disto teria sido feito. Portanto, a seguir deixarei narrado meus agradecimentos, quase numa *flamboyant* poesia para um deselegante como eu. Fundamentalmente, esse trecho inicial se trata de um hibridismo entre agradecimento e uma extensão da abreviada dedicatória. Assim sendo, agradeço aos meus pais, Celita e Juarez, e minha mana, Talita, pelo apoio e incentivo desde meu início na carreira acadêmica e por fazerem parte dessa trajetória. Numa jornada de acertos, erros (cf. *Omnia cinis aequat*) e hodiernas sombras na ciência, vocês sempre estiveram comigo, mesmo que muitas vezes não fisicamente. Felizmente, e muito felizmente, nem se quer uma pálida sombra de dúvida do que eu queria ser e fazer se embrionou entre vocês, tampouco repousou vindo de propágulos externos. A todos vocês, família Bogoni, meu ávido e atemporal muito obrigado, pela paciência, por acreditarem verdadeiramente em mim, por respeitarem minhas limitações intrínsecas, extrínsecas (adiei muita coisa, mas não dependia de mim, me desculpem), e por nunca colocarem em dúvida minha decisão de abraçar a academia. E aqui seguirei, e assim seguiremos juntos, ainda que a distância agora possa ser superlativa. Qualquer compêndio escrito nesse documento – de cerca de três centenas de páginas e um conjunto de mais de 9.000 dados ecológicos – não seria possível sem vocês. Logo – mãe, pai, mana – essa tese de doutorado também é de vocês, vocês me blindaram, foram, são, sempre serão, minha sombra tutelar e inspiração. Desejo vê-los sempre prósperos e escoltados pela mais elegante simplicidade que sempre o tiveram.

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RESUMO

A Mata Atlântica Sulamericana está entre as cinco ecorregiões com maior biodiversidade do mundo. Essa ecorregião apresenta uma grande variação na diversidade de hábitats e de formações vegetais que são acompanhadas por grandes variações nos padrões de diversidade e endemismo de vários grupos taxonômicos. Entretanto, a Mata Atlântica é também uma das regiões mais ameaçadas do planeta, por fatores como perda e fragmentação de hábitats, isolamento, defaunação e introdução de espécies exóticas. Da formação original restam cerca de 12% de cobertura vegetal com conectividade reduzida e fragmentos pequenos e perturbados. Na porção subtropical, as terras altas da Mata Atlântica são caracterizadas por mosaicos de vegetação de campo e florestas espacialmente restritos e amplamente ameaçados por mudanças climáticas e de uso do solo. Nas suas terras altas, a presença marcante da conífera ameaçada *Araucaria angustifolia* (Bertol) Ktze. (Araucária) formam a Floresta Ombrófila Mista (FOM), a qual tem sido usada como *proxy* para estratégias de conservação. A FOM teve forte influência antropogênica desde o período pré-colombiano—com Araucárias sendo expandidas pelos povos Xokleng e Kaingang—até as contemporâneas reduções na distribuição geradas pela exploração madeireira por quase um século, desde 1900 até meados dos anos 1980. A semente da Araucária (Pinhão) é possivelmente o principal recurso de sustentação da teia alimentar da FOM, com pico de produtividade no início do rigoroso inverno local, tendo também importância sociocultural e econômica para as populações humanas locais, assim como um forte produto do mercado extrativista do sul do Brasil. Em termos edáficos, as Araucárias ocupam o estrato superior das florestas e facilitando condições para o estabelecimento de outras espécies vegetais importantes, principalmente Myrtaceae e Lauraceae, que igualmente podem prover recursos à fauna que a elas se associam. Uma das espécies de Myrtaceae marcante nas terras altas é a *Acca sellowiana* (Berg) Burret (Feijoa), uma espécie que produz frutos grandes no início do outono, sendo considerada uma espécie incipientemente domesticada. O intrincado mecanismo de formação da estrutura da FOM depende dos processos históricos bem como de processos ecológicos mediados por animais, especialmente polinizadores, predadores e dispersores de sementes e frutos. Mamíferos são particularmente importantes neste cenário por desempenhar várias destas e outras funções ecológicas, além de serem amplamente ameaçados pela fragmentação de hábitats e pela caça que reduziu a diversidade da outrora majestosa Mata Atlântica. Existem muitas lacunas na biologia e ecologia de mamíferos, como carência de dados de abundância, desconhecimento das causas de variação nos padrões de diversidade, incertezas de distribuição e taxonomia das espécies. Os objetivos principais desta tese é avaliar os padrões de diversidade de mamíferos de médio e grande porte em regiões dentro da Mata Atlântica; quantificar as interações ecológicas entre os recursos (Pinhão e Feijoa) e a fauna de mamíferos (incluindo seres humanos); avaliar padrões, variações e causas da distribuição de espécies na FOM; e construir cenários teóricos da distribuição de espécies-chave da FOM em diferentes escalas temporais. Para isso, adotei diferentes metodologias em diferentes escalas espaciais ao longo da Mata Atlântica, especialmente dentro da região de FOM; fiz uso de dados secundários, de armadilhas fotográficas, de parcelas demográficas, de entrevistas com moradores locais e de modelagem de distribuição entre os anos de 2014 a 2017. Meu principal resultado mostra que existe uma variação de fundo na diversidade de mamíferos de 3.99 espécies de diferença entre um local e outro, mas que para áreas subtropicais essa diferença é de 2.17 espécies. Ainda, a alternância sazonal e espacial na produção de recursos (Pinhão e Feijoa) da FOM tem impactos diretos e indiretos, imediatos e postergados na estrutura das comunidades de vertebrados, especialmente de mamíferos. Questões históricas e fundiárias perpetuam influências na estrutura das florestas e na fauna nativa e cenários de mudanças climáticas podem alterar padrões e processos ecológicos e adicionar dificuldades em estratégias de conservação da FOM e seus elementos. A direção geral dos resultados contribui para o entendimento de como a união de processos históricos e ecológicos são capazes de alterar padrões de diversidade em áreas de grande importância para a conservação. Meus resultados evidenciam que processos históricos exercem influências diretas e indiretas nos padrões passados, atuais e futuros em paisagens dominadas por espécies com diferentes tipos de uso humano. Além disso, a fauna tem importância fundamental para a estrutura dos mosaicos de terras altas da Mata Atlântica subtropical, que vão desde consumo primário, passando pela dispersão de sementes, até a influência marcante dos predadores de topo. Essas perspectivas, portanto, contribuem para o conhecimento de padrões e processos na Mata Atlântica, especialmente na porção subtropical, e são capazes de capitanear políticas públicas de conservação diante de cenários de mudanças iminentes que poderão comprometer o funcionamento do ecossistema e seus serviços.

Palavras-chave: Mata Atlântica; Mamíferos; Diversidade; Floresta Ombrófila Mista; Araucária; Feijoa; Interações; Estruturação de comunidades; Conservação; Paisagem cultural, Construção de nicho.

ABSTRACT

The South American Atlantic Forest is one of five most biodiverse ecoregions in the world. This ecoregion comprises a wide variation in the diversity of habitats and vegetation formations that are accompanied by large variations on diversity patterns and on endemism of several taxonomic groups. However, the Atlantic Forest is also one of the most threatened regions in the planet, due to habitat loss, fragmentation and isolation, and to defaunation and introduction of exotic species. From the original Atlantic Forest formation there remains about 12% of vegetation cover in small and disturbed fragments with reduced connectivity. In their subtropical portion, the Atlantic Forest highlands are characterized by a mosaic of spatially-restricted vegetation fragments that are widely threatened by climate change and land use characterize. Within its highlands the outstanding presence of the threatened conifer *Araucaria angustifolia* (Bertol) Ktze. (Araucaria) compose the Mixed Ombrophilous Forest (FOM), which has been used as a proxy for conservation strategies. The FOM had a strong anthropogenic influence since the pre-Columbian period—with Araucarias being expanded by Xokleng and Kaingang ethnic groups—until the mid-1980's when it was the target of logging for almost a century. The Araucaria seed (Pinhão) is possibly the main staple resource of the FOM food web, whose productivity peaks at the beginning of the austral winter. Moreover, the Pinhão is also an important socio-cultural and economic resource for the local human populations. In edaphic terms, Araucarias occupy the upper strata of the forests and provide conditions for the establishment of other important plant species, especially Myrtaceae and Lauraceae, which can also provide resources to the associated fauna. One of the Myrtaceae species outstanding to the highlands is the *Acca sellowiana* (Berg) Burret (Feijoa), which produces large fruits in the early fall, and which has aspects of incipient domestication. In addition to historical processes, the intricated engineering of FOM formation and structure depends on current ecological processes mediated by animals, especially pollinators, seed dispersers and predators. Among these, mammals are particularly important for performing these and other ecological functions while are widely threatened in the Atlantic Forest by hunting and the destruction and fragmentation of habitats. Although widely studied, mammals there are many gaps in their biology and ecology, such as unknown abundance and causes of variations of diversity patterns, and uncertainties in distribution ranges and taxonomy. The overarching goal of this thesis is understand the neutral and niche influences on mammals diversity and structuring of communities. To do so, I evaluate the diversity patterns of medium- to large-bodied mammals in regions within the Atlantic Forest of South America; quantify the ecological interactions between the food resources (Pinhão and Feijoa) and the fauna (including local peoples); evaluate patterns, causes of variation in species distribution within FOM; and build theoretical scenarios of the distribution of FOM key species at different time scales. At different spatial scales throughout the Atlantic Forest, especially within the FOM region, I carried out this work between 2014 and 2017 employing different methodologies—such as, the use of secondary data, camera traps, demographic plots, interviews with local residents, species distribution models. My main result shows a background variation in mammal diversity between sampled places of 3.99 species, although this difference is 2.17 species for subtropical areas. Moreover, the results show that the seasonal and spatial alternation in the production of resources (Pinhão and Feijoa) of the FOM has direct and indirect, immediate and delayed impacts on the structure of vertebrate communities, especially mammals. Historical and land issues perpetuate influences on the structure of forests and native fauna; predictive scenarios of climate change can alter ecological patterns and processes and add difficulties in FOM conservation strategies and their elements. Overall, my results contribute to the understanding of how the combined effect of historical and ecological processes can change patterns of diversity in areas that are important for conservation. The results herein show that historical processes have direct and indirect influences on the past, present and future patterns in landscapes dominated by species with different types of anthropic use. In addition, this work reinforces that the fauna is fundamental for the structure of the highland mosaics of the subtropical Atlantic Forest, ranging from primary consumption, through the dispersion of seeds, to the marked influence of top predators on energy flow through food webs. This study, therefore, contributes to the knowledge of patterns and processes in the Atlantic Forest, especially in the subtropical portion and can propel public conservation policies in the face of scenarios of imminent changes that could jeopardize the ecosystem functioning and its services.

Key-words: Atlantic Forest; Mammals, Diversity; Mixed Ombrophilous Forest; Araucaria; Feijoa; Interactions; Communities structuring; Conservation; Cultural Landscape; Niche construction

LISTA DE SIGLAS

AIC - Akaike Information Criteria
CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
CBH - Circumference at Breast Height
CEL - Conhecimento Ecológico Local
CEPSH - Comitê de Ética com Pesquisa com Seres Humanos
CNPq - Conselho Nacional de Pesquisa
CXR - Coxilha Rica, Lages, Área Particular
ECOHE - Laboratório de Ecologia Humana e Etnobotânica, UFSC
FED - Florestas decíduas
FOD - Floresta Ombrófila Densa
FOM - Floresta Ombrófila Mista
FOM-AL - Mixed Ombrophilous Forest alluvial
FOM-UM - Mixed Ombrophilous Forest upper montane
FSD - Floresta semidecíduas
GPS - Global Positioning System
IBGE - Instituto Brasileiro de Geografia e Estatística
ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade
IUCN - International Union for Conservation of Nature
LECOTA - Laboratório de Ecologia Terrestre Animal, UFSC
MEC - Ministério da Educação e Cultura
NODF - Metric of network nestedness
PAA - Parque Nacional das Araucárias - Área A (porção Oeste)
PAB - Parque Nacional das Araucárias - Área B (porção Leste)
PARNA - Parque Nacional
PCA - Principal Component Analysis
PCNM - Principal Coordinate Analysis of Neighborhood Matrices
PPBio - Programa de Pesquisa em Biodiversidade
PSA - Parque Nacional de São Joaquim - Área A (Morro da Igreja)
PSB - Parque Nacional de São Joaquim - Área B (Campos de Santa Barbara)
RDA - Redundancy Analysis
RGF - RPPN Grande Floresta das Araucárias
RLM - RPPN Leão da Montanha
RPPN - Reserva Particular do Patrimônio Natural
SDMs - Species Distribution Models
UC - Unidade de Conservação

UFSC - Universidade Federal de Santa Catarina
VIF - Values of Variance Inflation

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APRESENTAÇÃO

Leopardus pardalis (Linnaeus, 1758) [jaguatirica] registrada em Mata de Araucária na data de 12 de agosto de 2016 na Reserva Particular do Patrimônio Natural Grande Floresta das Araucárias, Bom Retiro, Santa Catarina, Brasil (27°54’02” S; 49°23’26” O; 1.044 m.s.n.m).
Foto: Bogoni, 2016.

APRESENTAÇÃO

Um dos principais objetivos em ecologia é compreender os padrões, as tendências e as causas da distribuição e abundância das espécies na natureza; por essa razão, o arcabouço teórico meandra por muitas interfaces biológicas, físicas e sociais. Ademais, os sistemas ecológicos são, por natureza, complexos, autorregulados e dinâmicos no espaço e no tempo, complicando o desafio de entender padrões e processos nas diferentes escalas. Outros fatores, como políticas de conservação (ou a virtual ausência delas, na forma de deficiências de fiscalização) e questões históricas, também adicionam complexidade teóricas e práticas nos estudos ecológicos, especialmente em ecorregiões densamente ocupadas por assentamentos humanos contemporâneos e por locais com paisagens modificadas por ações humanas passadas.

As ecorregiões tropicais e subtropicais tendem a ser ecologicamente ainda mais complexas, têm um legado em seus padrões que é resultado das ações de populações humanas do passado e atualmente são intensamente perturbadas. Dentre essas regiões, destaca-se—de maneira dicotômica—a Mata Atlântica sulamericana. Essa região é um *hotspot* de diversidade mundial e ao mesmo tempo uma das áreas mais ameaçadas do planeta. Restam apenas cerca de 12% de sua cobertura original em fragmentos pequenos, perturbados, com baixa conectividade e em matrizes de paisagem intensamente modificadas por ações humanas, passadas e contemporâneas (Ribeiro et al. 2009). Na Mata Atlântica, as Florestas de Araucária *sensu stricto* (ou Floresta Ombrófila Mista [FOM]) são uma das formações vegetais mais reduzidas, as quais estão inseridas em agromosaicos e assentamentos humanos (Lacerda 2016). Essa formação vegetal é caracterizada pela presença marcante da Araucária (*Araucaria angustifolia* (Bertol.) Ktze.). Esta conífera ocorre em altitudes elevadas (> 600 m), sofreu importante influência antropogênica histórica e hoje é ameaçada de extinção (Mattos 1972; Reis et al. 2014; Lacerda 2016). Além disso, a Araucária fornece um recurso alimentar sazonal, temporalmente abundante, grande e altamente energético—o Pinhão. Potencialmente, Pinhão é o principal recurso de sustentação da teia alimentar da FOM, além de ter uma marcante importância sociocultural e econômica para as populações humanas locais (Reis et al. 2014).

Em termos edáficos, as Araucárias ocupam o estrato superior e geralmente fornecem condições para o estabelecimento de outras espécies vegetais importantes, principalmente Myrtaceae e Lauraceae, que igualmente podem prover recursos para a fauna. Dentre essas espécies ligadas as Florestas de Araucária–logo às terras altas–destaca-se a Feijoa (*Acca sellowiana* (Berg) Burret). Os frutos da Feijoa (localmente conhecida como goiabeira-serrana), assim como o Pinhão, são sazonais, grandes e energéticos, temporalmente abundantes e, sobretudo, disponíveis na época da ausência do Pinhão.

Entretanto, tanto para os padrões de diversidade, de distribuição de espécies na Mata Atlântica quanto para as espécies vegetais destacadas da FOM (i.e. Araucária e Feijoa) restam lacunas no conhecimento ecológico. Muitos estudos e muitas premissas teóricas, indicam que a intrincada engenharia da formação a estrutura das florestas depende dos processos ecológicos mediados pelos animais, especialmente polinizadores, predadores e dispersores de sementes e frutos (Dirzo et al. 2014; Peres et al. 2016). Simultaneamente, os recursos da FOM (especialmente o Pinhão e a Feijoa) por várias vias diretas (e.g. consumo de sementes) e indiretas (e.g. predadores de consumidores de sementes) têm o potencial de estruturar as comunidades animais espaço-temporalmente.

Entre as comunidades animais, as de mamíferos são particularmente mais influenciadas pelos recursos Pinhão e Feijoa. Ao mesmo tempo, mamíferos da região Neotropical são amplamente ameaçados pela destruição e fragmentação de hábitats e pela caça (Dirzo et al. 2014; Bogoni et al. 2016a; Peres et al. 2016). Os mamíferos são importantes ao redor do mundo por desempenhar importantes funções ecológicas (e.g. regulação de teias tróficas e estruturação de comunidades, incluindo outros grupos taxonômicos) e por contribuírem para a estrutura, dinâmica e regeneração das florestas (e.g. predação e dispersão de sementes) (Peres et al. 2016). Embora componham um grupo taxonômico amplamente estudado restam diversas lacunas no conhecimento dos padrões e causas das variações de diversidade até a associação com espécies vegetais e padrões de distribuição no tempo e espaço.

Portanto, os objetivos principais da minha tese de doutorado foi avaliar e entender os padrões de diversidade de mamíferos de médio e grande porte em regiões dentro da Mata Atlântica sulamericana para obter valores de variação de fundo (numa perspectiva neutra onde todas as espécies de mamíferos seriam equivalentes ecológicos [i.e., governados apenas por contingência]) que subsidiam o entendimento das variações ligadas à processos deterministas; quantificar as interações ecológicas entre os recursos (Pinhão e Feijoa), a fauna e o homem; avaliar padrões, estruturações espaço-temporais, variações e causas da distribuição de espécies da FOM e construir cenários teóricos da distribuição em diferentes escalas espaciais ao longo da Mata Atlântica, especialmente dentro da região de FOM. Para isso, este trabalho adota diferentes metodologias—incluindo o uso de dados secundários, de armadilhas fotográficas, de parcelas demográficas, de entrevistas com moradores locais e de modelagem de distribuição —entre 2014 a 2017. Eu exponho minha tese em uma introdução geral, na qual apresento as teorias que permeiam os meus trabalhos, minhas premissas, hipóteses e objetivos e, em seguida apresento minha região de estudo. Em sequência, apresento cinco capítulos na forma de artigos, que foram ou serão submetidos à publicação em revistas científicas indexadas. No final esses capítulos se encontram na conclusão geral de minha tese a respeito dos padrões, variações e causas da distribuição de diversidade em várias escalas espaciais e temporais na Mata Atlântica.

Especificamente, no primeiro capítulo busco, junto com os demais autores, compreender como varia a diversidade de mamíferos de médio e grande porte ao longo da Mata Atlântica inteira e em escalas mais reduzidas (e.g. na porção subtropical) sob um paradigma neutro em que todas as espécies são equivalentes ecológicos. No segundo capítulo, avaliamos como o fruto da Feijoa, um recurso alternativo para a época de escassez do Pinhão, é capaz de estruturar espaço-temporalmente as comunidades de mamíferos e aves interagentes. No terceiro capítulo, equacionamos como algumas dimensões do nicho influenciam a estrutura demográfica da Araucária e da Feijoa e como a produtividade varia espaço-temporalmente; avaliamos ainda as consequências desses fatores na estrutura das comunidades de mamíferos, tendo em vista a variação de fundo obtida no capítulo 1), e o papel dos mamíferos na estrutura demográfica e composição das Matas de Araucárias. No quarto capítulo, sob o arcabouço do Conhecimento Ecológico Local (CEL), avaliamos como aspectos socioambientais e históricos atuaram e atuam nos padrões e processos ecológicos em uma área de FOM, para entender a dimensão humana nos padrões de diversidade, construção de nichos, formação de paisagens culturais e os processos causais em escala local que afetaram a composição e estrutura das comunidades ao longo do tempo. Por fim, no último capítulo trazemos novamente uma abordagem biogeográfica, onde avaliamos a distribuição potencial passada (no Holoceno Médio, ~6.000 anos atrás), presente e futura (2060 e 2080) da Araucária, da Feijoa e dos mamíferos *Dasyprocta azarae* (cutia: principal mamíferos associado a

Araucária), *Eira barbara* (irara: principal mamífero associada a Feijoa), *Mazama gouazoubira* (veado-catingueiro: herbívoro mais abundante) e *Puma concolor* (puma: principal carnívoro) que formariam uma estrutura básica da teia-alimentar na FOM.

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INTRODUÇÃO

Campos de altitude (>1,650 m.a.s.l.) entremeados por manchas de Florestas de Araucária no Parque Nacional de São Joaquim, Urubici, Santa Catarina, Brasil.
Foto: Bogoni, 2016.

1. INTRODUÇÃO

1.1 A complexidade dos sistemas ecológicos e as escalas

Sistemas ecológicos são complexos e dinâmicos (May 1973; 1976) – especialmente em regiões tropicais (Wright 2002; Ricklefs 2004). Apresentam características de auto-organização, propriedades emergentes e, em muitos casos, retroalimentação (May 1973; Odum e Barrett 2007; Ricklefs 2009). Compreender os mecanismos, as semelhanças e as diferenças físicas e biológicas dentro dos sistemas auto-organizados fornece uma abordagem holística e contribui para a compreensão da dinâmica ecológica (Conway 1977; Solé e Goodwin 2000; Kirschner e Gerhart 2005).

Há muito tempo a Ecologia se preocupa com a relação estrutura-função (Watt 1947) e, assim, muitos estudos começam a partir de uma perspectiva estrutural (Cadenasso et al. 2006). A riqueza de maneiras pelas quais os sistemas ecológicos podem ser estruturados sugere que um *framework* seja determinado para que questões dentro da ecologia possam ser respondidas (Cadenasso et al. 2006). No entanto, o principal gargalo em estudos ecológicos—tanto do ponto de vista de padrões e processos, quanto de funcionamento—é compreender como estruturas relativamente simples levam a comportamentos complexos (Bak e Chen 1991). Porém, este *framework* pode se basear em uma definição de biocomplexidade: como o grau em que os sistemas ecológicos – que compreendem componentes de características biológicas, sociais e físicas – incorporam a heterogeneidade espacialmente explícita, a conectividade organizacional e a contingência histórica (i.e., eventos estocásticos) ao longo do tempo (Cadenasso et al. 2006).

A determinação da escala de trabalho é outro problema que a maioria dos estudos ecológicos enfrenta (Freckleton 2004). As escalas (espaciais e temporais) em que pretendemos prever as dinâmicas dos sistemas ecológicos são muito maiores do que aquelas em que possivelmente poderíamos observar (Freckleton 2004). As relações espaciais vão desde a escala de indivíduo até a escala biogeográfica (Ricklefs 2004; 2008); já as relações temporais no sistema vão desde questões contemporâneas diretas e indiretas até as contingências históricas (Cadenasso et al. 2006). Por não interagir de forma linear, mas frequentemente com atrasos e retroalimentação (Ecological Modelling Editorial Note 2002), ações passadas geradas por “engenheiros” humanos em paisagens co-construídas com a natureza persistem nos ecossistemas. Essas ações passadas têm importantes implicações para padrões de diversidade e processos ecológicos atuais (McKey et al. 2010; Levis et al. 2012; 2017). As ações agem direta e indiretamente através de construção ou manutenção de espaços de nicho (Zeder 2016). Tanto as ações passadas como as perturbações contemporâneas podem promover inúmeras alterações de funcionamento. Por exemplo, podem deslocar o ecossistema para um estado alternativo estável diferente do original (Lewontin 1969; May 1976) e reorganizar os espaços e dimensões de nichos (Pearman et al. 2008; Colwell and Rangel 2009). Em conjunto, estas perturbações alteram a probabilidade de persistência de uma espécie e consequentemente a composição das comunidades (Hutchinson 1957; Levis et al. 2012; 2017; Bogoni et al. 2016a).

1.2 A Mata Atlântica sulamericana e as ações humanas

As alterações oriundas de ações antrópicas moldaram muitos ecossistemas terrestres direcionando-os a mudanças não-randômicas, ou seja, determinísticas (Levis et al. 2017). Considerando ambientes em mudança, a Mata Atlântica historicamente tem sofrido com a expansão da fronteira agropecuária, construção de infraestrutura, crescimento das cidades e exploração não sustentável das florestas (Myers et al. 2000; Ribeiro et al. 2009). Essa ecorregião é a segunda maior região tropical da América do Sul, ocorrendo ao longo de um grande gradiente latitudinal (3°S e -30°S), longitudinal (-35°O e -60°O), e altitudinal (0 a 2.900 metros acima do nível do mar [masl]) conferindo-lhe uma grande heterogeneidade ambiental e compreendendo uma série de formações vegetais (Ribeiro et al. 2011). Engloba grandes blocos de florestas “sempre-verdes” (Floresta Ombrófila Densa [FOD]) à semidecíduas (FSD), mas também florestas decíduas (FED), manguezais, pântanos, afloramentos rochosos, prados de grande altitude (Campos Rupestres e Campos de Altitude), e as florestas de pinheiros brasileiros (Araucárias) (Scarano 2002; Camara 2003).

Entretanto, a definição de florestas Atlânticas deveria ser tão abrangente quanto a definição das Florestas amazônicas (Oliveira-Filho e Fontes 2000), sendo principalmente ligadas aos regimes de chuva, temperatura, gradientes altitudinais e distância do oceano (Salis et al. 1995; Scudeller et al. 2001; Joly et al. 2014). Essa diversificação de formações e hábitats, conjuntamente com as ameaças à conservação, faz com que a Mata Atlântica seja um *hotspot* de diversidade com mais de 20 mil espécies de plantas, 318 mamíferos (90 endêmicos), 936 aves, 306 répteis e 475 anfíbios (Mittermeier et al. 2005; Paglia et al. 2012; Graipel et al. 2016).

Com a perda de aproximadamente 88% da cobertura de floresta original de Mata Atlântica e com remanescentes incorporados em dinâmicas de agromosaicos, monoculturas de espécies exóticas e assentamentos humanos (Tabarelli et al. 2010), inevitavelmente há implicações nos padrões de diversidade, processos ecológicos e funcionamento do ecossistema (Pimm 2007; Cabral et al. 2012). A distância média de isolamento para fragmentos da Mata Atlântica é de aproximadamente 1,5 km, variando de poucos metros a dezenas de quilômetros e os 11,73% (16,377,472 ha) da cobertura vegetal original compõem principalmente fragmentos remanescentes perturbados e/ou pequenos (Ribeiro et al 2009). Aliado a isso, para quase todos os grupos há lacunas sobre distribuição geográfica das espécies, lacunas de taxonomia, de padrões populacionais, hiatos nos padrões e processos evolutivos, nos padrões de diversidade funcional e funções ecossistêmicas, lacunas de padrões de tolerâncias abióticas e lacunas sobre interações ecológicas, o que tem sido chamado de deficiências *Wallaceana*, *Linneana*, *Prestoniana*, *Darwiniana*, *Raunkiaerana*, *Hutchinsoniana* e *Eltoniana* respectivamente (Whittaker et al. 2005; Hortal et al. 2015). Essas lacunas se afloram especialmente em regiões subamostradas, como na Mata Atlântica subtropical (Cáceres et al. 2007).

1.3 As terras altas da Mata Atlântica subtropical e a domesticação dos elementos e paisagens

Na porção subtropical da Mata Atlântica encontra-se uma das formações vegetais mais reduzidas e ameaçadas que têm sido utilizadas como um proxy para estratégias de conservação (Veloso 1991; Lacerda 2016). A paisagem dessas terras altas é formada de mosaicos de vegetação (e.g. ecótonos de floresta-campo), restritos espacialmente e altamente ameaçados, principalmente por mudanças climáticas e de uso do solo (Lima et al. 2015; Lacerda 2016; Souza et al. 2016) e geralmente mantidos pelo manejo feito por populações humanas locais (Duarte et al. 2006). As manchas de floresta dessa formação são compostas por Florestas de Araucárias ou Floresta Ombrófila Mista (FOM), caracterizadas pela presença marcante da espécie ameaçada *Araucaria angustifolia* ((Bertol.)

Kuntze 1898) (Araucária) (Mattos 1972). A Araucária é uma conífera dioica com diferentes variedades (Mattos 2011) e o estróbilo feminino dessa espécie (pinha) é composto por sementes viáveis (pinhões), sementes não-viáveis (chochos) e escamas estéreis (falhas), ficando maduras cerca de quatro anos após a fertilização pelos indivíduos machos através do vento (Shimoya 1962; Mattos 2011). A maturação da pinha depende da variedade da Araucária, mas o pico de produtividade se dá entre os meses de abril e junho (Shimoya 1962; Reitz et al. 1988). O Pinhão é, portanto, um recurso sazonal, com pico no rigoroso inverno local e com importantes características energéticas (Rosado et al. 1994; Solórzano-Filho 2011). É explorado como alimento desde a época pré-colombiana por grupos humanos (Reis et al. 2014) e compartilhado por inúmeras espécies da fauna nativa (Solórzano-Filho 2011; Iob e Vieira 2008; Schüssler 2014; Batista 2015), tornando-se um dos principais recursos estruturadores das comunidades animais locais, que se distribuem pelas manchas imersas no mosaico de vegetação.

Nas manchas de floresta imersas neste mosaico, as Araucárias dominam o estrato superior, enquanto que as Myrtaceae e Lauraceae são as principais famílias que formam os estratos médio e inferior da estrutura das florestas (Rambo 1951; Souza 2007). A expansão da Araucária sobre as áreas degradadas ou pastagem, e áreas de campos (nativos ou não) é um facilitador para o estabelecimento de espécies florestais lenhosas e a conservação de dispersores pode aumentar essa expansão (Duarte et al. 2006). Enquanto que nas florestas chuvosas de baixa altitude podem ser encontradas mais de 50 espécies de Myrtaceae em um espaço relativamente reduzido (~1 ha) (Landrum e Kawasaki 1997; Tabarelli e Mantovani 1999), algumas espécies dominam a flora nessas terras altas, geralmente táxons caracterizados por pequenos frutos (<1 cm de diâmetro; e.g. *Myrceugenia* spp.), tornando as manchas "*quasi-monoespecíficas ou quasi-monogenéricas*" (Gressler et al., 2006; Mazine e Souza 2008). Uma exceção a esse padrão de frutos pequenos é a presença nas manchas da *Acca sellowiana* [Berg] Burret (Feijoa), uma árvore nativa do sul do Brasil e do norte do Uruguai, com ocorrência restrita a áreas com altitude superior a 800 metros acima do nível do mar (Santos et al. 2009; Amarante e Santos 2011). A Feijoa é polinizada por pássaros e abelhas (Popenoe 1912; Hickel e Ducroquet 2000), produz frutos grandes (20 a 250 g) com sementes pequenas (~ 3 mm) (Gressler et al. 2006; Bogoni et al. dados não publicados) e tem um certo grau de influência humana na forma de domesticação (Santos et al. 2009).

A domesticação de plantas e animais é o desenvolvimento mais importante da história humana desde 13.000 anos atrás, e mudou o curso da humanidade (Diamond 2002). Desde Darwin (1859), os sistemas domesticados têm um papel crítico no desenvolvimento e teste da teoria evolucionária (Purugganan e Fuller 2009). A gestão dos frutos nativos *in situ*, tanto por populações indígenas como por agricultores locais, é uma prática de conservação reconhecida, contribuindo para a diversidade genética e para vários processos ecológicos, através de uma propagação à jusante dentro de redes biológicas (Miller e Gross 2011; Olsen e Wendel 2013; Lins Neto et al. 2014). Outra característica marcante da domesticação da paisagem local – a intervenção humana nos componentes paisagísticos, resultando em mudanças na evolução, ecologia, interações e demografia de espécies (Clement 1999) – é a presença do gado (*Bos taurus*) e seus impactos (Mello e Peroni 2015). O gado é um elemento de alóctone administrado por longos anos (> 100 anos) por pequenos proprietários locais em planaltos subtropicais com a presença da Araucária (Mello e Peroni 2015).

A Araucária teve sua expansão favorecida por atividades antropogênicas, principalmente por povos indígenas do tronco Jê (Kaingangs e Xoklengs) (Bitencourt e Krauspenhar 2006) e sofreu com a exploração madeireira desde 1920 até meados dos anos 1990 (Eduardo 1974; Mattos 2011). Exemplos de uso e manejo de espécies do mesmo gênero ou família são registrados na América Latina por populações tradicionais, que, devido às pressões de exploração e desmatamento podem comprometer essa dependência social e histórica (Herrmann 2006; Santos et al. 2009). Tal como as paisagens locais e a Araucária, a Feijoa tem recebido influência antropogênica histórica, promovendo um certo nível de domesticação de algumas populações *in situ* (Bitencourt e Krauspenhar 2006; Reis et al. 2014; Mello e Peroni 2015). Dentro da FOM, a Feijoa tem vários usos por parte da população local, que gerenciou a espécie com poda, transplante, aplicação de pesticidas, afinamento, propagação por sementes e propagação vegetativa. Os níveis de práticas de manejo em Feijoa variam de mantenedores: pessoas que "mantêm" as plantas em suas propriedades e representam o menor nível de interação; Gerentes: inclui pessoas que "gerenciam" Feijoa; Cultivadores: pessoas que estabelecem ativamente pomares de Feijoa e que se concentram na comercialização de Feijoa; E usuários: pessoas que usam a fruta Feijoa para cozinhar, bonsai plantas, reflorestamento, produção e venda de mudas, e outras atividades (Santos et al. 2009), e assim como a Araucária, a Feijoa tem forte interação com espécies da fauna nativa (Bogoni et al. dados não publicados).

1.4 As variações na diversidade de mamíferos da Mata Atlântica

Entender processos que influenciam a distribuição de uma espécie é um ponto crítico para a ecologia e conservação (Phillips et al. 2004). Ainda, as condições ambientais e paisagísticas, como a fragmentação, o tipo de habitat, o uso do solo e a disponibilidade de recursos, variam entre escalas espaciais (Declerck et al. 2011; Bogoni et al., 2016a). Estas características e suas variações levam a mudanças determinísticas nas comunidades de plantas e animais, alterando os padrões de diversidade (por exemplo, riqueza de espécies e diversidade funcional) e processos ecológicos (por exemplo, teia trófica, dispersão de sementes e cadeia de detritivoros) (Galetti et al. 2009; Bogoni et al., 2016a, 2016b).

A estrutura da comunidade foi recentemente reavaliada e reinterpretada dentro de um quadro metacomunitário (Leibold et al. 2004). Metacomunidade foi definida como um conjunto de comunidades locais conectadas pela dispersão de muitas espécies que potencialmente interagem entre si (Leibold et al. 2004). Os paradigmas da teoria da metacomunidade (i.e., *patch dynamics*, *species sorting*, *mass effects* e *neutral model*) dependem da escala espacial, extensão ou distâncias espaciais entre áreas (Declerck et al. 2011). Os paradigmas também dependem do ambiente e do grupo taxonômico, devido às idiossincrasias do tipo de ecossistema e seus filtros, e devido à habilidade de dispersão e colonização e das interações entre espécies (Hollyoak et al. 2005). *Patch dynamics* (dinâmica de manchas) é uma perspectiva que pressupõe que as manchas florestais são idênticas e que cada mancha é capaz de conter populações, as manchas podem estar ocupadas ou desocupadas e a diversidade de espécies nas manchas são limitadas pela dispersão. Nesse paradigma a dinâmica espacial é dominada pela extinção local e pela colonização (Leibold et al. 2004). *Species sorting* (classificação de espécies) é uma perspectiva que enfatiza os gradientes de recurso ou os tipos de manchas causam diferenças na demografia local das espécies, portanto numa abordagem de nicho (Leibold et al. 2004). *Mass effects* (efeitos em massa) focaliza o efeito da imigração e da emigração sobre a dinâmica da população local (Leibold et al. 2004). *Neutral model* (modelos neutros) é o paradigma mais simples de uma metacomunidade e pode ser útil para entender a diversidade de espécies de uma perspectiva em que todas as espécies são semelhantes em sua capacidade competitiva, movimento e aptidão (Hubbell 2001; Leibold et al. 2004).

Avanços analíticos e na teoria ecológica permitem identificar as espécies e áreas que mais contribuem para a diversidade ao longo dos gradientes ecológicos, dividindo a variância dos conjuntos de dados da comunidade para estimar os componentes da diversidade (Jost 2007; Legendre & De Cáceres 2013). A diversidade alpha, beta e gamma são componentes clássicos da diversidade, definidos como o número de espécies em uma localidade ou habitat, o *turnover* de espécies entre hábitats ou localidades e o número estimado de espécies presentes numa área maior, respectivamente (Whittaker et al. 1975). Outras métricas de diversidade baseadas no conceito de entropia, definida como uma medida de incerteza calculada a partir da distribuição de frequência de uma comunidade, mostram propriedades importantes, como o número de espécies igualmente frequentes que representa o mesmo nível de diversidade dos dados que podem ser convertidos em "diversidade verdadeira" (Jost 2006; Jost 2007).

1.5 A defaunação e a interação entre a fauna e os recursos

Somando-se a esses fatores e numa escala de tempo atual existe as consequências da defaunação, um processo de extinção, especialmente de vertebrados, causado por impactos humanos (Redford 1992; Dirzo et al. 2014; Ceballos et al. 2015). As principais causas humanas de defaunação e mudanças de composição das comunidades são a perda de habitat, a fragmentação, a caça e a conversão florestal (Canale et al. 2012; Galetti e Dirzo 2013; Bogoni et al. 2016a). As mudanças de composição das comunidades e a perda seletiva de espécies podem produzir efeitos negativos no funcionamento dos ecossistemas, promovendo efeitos de cascata em várias escalas (Galetti e Dirzo 2013). Estes efeitos incluem mudanças evolutivas (e.g. diminuição do tamanho das sementes) e afetam a dinâmica das populações e a estruturação das comunidades (e.g efeitos em cascata ao longo da rede de detritivores, mudanças nos padrões de dispersão e predação de sementes, alterações em teias tróficas e reorganização de forças *bottom-up* e *top-down*) (Galetti e Dirzo 2013; Kurten 2013; Bogoni et al. 2016b). Esses padrões de defaunação e seus efeitos afetam a Mata Atlântica como um todo, incluindo a região subtropical, onde os índices médios de defaunação são de 50% (Giacomini e Galetti 2013; Bogoni et al. 2016a).

1.6 Os feedbacks dos recursos para os mamíferos e dos mamíferos para as florestas

As perdas e alterações de áreas nativas e a redução gradativa de populações de mamíferos podem alterar toda a dinâmica de estruturação das comunidades biológicas, e isso é particularmente importante pois mesmo em uma floresta intacta, mas sem associação com a fauna, há descaracterização do sistema ecológico funcional original e desestruturação de comunidades biológicas (Redford 1992). Apesar de haver um pluralismo de processos envolvidos, tanto os mecanismos de estruturação *bottom-up* quanto *top-down* são influenciados pela competição por recursos (Hairston et al. 1960). A proposta *top-down* prediz que organismos são limitadores, tanto como predador ou como recurso, dependendo de sua posição nas cadeias alimentares, e a eficácia relativa das forças *top-down vs. bottom-up* na cadeia dependerá, em parte, da eficiência com que consumidores exploram suas presas (Hairston et al. 1960; Power 1992). A teoria ecológica postula que grandes mudanças nos ecossistemas, como a perda e fragmentação de hábitat, podem acompanhar grandes mudanças na abundância e distribuição de organismos, especialmente de consumidores, e há acúmulo de evidências teóricas e empíricas mostrando uma perspectiva de alteração no mecanismo *top-down* que força a dinâmica do ecossistema sugerindo efeitos em cascata (Hairston et al. 1960; Fretwell 1987; Power 1992; Estes et al. 2011).

O uso de determinadas espécies (e.g. Feijoa) poderia ter uma função mais ampla na economia local e contribuir para a conservação da biodiversidade (Santos et al. 2009). Além de destacarem-se pela qualidade madeireira, a Araucária e a Feijoa são fonte de alimento para a fauna, para o homem e/ou criações domésticas, e a extração desses recursos pode ter implicações importantes para os animais silvestres em época de escassez alimentar (Reitz e Klein 1966; Holz et al. 2009; Paludo et al. 2009). Essa condição pode ser particularmente importante e constante ao longo do ano por haver diferentes variedades de Araucária com pinhões maduros de fevereiro a dezembro (Zechini et al. 2012; Adan 2013) provendo recursos constantes à fauna.

1.7 Passado, presente e futuro frente às mudanças ambientais

O hipervolume do nicho *Hutchinsoniano* promove que muitos são os fatores causais da distribuição das espécies, mas os tratamentos teóricos do nicho enfatizam apenas alguns recursos, requerimentos ou fatores limitantes (Franklin 2009). Nesse aspecto, os impactos *Eltonianos* (definição funcional do nicho, de escala local com enfoque bionômico e nas interações) e os requerimentos *Grinnellianos* (definição das influências no nicho e a respeito das condições de larga escala) das espécies são interligados na redefinição contemporânea de nicho como: condições ambientais que permitem uma espécie satisfazer as exigências mínimas de modo que a taxa de nascimento é igual ou superior a taxa de mortalidade, aliado ao conjunto *per capita* dos efeitos da referida espécie sobre as condições ambientais (Chase e Leidold 2003).

O conceito de nicho fornece uma maneira para conceituar e analisar distribuições biogeográficas em relação aos padrões ambientais espaciais (Brown 1995). A extensão espacial do que é chamado de biótopo por *Hutchinson*, é conhecida como um “mapa” e em seus pontos, além das coordenadas, caracterizam-se os valores locais de *n* atributos em um determinado momento e se define o espaço de nicho correspondente (Colwell e Rangel 2009). Isso permite projeções recíprocas – reais ou potenciais – da distribuição geográfica de uma espécie – no passado ou futuro – isto é, modelos estocásticos que englobam desde especiações à adaptação evolutiva a ambientes em mudança (Colwell & Rangel 2009; Peterson et al. 2011).

Ainda, outras ferramentas como modelos de distribuição de espécies (SDMs) servem para estimar a relação entre os registros de espécies e o ambiente e/ou características espaciais dos locais (Franklin 2009) sendo amplamente utilizados na biogeografia, ecologia e conservação biológica (Elith e Leathwick 2009; Franklin 2009; Elith et al. 2011). Devido à capacidade matemática de se associar a presença de uma espécie com um grupo de variáveis ambientais, os métodos de modelagem constituem uma ferramenta preditora de padrões de distribuição, com o advento de gerar mapas ilustrativos de distribuições em diferentes condições ambientais e/ou climáticas. A modelagem fundamenta-se no conceito de nicho, que considera a soma dos fatores ambientais que exercem influências sobre um organismo, ainda que na natureza observam-se nichos ecológicos realizados, ou seja, partes do nicho fundamental disponível onde a espécie não foi excluída por interações bióticas e/ou limitações de recursos (Guisan e Thuiller 2005). Atualmente existem diversos algoritmos que exploram a associação da ocorrência de espécies com variáveis ambientais explicativas (Elith et al. 2006). Com base na máxima entropia a modelagem tem sido usada para previsão da abundância relativa de um conjunto de espécies conhecidas, com os valores característicos de cada espécie e os valores característicos de comunidades agregadas de um local e baseia-se na melhoria na escala do algoritmo iterativo (Shipley et al. 2006; Sonnier et al. 2009).

Essa abordagem permite explorar algumas questões na conservação, ecologia e evolução como: (a) definir áreas prioritárias para conservação (Chen e Peterson 2002; Garcia 2006; Lópes-Arévalo et al 2011; Faleiro et al. 2013); (b) entender processos invasivos de espécies (Ficetola et al. 2007; Giovanelli et al. 2008); (c) realizar modelos preditores sobre distribuições futuras (Siqueira e Peterson 2003); (d) propor modelos de distribuição de uma determinada espécie no passado (Hugall et al. 2002; Carnaval e Moritz 2008); e (e) gerar modelagem de nicho ecocultural heurísticas que refletem influências ecológicas na distribuição geográfica de culturas humanas (Banks et al. 2008). A disponibilidade de dados detalhados, juntamente com avanços computacionais, alimenta um aumento de estudos com modelagem de distribuição de espécies e de dados ambientais em alta resolução disponíveis para esses estudos (Phillips et al. 2006). Recentemente estão sendo feitas projeções para cenários de mudanças climáticas na Mata Atlântica, cujos resultados demonstram, além da perda de diversidade, uma conjuntura de redistribuição de espécies, principalmente as ameaçadas e/ou endêmicas (e.g. Colombo e Joly 2010; Souza et al. 2011).

1.8 As lacunas no conhecimento

Com base no conhecimento atual sobre a Araucária, sobre a Feijoa e sobre a fauna de mamíferos, é possível identificar algumas importantes lacunas nos conhecimento e ligações entre esses elementos da Mata Atlântica. Uma delas é de que existe uma variação de fundo nos padrões de diversidade de mamíferos ligados às escalas espaciais e temporais. Na Mata Atlântica subtropical a Araucária é o principal estruturador da FOM, existe a dependência ecológica da Feijoa nessa formação e há dependência ecológica da fauna de mamíferos das duas espécies vegetais (e a relação inversa potencialmente é recíproca). Além disso, a interação das populações locais com recursos da FOM forma um complexo sistema socioecológico, fundamentado em dimensões tanto em escalas temporais quanto espaciais nas terras altas sulbrasileiras. Explicitadas as dependências entre os grupos, suporto que a confecção de modelos teóricos parametrizados por dados de literatura e de campo podem fornecer importantes cenários preditivos em diferentes escalas na Mata Atlântica sulamericana. Suporto também que em escala local as perspectivas abordadas podem ter influências ou lacunas preenchidas pelo conhecimento ecológico local, principalmente questões de histórico de uso das espécies e das paisagens onde estão distribuídas as espécies.

2. PREMISSAS, HIPÓTESES E OBJETIVOS

As perguntas que norteam meu estudo são: (1) Como varia a estrutura das comunidades e quais os valores de diversidade de mamíferos de médio e grande porte ao longo da Mata Atlântica avaliados em diferentes cenários teóricos de metacomunidades sob um paradigma neutro? (2) Quais as principais espécies de mamíferos e aves associados à Feijoa e qual a importância dos mamíferos e das aves no seu sucesso reprodutivo (remoção de frutos e sementes)? (3) Como é o padrão demográfico da Araucaria e da Feijoa e o que ou quem os afeta? Qual a ligação entre os padrões ecológicos (i.e. demografia e produtividade) da Araucária e da Feijoa com a mastofauna? Como a oferta de recursos (Pinhão e frutos da Feijoa) estrutura a mastofauna em diferentes locais e em diferentes épocas e como os mamíferos podem influenciar os padrões de distribuição de Araucária e Feijoa e na composição arbórea-arbustiva da floresta? (4) Como as questões fundiárias e históricas exercem (ou exerceram) influência na distribuição e abundância local de Araucarias e Feijoas e/ou influenciam a estrutura da fauna de mamíferos (incluindo as associações ecológicas com as espécies vegetais)? (5) Como era a distribuição de espécies-chave da FOM no passado (Holoceno-médio: 6.000 anos atrás), como potencialmente é a distribuição atual e como será no futuro diante de diferentes condições climáticas?

A partir dessas perguntas fundamentei as seguintes hipóteses: (1) A diversidade alfa e beta de mamíferos de médio e grande porte sob uma perspectiva neutra dependem da delimitação do modelo metacomunidade, mas diminuem em congruência com a diminuição de escala (e.g. subtropical e local), permanecem iguais em comparação a modelos nulos que têm probabilidade de ocorrência das espécies igual ao observado; (2)

Mamíferos e aves que removem frutos de Feijoa – além do gado e assumindo *a priori* sítios já defaunados, restando apenas uma diversidade relictual – são frugívoros/onívoros de tamanho corporal pequeno a médio. Em contrapartida a Feijoa, por ser um recurso sazonal, estrutura as comunidades de vertebrados no tempo e espaço, mantendo a diversidade residual em congruência com a oferta de frutos, e o número de interações está relacionado aos padrões ambientais, intensidade de domesticação das árvores, distâncias espaciais e produtividade; (3) As diferentes épocas de produção de recursos das espécies vegetais irão estruturar espacial e temporalmente as comunidades de mamíferos por competição e há congruência espacial entre os padrões ecológicos da Araucária e da Feijoa e a estrutura das comunidades de mamíferos; (4) A manutenção dos mosaicos de florestas e campos de altitude nas terras altas da Mata Atlântica subtropical tiveram e ainda têm grande influência humana, com importantes implicações não somente para as paisagens, mas para a diversidade de mamíferos. Ainda, a população humana local, a fauna nativa e os animais domésticos, compartilham os recursos da FOM (Pinhão e Feijoa) influenciando a dinâmica dos mosaicos e paisagens como um todo, ao longo do tempo decorrente e com implicações futuras; (5) Com base nas principais dimensões do nicho ecológico-climático fundamental, no passado a distribuição geográfica da Araucária, da Feijoa e da mastofauna interagente foi mais reduzido do que atualmente o é, e no futuro espera-se uma distribuição ainda mais restrita devido às condições climáticas inapropriadas. Espero, no entanto, ainda haver sobreposição na distribuição das espécies vegetais e da fauna (coocorrência), do contrário, potencialmente pode haver um comprometimento dos padrões ecossistêmicos dependentes desses grupos na Mata Atlântica.

2.1 Objetivo Geral

Sob paradigmas neutros (contingência) e de nicho (determinismo), objetivei entender os padrões de diversidade e estruturação das comunidades de mamíferos de médio e grande porte em regiões dentro da Mata Atlântica, quantificar as interações ecológicas entre os recursos-chave da FOM (Pinhão e frutos da Feijoa), a fauna e o homem, avaliar padrões, variações e causas da distribuição de espécies na FOM e construir cenários teóricos da distribuição de espécies-chave da FOM em diferentes escalas temporais.

2.2 Objetivos Específicos

1) Particionar a diversidade de mamíferos desde escalas locais à biogeográfica, para avaliar e indicar qual cenário teórico de metacomunidades sob um paradigma neutro dentro da Mata Atlântica tem maior diversidade alpha e beta e compreender a relação entre a entropia da diversidade beta (uma medida de desordem) e variáveis biogeográficas;
(Capítulo 1 [Hipótese 1]: "What would be the diversity patterns of medium- to large-bodied mammals if the fragmented Atlantic Forest was a large metacommunity?")

2) Gerar um cenário das relações tróficas entre a Feijoa e a fauna de vertebrados para avaliar a congruência espaço-temporal entre a produtividade de frutos e os padrões de diversidade;
(Capítulo 2 [Hipótese 2]: "The ecological footprint of *Acca sellowiana* domestication maintain the residual vertebrate diversity in threatened highlands of Atlantic Forest")

3) Investigar se os padrões de distribuição, abundância, produção de recursos e demografia e das espécies vegetais (Araucária e Feijoa) possuem relação com a composição e abundância relativa das comunidades de mamíferos e apurar como espacial e temporalmente as comunidades de mamíferos são estruturadas pela competição pela oferta potencial de recursos;
(Capítulo 3 [Hipótese 3]: Spatio-temporal congruence between resources availability and mammals diversity in threatened Brazilian highlands)

4) Dentro e no entorno de uma Unidade de Conservação (UC) localizada nas terras altas da Mata Atlântica subtropical, acessar a relação entre a população humana local, a paisagem e seus componentes para entender o histórico dos mosaicos de Florestas da Araucárias e Campos de Altitude, a potencial construção e manutenção de nichos, a relação e o conhecimento local sobre mamíferos nativos e suas interações com o Pinhão e a Feijoa, a linha de tempo dos principais eventos capazes de

modificar a paisagem e criar novos espaços de nicho e gerar uma perspectiva socioecológica futura através da percepção dos moradores locais;

(Capítulo 4 [Hipótese 4]: "The human dimension of Araucaria Forest: resource and landscape uses, niche construction and ethnozoology")

5) Com base no nicho climático fundamental gerar cenários de distribuição de espécies para condições passadas (Holoceno médio, ~6000 anos antes do presente), presente (condições de 1950 a 2000) e futuras (cenários de mudanças climáticas para 2060 e para 2080) para os principais elementos da FOM – Araucária – Pinhão, Feijoa – frutos *Dasyprocta azarae* (cutia, ligada ao Pinhão), *Eira barbara* (irara, ligada a Feijoa), *Mazama gouazoubira* (veado-catingueiro, principal e mais abundante pastador) e *Puma concolor* (puma, principal predador) – que compõe uma estrutura básica de rede trófica na FOM.

(Capítulo 5 [Hipótese 5]: "Run to the hills: Past, present and future biogeographic distribution of Araucaria Forest elements")

3. META-REGIÃO DE ESTUDO

Cada capítulo da minha tese foi desenvolvido em diferentes áreas da Mata Atlântica sulamericana e em diferentes escalas espaciais, variando de escalas biogeográfica, contemplando escalas regionais, até escalas locais. O primeiro capítulo, numa escala biogeográfica, envolveu dados secundários de mamíferos de médio e grande porte de áreas ao longo de toda a Mata Atlântica (-2°S a -38°S; -32°O a -58°O; Tabela 1; Figura 1A). O segundo capítulo, em escala regional, foi desenvolvido em quatro áreas inseridas em três Unidades de Conservação (UCs) (Parque Nacional de São Joaquim (duas áreas), Reserva Particular do Patrimônio Natural [RPPN] Grande Floresta das Araucárias e RPPN Leão da Montanha) localizadas nos planaltos e terras altas de Mata Atlântica subtropical no estado de Santa Catarina (-27°50’S a -28°10’S; 49°20’O a 49°40’O; Tabela 1; Figura 1B). O terceiro capítulo também em escala regional, foi desenvolvido em sete áreas, seis delas inseridas em quatro UCs (Parque Nacional das Araucárias [duas áreas: PAA e PAB], Parque Nacional de São Joaquim [duas áreas: PSA e PSB], RPPN Grande Floresta das Araucárias [RGF] e RPPN Leão da Montanha [RLM]) e uma área particular no município de Lages (localidade Coxilha Rica [CXR]) localizadas na Mata Atlântica subtropical no estado de Santa Catarina (-26°40’S a -28°10’S; -49°20’O a -52°10’O; Tabela 1; Figura 1C). O quarto capítulo, em escala local, foi feito no Parque Nacional de São Joaquim e entorno (-28°08’S; -49°30’O; Tabela 1; Figura 1D) e o quinto capítulo, em escala biogeográfica, foi desenvolvido com dados próprios e secundários ao longo das latitudes -10°S a -35°S e longitude -60°O a -35°O (Tabela1; Figura 1E).

A Mata Atlântica como um todo tem várias condições climáticas (e.g. Af, Am, Aw, Cfa, Cfb, Cwa, Cwb e Bsh) de acordo com a classificação de Köppen-Geiger. No geral, índices pluviométricos vão acima de 1.000 mm³/ano e temperaturas são altamente variáveis ao longo de toda sua distribuição (Peel et al. 2007). Além disso, o solo e o relevo na Mata Atlântica também são fatores altamente variáveis e influenciam todo o meio biótico (Resende e Resende 1983; Rossi e Queiroz-Neto 2001). A região das terras altas do Planalto Catarinense é de clima subtropical úmido (clima Cfa), têm estações bem definidas e chuvas bem distribuídas ao longo do ano, com uma média de precipitação anual de 1.700 mm. Nessa região as temperaturas variam consideravelmente ao longo do ano, entre -10°C e 40°C, com média anual de entre 11°C e 19°C (Monteiro 2001; Peel et al. 2007).

A vegetação da Mata Atlântica, assim como seu clima e relevo, é amplamente variável contendo diferentes ecossistemas representado por um conjunto de formações florestais ao longo da variação dos gradientes ambientais (Veloso et al. 1991). Engloba grandes blocos de florestas “sempre-verdes” (Floresta Ombrófila Densa [FOD]) à semidecíduas (FSD), mas também florestas decíduas (FED), manguezais, pântanos, afloramentos rochosos, prados de grande altitude (Campos Rupestres e Campos de Altitude), e as florestas de pinheiros brasileiros (Araucárias) (Scarano 2002; Camara 2003). A vegetação da região do Planalto Catarinense é principalmente Florestas de Araucária (ou Floresta Ombrófila Mista [FOM]) e suas variações de classificação, tais como FOM alto-montanas (matas nebulares), FOM montanas, FOM aluviais e campos de altitude (Veloso et al. 1991). Em escala biogeográfica a distância linear média entre as áreas estudadas (desconsiderando os pontos de presença das espécies e considerando apenas áreas ou comunidades de mamíferos) é de 846.1 km (± 596.8), em escala regional a distância linear média entre as áreas estudadas é de 148,3 (±118,4) km, com mínima de 4,8 km e máxima de 290,0 km. A altitude das áreas na escala regional varia em 662 metros, com mínima média de 887 m.a.s.l. e máxima média de 1.549 m.a.s.l..

As áreas estudadas na escala regional (i.e. PAA, PAB, PSA, PSB, RGF, RLM e CXR) são desiguais no tempo e nos termos de proteção, mas compartilham semelhanças na gestão e na exploração histórica (Eduardo 1974, Mello e Peroni 2015). As áreas apresentam elementos de paisagens culturais; pois são visualmente configuradas em florestas antropogênicas com diferentes intensidades de uso passado e presente (Reis et al. 2014, Mello e Peroni 2015) e apresentam diferentes estágios de regeneração. Outra característica marcante da domesticação da paisagem regional é a presença do gado (*Bos taurus*) (ou o fantasma do seu passado) e seus impactos (Mello e Peroni, 2015). O gado é um elemento de alóctone administrado por longos anos (> 100 anos) por pequenos proprietários de terras nos planaltos subtropicais (Mello e Peroni 2015). Além do gado, a exploração madeireira e a exploração da erva-mate (*Ilex paraguariensis*) foram e ainda são fatores altamente relevantes e que influenciaram as formações vegetais da região (Eduardo 1974). A exploração madeireira iniciou com maior intensidade no começo do século XX e a exploração da erva-mate é uma atividade que passou a ser um importante produto na economia catarinense no final do século XIX, com cerca de 7.260 toneladas exportadas entre 1884 e 1887 (Eduardo 1974) e ainda é fortemente explorada.

Tabela 1. Abreviação, município, localidade, georreferência, altitude, tamanho político e respectivos capítulos da tese desenvolvida em áreas de Mata Atlântica para avaliar os padrões de diversidade de mamíferos de médio e grande porte em regiões dentro da Mata Atlântica, quantificar as interações ecológicas entre os recursos (*Araucaria angustifolia*: Pinhão e *Acca sellowiana*: Feijoa), a fauna e o homem, avaliar padrões, variações e causas da distribuição de espécies na Floresta Ombrófila Mista (FOM) e construir cenários teóricos da distribuição de espécies-chave da FOM em diferentes escalas temporais. B: biogeográfica; R: regional; L: local.

Área	**Escala**	**Abrev.**	**Município**	**Localidade**	**Lat (S)**	**Long (O)**	**Altitude**	**Tamanho Político (ha)**	**Capítulo**
Mata Atlântica Sulamericana	B	-	-	-	-	-	-	-	1
Parque Nacional das Araucárias - Área A	R	PAA	Ponte Serrada	Porção Oeste	26°48’	51°59’	887	12.841	3,5
Parque Nacional das Araucárias - Área B	R	PAB	Passos Maia	Porção Leste	26°49’	51°48’	1122	12.841	3,5
Área Particular	R	CXR	Lages	Coxilha Rica	28°04’	50°18’	1045	143*	3,5
RPPN Leão da Montanha	R	RLM	Urubici	Rio Canoas	27°59’	49°23’	1130	127	2,3,5
Parque Nacional de São Joaquim - Área A	R/L	PSA	Urubici	Morro Igreja	28°06’	49°30’	1549	49.3	2,3,5
Parque Nacional de São Joaquim - Área B	R/L	PSB	Urubici	Santa Bárbara	28°09’	49°30’	1539	49.3	2,3,4,5
RPPN Grande Floresta das Araucárias	R	RGF	Bom Retiro	Campo Novo	27°54’	49°23’	1000	4.019	2,3,5
Lat. -10°S a -35°S; Long. -60°O a -35°O	B	-	-	-	-	-	-	-	5 **

* Nesse caso em especial, por ser uma área não protegida, o tamanho da área é representado pelo tamanho do fragmento, desconsiderando áreas de campo; ** Dados próprios, de escala regional, também foram usados no capítulo 5.

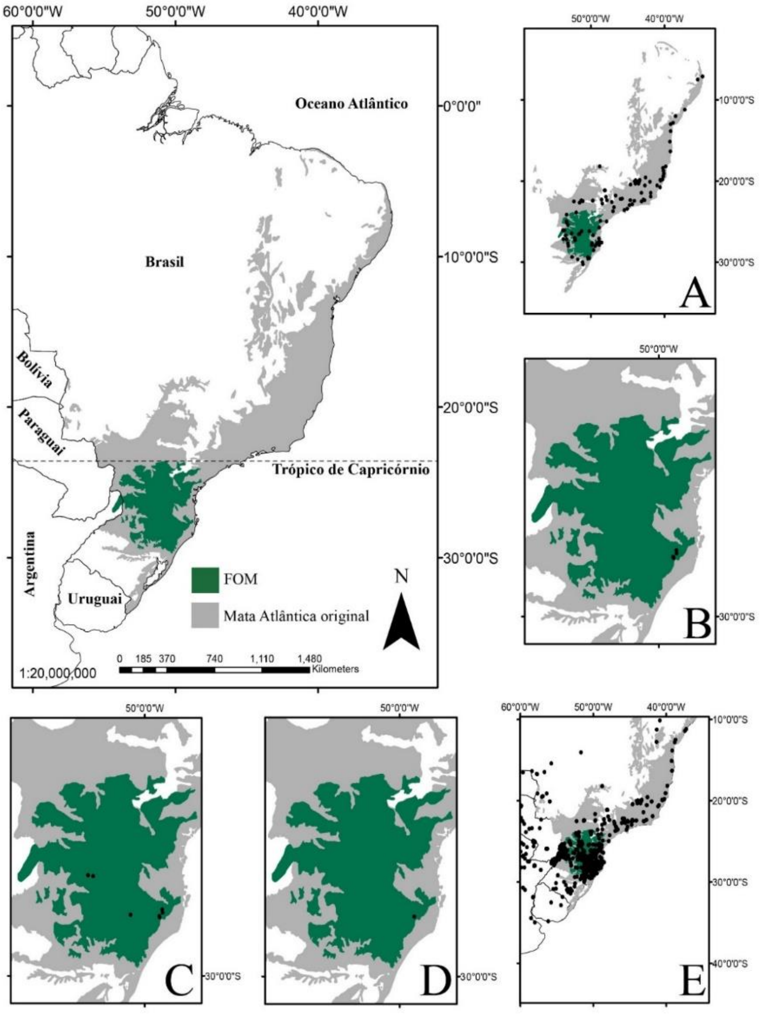

Figura 1. Região de estudo localizada em áreas de Mata Atlântica. (A) Áreas de estudo do capítulo 1; (B) Áreas de estudos do capítulo 2; (C) Áreas de estudo do capítulo 3; (D) Área de estudo do capítulo 4; (E) Área de estudo e pontos de presença do capítulo 5.

CAPÍTULO 1

What would be the diversity patterns of medium- to large-bodied mammals if the fragmented Atlantic Forest was a large metacommunity?

(Quais seriam os padrões de diversidade de mamíferos de médio a grande porte se a fragmentada Mata Atlântica fosse uma grande metacomunidade?)

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Mazama americana (Linnaeus, 1758) [veado-mateiro] registrado em 12 de julho de 2016 na Reserva Particular do Patrimônio Natural Leão da Montanha, Urubici, Santa Catarina, Brasil (28°01’03” S; 49°25’33” O; 1.079 m.a.s.l.). Foto: Bogoni 2016.

What would be the diversity patterns of medium- to large-bodied mammals if the fragmented Atlantic Forest was a large metacommunity?

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ABSTRACT

Mammals play innumerous ecological functions in terrestrial ecosystems and are in decline in the Atlantic Forest. Using a biogeography approach with tools to analyze metacommunities, this study aimed to understand how mammal diversity would vary spatiotemporally across the Atlantic Forest. Secondary data about mammal communities was obtained using search engines. A nestedness analysis and spatial autocorrelations were used to evaluate the spatial patterns of richness. Metacommunity models were used based on species-neutral diversity to measure partitioning and estimate and compare diversity at different spatial and temporal scales, and regression models were made to evaluate the diversity variation obtained in relation to biogeographical predictors. The richness of mammals had intermediary nestedness and a spatial autocorrelation. We obtained high beta diversity for the entire Atlantic Forest, which was similar to simulated values and decreased at smaller spatial and temporal scales. The diversity of medium- to large-bodied mammals along the Atlantic Forest is composed of a nested summary of local to regional diversities, yet the tropical region was very important to the composition of the overall diversity. The different multiscale approaches and results may contribute to better understanding the diversity of medium- to large-bodied mammal communities and how they vary in the Atlantic Forest. Both the neutral paradigm and other metacommunity paradigms have complementary strengths in species diversity at several scales. We conclude that conservation strategies should consider all scales in the Atlantic Forest, because the diversity of mammals is dependent both the local and regional pool of mammals. Some of the most important standing issues are to find out whether dispersal across regional landscapes occurs for most species and, if it does, to ensure that this is maintained or increased, to maintain species diversity and ecological processes.

Keywords: Mammals, Diversity, Atlantic Forest, Metacommunity, Diversity partitioning, Alpha and Beta diversity.

1. Introduction

Mammals play many important ecological functions, such as community structuring and forest regeneration (Roemer et al., 2009; Galetti and Dirzo, 2013). Their populations are under decline in many terrestrial biomes (Davidson et al., 2009; Ceballos et al., 2015), especially in the Brazilian Atlantic Forest (Galetti et al., 2015). In terms of biodiversity and endemism, the Atlantic Forest is in one of the five most important ecoregions in the world (Myers et al., 2000) and has 318 mammal species, of which 90 are endemic (Paglia et al., 2012; Graipel et al., 2016). Although mammals are the focus of several studies, there are shortfalls in biology, such as lack of abundance data, uncertain in the geographic distribution and taxonomy of species (Rosado et al., 2016). There are several geographic sampling gaps and large differences in sampling methods and efforts – factors that can affect the estimative of local richness (Lyra-Jorge et al., 2008). Mammals of the Atlantic Forest are extremely threatened to result in high defaunation caused by several factors, including biological invasions, hunting, habitat loss, fragmentation and isolation (Galetti et al., 2009; Bogoni et al., 2016a).

The average isolation distance for Atlantic Forest fragments is ~1.5 km, varying from a few meters to dozens of kilometers, and the remaining 11.73% (16,377,472 ha) of the original vegetation cover comprises mostly disturbed and small remnant fragments (Ribeiro et al., 2009). These small (< 50 ha) fragments may serve as steppingstones between larger fragments (Haddad et al., 2003), increasing landscape connectivity (Magioli et al., 2015). For the Atlantic Forest, the major functional connectivity occurs in the highland region (i.e., Serra do Mar and Serra Geral) that spreads from the state Rio de Janeiro to the state of Rio Grande do Sul (Ribeiro et al., 2009). The patch size affects abundance and diversity of mammal species (Canale et al., 2012; Magioli et al., 2016), and the landscape-scale features, such as the intensity of human occupation, change the composition of communities (Bogoni et al., 2016a). Environmental and landscape conditions, such as fragmentation, habitat type, land use and resource availability, vary across spatial scales (Declerck et al., 2011). These aforementioned characteristics and their variations lead to non-random shifts in plant and animal communities, changing the diversity patterns (e.g., species richness and functional diversity), ecological processes (e.g., the trophic web, seed dispersal, detritivore webs) and community structure (Galetti et al., 2009; Bogoni et al., 2016a, 2016b).

Community structure has recently been reevaluated and reinterpreted within a metacommunity framework (Leibold et al., 2004). Metacommunity was defined as a set of local communities connected by the dispersal of many species that are potentially interacting (Leibold et al., 2004). The paradigms of metacommunity theory (i.e., patch dynamics, species sorting, mass effects and neutral model) depend on spatial scale, extent, or spatial distances between areas (Declerck et al., 2011; Chase, 2014). The paradigms depend on the environment and taxonomic group, due to the idiosyncrasies of the ecosystem type and its filters, and due to dispersal, colonization and interactions among species (Holyoak et al., 2005; Logue et al., 2011). Neutral models are the simplest paradigm of a metacommunity and can be useful to understand species diversity from a perspective where all species are similar in their competitive ability, movement and fitness (Hubbell, 2001; Leibold et al., 2004).

Analytical advances allow the identification of species and areas that contribute the most to diversity along ecological gradients by partitioning the variance of community datasets to estimate diversity components (Jost, 2007; Legendre and De Cáceres, 2013) and can be compared to values obtained from null models based on several scenarios (Gotelli and Graves, 1996; Gotelli and Ulrich, 2012). Alpha, beta, and gamma diversity are classical diversity components defined as the number of species in a locality or habitat, the turnover of species between habitats or localities, and the estimated number of species present within a larger area, respectively (Whittaker, 1975). Other diversity metrics based on the entropy concept defined as a measure of uncertainty calculated from the frequency distribution of a community (Jost, 2006). These metrics show important properties, such as the number of equally frequent species that represents the same level of diversity of the data that can be converted into “true diversity” (Jost, 2006, 2007).

Beta entropy has no intuitive interpretation in general (Marcon and Hérault, 2015), defined as the information gain brought by the knowledge of each community composition (Marcon et al., 2014). Beta entropy gives a value of divergence between each local community's species probabilities and the metacommunity species probabilities, with proprieties interpretable, self-contained, and with a generalized information function (Marcon et al., 2014). Another phenomenon that influences beta diversity is nestedness, which occurs when the biota of an area with a lower number of species is a subset of a biota with a greater number of species (Baselga, 2010a, 2010b). In this case, the dissimilarity among sites is because of differences in species richness and occurs even in the absence of actual species turnover (Koleff et al., 2003a, 2003b; Baselga, 2012). The occurrence and persistence of mammal species in different patches within a landscape are related to ecological traits, especially body size and diet, influencing both the nestedness such as the dissimilarity among areas (Canale et al. 2016; Bogoni et al., 2016a).

In areas of the Atlantic Forest, few studies have dealt with mammal distributions at continental scales and investigated dissimilarities in species composition among areas (Melo et al., 2009). Still, it is expected that beta diversity is not seasonal, and that it increases because of endemic species, local extinctions and the presence of some species with low dispersal capacity, and decreases because of large spatiotemporal scales and by other species with high dispersal capacity (Leibold et al., 2004; Declerck et al., 2011). In this study, mammal inventories along the Atlantic Forest were compiled and the mammal diversity was partitioned into different spatial and temporal scales. By generating an overview of the richness and composition of several communities of medium to large mammals that occur along the Atlantic Forest, based on the neutral paradigm of the metacommunity framework, two goals for this study were defined: (1) to evaluate the nestedness and spatial autocorrelation of richness and biomass among mammal communities distributed along the Atlantic Forest; and (2) to partition mammal diversity from local to biogeographical scales, in order to evaluate and indicate which spatiotemporal theoretical scenario of the metacommunities within the Atlantic Forest has greater alpha and beta diversity, understand the relationship between the beta entropy and biogeographical variables, and list the species that contribute the most to the metacommunity model with the greatest spatial extent.

Our two main hypotheses are: (1) mammal nestedness is high (> 70%), and higher than expected at random, due the large distribution of most species, and richness and biomass are spatially autocorrelated due to the homogenization of composition caused by a decrease in distance; and (2) in a neutral metacommunity paradigm, the alpha and beta diversity depend on the delimitation of the metacommunity model. The predictions of our second hypothesis are: (a) the diversity metrics increase in congruence with an increase in scale, remaining equal in comparison to null models that have equal probability of observed species occurrence and larger beta diversity than expected randomly when the species presence or absence probability is symmetric (i.e., 50%); (b) the beta entropy is negatively related to alpha diversity, species richness and fragment size, because the entropy of communities is buffered by the largest pool of species in large fragments; (c) the beta diversity is greater in the tropical portion of the Atlantic Forest compared to the subtropical portion, due to the endemism in some tropical areas; and (d) the species that contribute to decreasing the beta diversity have wide distributions, tolerate habitat changes, and have a higher probability of occurrence in the theoretical metacommunity model.

2. Material and methods

2.1. Data source and organization

Secondary data of mammal communities along the Atlantic Forest was obtained using search engines regardless of publication year. We used the terms (in English, Portuguese and Spanish) "medium-to(and) large-sized(bodied) mammals" and "Atlantic Forest" in Scopus (http://www.scopus.com/), Web of Science (https://apps.webofknowledge.com/) and Scielo (http://www.scielo.br/), in addition to searching the first 200 results of Google Web Search (https://www.google.com) and ResearchGate (https://www.researchgate.net/) (Allen et al., 2011; Maglioli et al. 2015). The data search was conducted between 15 June 2015 and 30 December 2015 and included published and *in press* peerreviewed papers of studies throughout most of the original extent of the Atlantic Forest (Fig. 1). We considered all medium- to large-sized species (i.e., with an adult weight ≥ 1 kg; Chiarello, 2000); indeterminate species (listed at the genus level) were not included in the presence-absence data set. Taxonomy and body mass follow Paglia et al. (2012). Based on this reference, mammal species were classified into the trophic guilds: carnivores/piscivores, herbivores/frugivores and omnivores/insectivores, the habits in: arboreal or scansorial, terrestrial and semi-aquatic. Recent taxonomic issues concerning *Sapajus, Galictis* and *Coendou,* and consequently their species distributions, were resolved using IUCN (2015) distribution maps (Voss, 2011; Bornholdt et al., 2013). Additional taxonomic changes along the period of the study did not compromise the current classification.

For each study, we counted how many methodologies were used in the inventories, assessed the possibility of arboreal species records with the methods employed, and noted the study region (subtropical or tropical, divided into latitude −23.44° [Tropic of Capricorn]). In addition, the main vegetation physiognomy in each area, the fragment size (or area when the research included more than a forest patch, depending on the methods), and geographic coordinates were recorded. Missing data for vegetation type and geographic coordinates were estimated using digital maps (IBGE, 2004), maps provided in the articles, Google Earth® and Google Search (Google Earth, 2015). Based on the descriptions in each article, the vegetation physiognomy was grouped into: Dense Ombrophilous Forest (FOD), including lowland forest; Mixed Ombrophilous Forest (FOM), including altitudinal grasslands; and Deciduous (or Semideciduous) Seasonal Forest (FED), including dry forest. Articles describing communities for more than one area were separated according to the authors of the articles, and only the most recent information was included for articles conducted in the same location.

2.2. Data analysis

2.2.1. General patterns, nestedness and spatial autocorrelation

We analyzed the data using three traditional diversity descriptors: total richness, richness of trophic guilds, and richness of habits (Magurran, 2004). To develop the first objective of our study, we made a network plot to summarize the presence of species along the areas, organizing the matrix according to the degree of species (i.e., number of each species presence along the communities). We calculated the total degree of nestedness (N) for the binary network using NODF criteria (metric based on overlapping and decreasing fill) (Bascompte et al., 2003; Guimarães and Guimarães, 2006; Almeida-Neto et al., 2008). NODF ranges from 0, when the matrix is non-nested, to 100, when the matrix is perfectly nested (Pires et al., 2014). We also compared the nested value of the network with the value generated by 1000 null models, adopting as the p-value (significance at $p < 0.05$) the ratio of how many times the observed N was greater or equal to the N values in the null models (Bascompte et al., 2003).

Still, a Mantel test based on 1000 permutations was performed to evaluate the spatial autocorrelation of the mammal composition and mammal body size matrixes among the areas (Legendre and Legendre, 1998). Moran's test was conducted to evaluate the spatial autocorrelation of mammal richness (Legendre and Legendre, 1998; Legendre et al., 2015); the asymmetry of the data was corrected by the Hellinger transformation (Legendre and Legendre, 1998) with the spatial matrix of the distance obtained from geographic data (Legendre et al., 2015). For the significant results of Mantel or Moran test, we performed a principal coordinate analysis of neighborhood matrices (PCNM) to determine significant spatial components obtained from the truncated distance matrix among areas (Borcard et al., 2004). The positive PCNMs were selected according to the spatial autocorrelation obtained via the Moran index (Borcard et al., 2004). As a predictor of respective variable response (e.g. species richness), we used the first three PCNMs (Borcard et al., 2004; Borcard et al., 2011) in the regression model (Dobson, 1990; Johnson and Omland, 2004). The regression model was validated by checking normality and variance diagnostic plots (Johnson and Omland, 2004; Bolker, 2008).

2.2.2. Metacommunity models and diversity partitioning analysis

To develop the second objective of our study we used metacommunity theoretical models based on species-neutral diversity (Hubbell, 2001; Hu et al., 2007) in a multiplicative framework (Ellison, 2010; Veech and Crist, 2010; Chao et al., 2012) to measure, partition, estimate and compare the diversity of the mammal communities. We based the analysis on two approaches: (1) binary, only presence/absence data; and (2) weighted, with the data weighted by both occurrence probability and species body size. In the “weighted” approach, the occurrence probability values were obtained by Eq. (1) and weighted by species body size (Eq. (2)). The equations were self-created based on MacKenzie et al., 2006 and Brown et al., 2004 concepts for species occurrence probabilities and considering the implications for the species metabolism according to their body sizes.

$$P_i = \sum_i c_i \left(\frac{p_i}{sc_i}\right) \tag{1}$$

Where:
P_i = occurrence probability of the *i*-th species
c_i = *i*-th species occurrence in all communities (total records for *i*-th species)
p_i = presence of *i*-th species in the community (i.e. 1 or 0)
sc_i = species richness of the community

$$Pbs_i = \frac{Pi}{1+\sqrt{(wmax-w_i)^{3/4}\,p_i}} \tag{2}$$

Where:
Pbs_i = occurrence probability of *i*-th species weighted by body-size
P_i = occurrence probability of *i*-th species (derived from Equation 1)
wmax = max species body-size from all communities
wi = body-size of *i*-th species.

To create the composition matrix of the communities, several theoretical metacommunity models were used. The binary approach included the Total Binary metacommunity – TotBin, with all mammal communities. The weighted approach included the following: (1) Total Weighted metacommunity – TotWgt, with all mammal communities; (2) Random Symmetrical metacommunity – RandSym, redistributing the presence and absence of species at random in all communities based on 1000 models with equal probability (i.e., 50%) of presence and absence; (3) Random Asymmetrical metacommunity – RandAsym, redistributing the presence and absence of the species based on 1000 random models with greater probability of absence (i.e., 76%) than presence (i.e., 24%), which is similar to what was observed in our data set (obtained by the ratio between the total number of mammal records and the number of total possibilities in the matrix); (4) Subtropical metacommunity – Sub, only subtropical areas (latitude ≤ 23.44° S); (5) Tropical metacommunity – Trop, only communities in tropical areas; (6) Local metacommunities – Local, for groups of mammal communities ≤ 14.4 km apart (~10 times the mean distance between Atlantic Forest fragments [Ribeiro et al., 2009], resulting in 10 subsets with 2 to 5 communities each); (7) Temporal metacommunities – Temp, data for the entire Atlantic Forest separated by decades.

Moreover, for the partitioning analysis we gave different importance weights for each community (Hérault and Honnay, 2007) defined by an interaction of fragment size, number of methods employed, and average of spatial distance of each community in relation to the other communities (due to differences in the data magnitude, the values were log-transformed). Fragment size and the number of methods were used because species richness and biomass increase in congruence with these factors (Lyra-Jorge et al., 2008; Canale et al., 2012), and spatial distance was used because it is likely to be the main limitation for dispersal (Munguía et al., 2008). The diversity partition of metacommunity metrics was summarized into average alpha diversity (i.e. mean of alpha diversity for each community), beta diversity (i.e. derived from beta entropy of each community), gamma diversity, and true diversity (Jost, 2007; Marcon et al., 2012, 2014). In the TotWgt we analyzed the relationship between alpha diversity and beta entropy in each community using a correlation analysis. Additionally, we performed multiple linear regression between TotWgt beta entropy and predictive variables to selected a best predictor model, based on combination of the best AIC value, residual validation, values of variance inflation (VIF ≤ 2) and best model overdispersal (Dobson, 1990; Johnson and Omland, 2004), verifying what factors that are associated significativelly with the variation of the beta entropy along the Atlantic Forest. In the regression models, the following set of predictors were used to model the variation in beta entropy: (a) vegetation type, (b) fragment size, (c) region (tropical/subtropical), (d) species richness, (e) average spatial distance among communities, (f) total biomass, and (g) number of species with a restricted distribution and/or with locomotion via brachiation (Paglia et al., 2012).

We compared the observed beta diversity of the TotWgt in relation to the beta diversity found in simulated communities (i.e., RandSym and RandAsym), adopting as the p-value (significance at p <

0.05) the ratio of how many times the observed beta diversity was less than or equal to the beta diversity values in the null models, divided by the number of null models (i.e., 1000). To perform the analysis, the program R (R Core Team, 2016) and the packages vegan (Oksanen et al., 2013), bipartite (Dormann et al., 2008), ade4 (Dray and Dufour, 2007) and entropart (Marcon and Hérault, 2015) were used.

3. Results

3.1. Search panorama, nestedness and spatial autocorrelation

The search using the search engines returned 618 results. However, only 72 papers met the inclusion criteria, resulting in 118 independent areas (Fig. 1; Supporting information S1 and S2). These studies were carried out from 1983 to 2013. Overall, we compiled 1735 presence records, belonging to 62 species and varying from 4 to 31 species per area (Supporting information S3 and S4) which resulted in a 0.24 average probability of species presence. Nestedness was statistically higher than simulated with the null models [$N_{obs} = 52.9$; $N_{null} = 32.5$; $p < 0.001$] (Supporting information S5). Species richness of carnivores was 9 species (0–8 per area), herbivore richness was 26 species (0–11) and omnivore richness was 27 species (1–16). Moreover, 38 species (1–24) were terrestrial, 20 arboreal or scansorial (0–7), and 4 semi-aquatic (0–3). Spatial distance between areas was, on average, 846.1 km (± 596.8) and ranged from 0.36 to 2837.4 km. Sampling area size varied from 5.4 ha to 468,760 ha, adding up to 1,124,465.7 ha.

Spatial autocorrelation was not significant for mammal composition and mammal body size among the areas [$r = -0.03$; $p = 0.99$ and $r = -0.04$; $p = 0.99$]. Yet, mammal richness was autocorrelated spatially [$M_{obs} = 0.15$; $M_{exp} = -0.01$; $p < 0.001$] and PCNMs derived 26 positive and significant eigenvectors. Among the three main vectors (Moran Index ≤ 0.2; Supplementary material 6) only the second eigenvector are significant [$t = 2.16$; $df = 114$; $p = 0.04$] to predict the species richness in regression model.

3.2. Diversity variations

The results of the diversity partitioning analysis showed that for the TotWgt the “true diversity” was 39.32 species (63.4% of total richness

[62]), with a mean alpha diversity of 9.86 (67.1% of the average richness [14.7] of the 118 communities), turnover (beta diversity) of 3.99 and gamma diversity of 39.32 (Fig. 2A; Table 1). The probability of occurrence of each species in the TotWgt scenario ranged from <0.001 to 0.065 (0.016 ± 0.016). The five species with the highest occurrence probabilities were *Cerdocyon thous*, *Nasua nasua*, *Dasypus novemcinctus*, *Procyon cancrivorus* and *Tamandua tetradactyla*. The species with the lowest occurrence probabilities were endemic, which had restricted distributions or were locally extinct (Supporting information S7).

The binary approach (i.e., TotBin), "true diversity" and gamma diversity were similar to the weighted approach, as well as the probability values and species that contribute most in both scenarios. However, numerically, these two approaches differed greatly for alpha and beta diversity (Table 1). The values of the diversity index obtained for the TotWgt and TotBin varied greatly compared to the values obtained for the RandSym and RandAsym especially for "true diversity," alpha diversity and gamma diversity (Table 1). Beta diversity of the TotWgt was significantly higher than beta diversity of the null models for the RandSym [$\beta_{obs} = 3.99$; $\beta_{null} = 2.02$; $p < 0.01$], and lower than in the null models for the RandAsym [$\beta_{obs} = 3.99$; $\beta_{null} = 4.27$; $p < 0.01$] (Fig. 2B). Alpha diversity of the TotWgt was statistically lower than in the RandSym [$\alpha_{obs} = 9.86$; $\alpha_{null} = 14.29$; $p < 0.001$] (Fig. 2C). The variation in diversity metrics over time was also great. Communities sampled before 2000 showed a higher species richness, alpha diversity and "true diversity" than the communities sampled after 2000; beta diversity, in turn, was lower for samples taken before 2000 (Fig. 2D; Table 1).

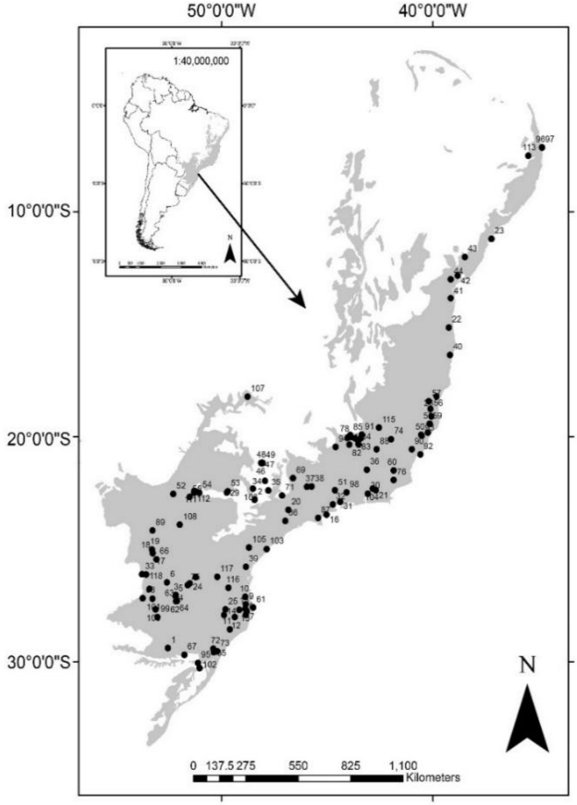

Fig. 1. Location of secondary data of medium- to large-bodied mammals communities using search engines along Atlantic Forest to evaluate patterns of diversity at a neutral metacommunity paradigm.

Both alpha and beta diversity of the TotWgt lacked a spatially autocorrelated pattern (Fig. 3). Alpha diversity of communities in the TotWgt was negatively correlated with beta entropy [$r = -0.78$; $df = 116$; $p < 0.001$] (Fig. 3). The model selection showed that the main predictors of beta entropy were an interaction between species richness and number of species with restricted distributions and/or with locomotion via brachiation [AIC = 48.66; VIF = 1.24; overdispersal = 0.08; df = 117] (Table 2). When the scale was reduced to the subtropical area, the “true diversity” was 31.81, with an average alpha diversity of 14.49, beta diversity of 2.17, and gamma diversity of 31.52. The “Tropical metacommunity" had a "true diversity" of 40.80, with an alpha diversity of 14.62, beta diversity of 2.76, and gamma diversity of 40.28 (Table 1). We obtained 10 "Local" metacommunity models (Supporting information S8) involving communities located < 14.4 km apart. This set of Local metacommunities had an average "true diversity" of 22.22 (±15.35; ranging from 7.42 to 44.26) and an average richness of 10.43 (±6.44), showing that the "true diversity" is approximately two times the observed richness in the local communities. The average alpha diversity in the local communities was 9.34 (±6.10), the average beta diversity was 1.49 (±0.23) and average gamma diversity was 13.17 (±6.84) (example in Fig. 4; Table 1).

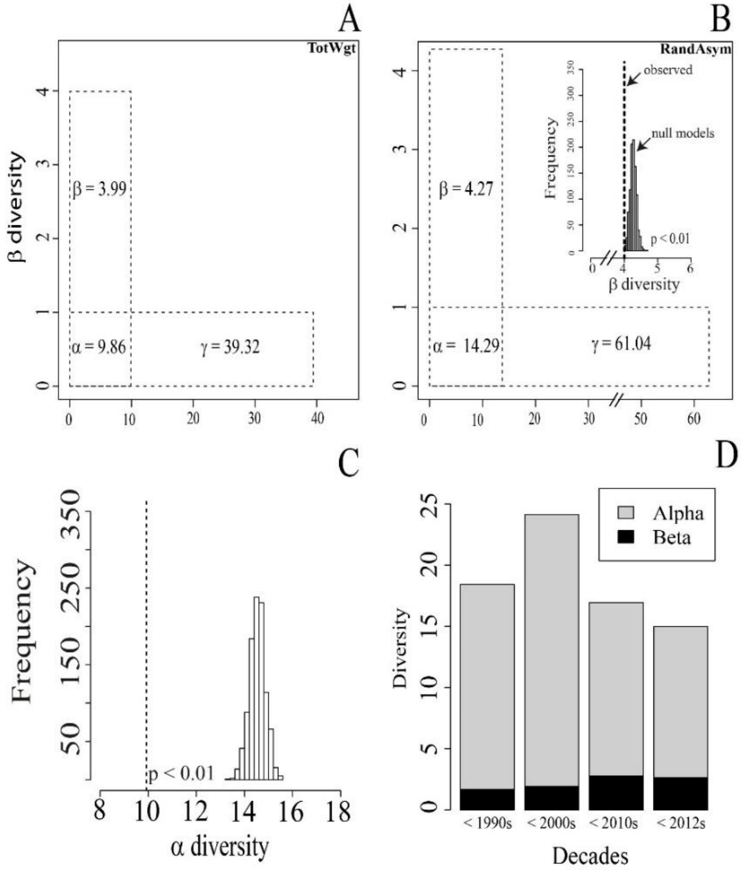

Fig. 2. (A) Total Weighted metacommunity values of diversity indexes for medium- to large-bodied mammals of the entire Atlantic Forest; (B) Random Asymmetric metacommunity values of diversity indexes based on1000 null models, histogram of the distribution of beta diversity for each null model (gray) compared with beta diversity for Total Weighted metacommunity (dotted line); (C) alpha diversity values of Random Asymmetric metacommunity null models (bar) in comparison to the Total Weighted metacommunity (dotted line); and (D) diversity variation among decades.

4. Discussion

Understanding the relationships between species richness, turnover, and spatial broad-scale features can provide important insights into the processes driving species diversity (Melo et al., 2009; Rouquette et al., 2013). The main result of our study showed a large beta diversity for medium- to large-bodied mammals compared to the average alpha diversity and beta diversity at smaller spatial scales (e.g., tropical and subtropical areas, and Local metacommunity scenarios). The largest diversity at the greatest scales was composed of a summary of the diversity of smaller regions, but our results showed that the tropical area was very important to Atlantic Forest mammal diversity. The values of diversity in the tropical region and the results of regressions to predict the beta entropy reinforce this issue. For example, all diversity metrics were higher in the tropical region compared to the subtropical region. Potential drivers for this distinction are the absence of endemic species, few species with restricted distributions and/or species with low locomotion capacity in the subtropical region (Graipel et al., 2016). The difference in diversity among scales could have been determined by historical factors, habitat heterogeneity, environmental stress or stability, area size and disturbance (Whittaker et al., 2001; Jenkins et al., 2015; Oliveira et al., 2016).

Thus, both stochastic (neutral paradigm) and deterministic (other metacommunity paradigms) processes have complementary strengths, and the window of observation influences the perception of which process is more important (Mikkelson, 2005; Chase, 2014). Our result is in accordance with this ambiguity. Mammal diversity reduces gradually as the scale decreases. This pattern points to an action of local filters or to a local community disassembly process (Gonzalez, 2005). Still, with the decline of the sampling scale (encompassing fewer individuals and less habitat heterogeneity), the relative contribution of the stochastic events that influence the structure of the community increases (Chase, 2014). An increase in mammal beta diversity with increasing spatial extent seems to be due to species dispersal limitations because of a combination of habitat fragmentation, presence of geographical barriers (Silva and Hernández, 2014) and changes in environmental conditions (Melo et al., 2009). However, neutral processes are also important at larger spatiotemporal scales, and are a result of random probabilities of the gain and loss of species, which requires much more of the extinction and speciation processes (Leibold et al., 2004). Another factor that highlights this ambiguity is that the beta diversity obtained for the entire Atlantic Forest in the weighted approach (TotWgt) is lower than expected at random, with a similar presence probability (RandAsym). RandAsym is the null scenario that is more similar to real data (TotWgt) in a neutral perspective. Yet, the beta diversity obtained is higher compared to the models where presence and absence had the same probability (RandSym), composing a more stochastic null scenario.

The high beta diversity is evidence that among the 118 mammal communities evaluated the spatial species turnover is 3.99, or approximately 4 different species in each community (41% of average alpha, 11% of gamma diversity and 27% of average richness). When alpha diversity a component of total diversity, only shows diversity values of each area (Lande, 1996), beta diversity produced by compositional differences among areas, showed a large range of change in community composition in space and time (Whittaker, 1960). In our other spatial approaches, beta diversity and alpha diversity ratio decreased (i.e., showing the greater similarity between areas close to each other) at smaller spatial extents, even though gamma diversity and "true diversity" also declined.

Table 1

Results of the metacommunity's approach analysis of diversity partitioning to medium- to large-bodied mammals of Atlantic Forest communities. N: number of communities; Prob: the ratio between presences in relation to the full potential (N× St); St: total mammals richness; Sm: average mammals richness; and TD: “true diversity”.

Approach	Metacommunities	N	Prob	St	Sm	TD	α	β	γ
Binary	Total Binary metacommunity – TotBin	118	0.24	62	14.71	40.17	14.56	2.74	39.83
Weighted	Total Weighted metacommunity – TotWgt	118	0.24	62	14.71	39.32	9.86	3.99	39.32
Weighted	Random Symmetric metacommunity – RandSym [a]	118	0.50	62	30.99	61.72	30.61	2.02	61.70
Weighted	Random Asymmetric metacommunity – RandAsym [a]	118	0.24	62	14.86	61.06	14.29	4.27	61.04
Weighted	Subtropical metacommunity – Sub	49	0.35	44	15.25	31.81	14.49	2.17	31.52
Weighted	Tropical metacommunity – Trop	69	0.25	57	14.32	40.80	14.62	2.76	40.28
Weighted	Local metacommunity – Local [b]	10	0.65	15.7	10.43	22.22	9.34	1.49	13.17
Weighted	< 1990's metacommunity	4	0.54	34	18.25	33.24	16.77	1.66	27.85
Weighted	< 2000's metacommunity	8	0.46	50	23.00	64.91	22.22	1.90	42.31
Weighted	< 2010's metacommunity	85	0.24	60	14.33	39.71	14.17	2.77	39.26
Weighted	< 2012's metacommunity	21	0.27	46	12.38	33.54	12.36	2.62	32.38

[a] Average of 1000 null models; [b] Average of 10 real nearby (≤14.4 km) communities.

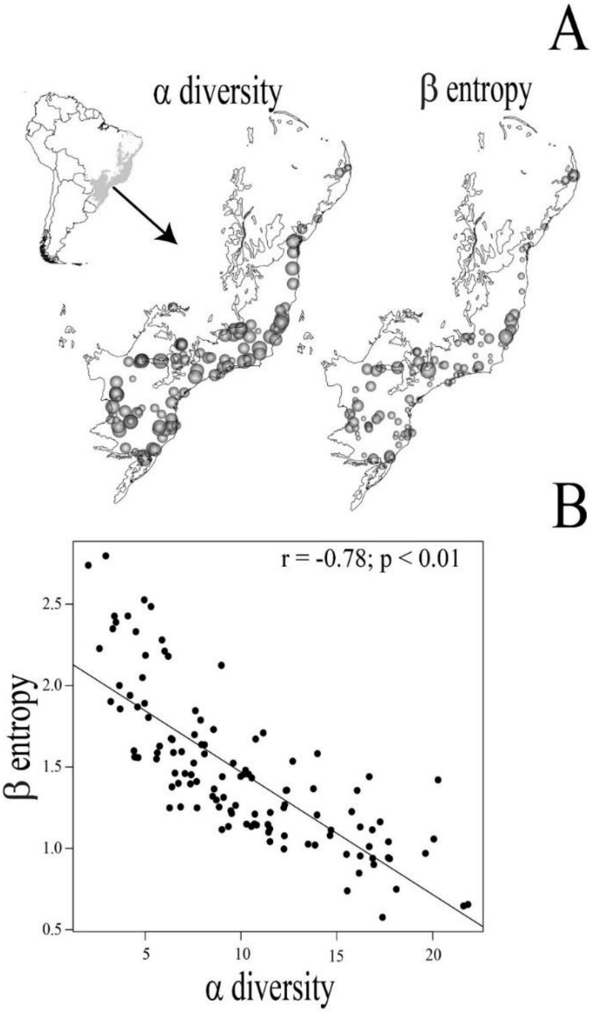

Fig. 3. (A) Spatial representation of alpha diversity and beta entropy of each mammals community in the Total Weighted metacommunity approach; and (B) negative relationship between beta and alpha diversity in the Total Weighted metacommunity approach across 118 medium to large-bodied mammals communities in Atlantic Forest, Brazil.

The beta entropy of each community decreased with species richness and richness of species with restricted distributions, whereas alpha diversity increased with the same variables, and both (beta entropy [disorder] and alpha diversity) had a negative relationship. Although the spatial turnover implies the replacement of some species by others, little consensus has been reached about general features of spatial variation in beta diversity (Koleff et al., 2003a, 2003b). Turnover is highly variable in space and has been related to transitions between habitats or ecosystems, topographic variation (McDonald et al., 2005), and increased beta diversity at larger spatial extents because of larger distances separating communities (Legendre et al., 2005; Steinitz et al., 2006). These three factors can explain the high beta diversity in the Atlantic Forest because of its large extent and heterogeneity (Ribeiro et al., 2009), making it impossible for an individual to be dispersed throughout the entire Atlantic Forest. Another factor that influenced the richness was the spatial autocorrelation because, based on the patch dynamics concept, areas with high richness can serve as a source for nearby areas with low richness (Leibold et al., 2004). Our results also confirm these patterns; we found a spatial autocorrelation of species richness, reinforcing the importance of regional pool of species.

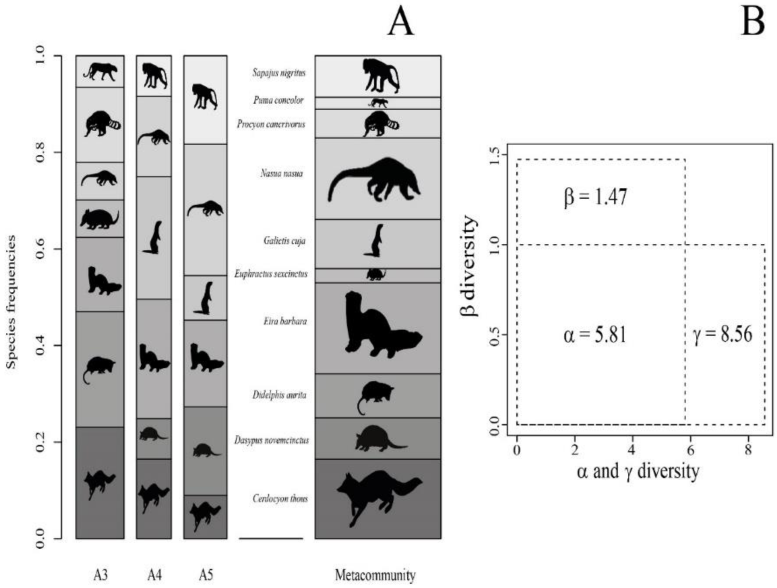

Fig. 4. (A) Species frequencies in each community and in the theoretical metacommunity. The left-bar width shows the contribution of each community to the metacommunity; bar height represents the species contribution to each community and to the metacommunity. (B) Diversity partition in alpha, beta and gamma diversity. Data from Bogoni et al. (2013) (A3, A4 and A5), in three neighboring (3.4 ± 3.0 km) fragments (~50 ha each) of Seasonal Deciduous Forest (FED) in the agromosaic of the subtropical Atlantic Forest, Brazil. Total richness observed is 10 (average of 6.33) and “True diversity” was 9.42.

Table 2

Regression models using biogeographic and ecological patterns to predict de beta entropy of medium- to large-bodied mammals in “Total Weighted metacommunity” (TotWgt) approach along Atlantic Forest.

Response	**Predictive**		**Parameters**						
Variable	**Model**	**Model description**	**k**	**df Total**	**AIC**	**ΔAIC**	**Passed residuals’ validation**	**VIF**	**O**
Beta Entropy of TotWgt approach	M9	R * S * F	7	117	44.64	0	yes	< 255.9	0.08
	M8	R * S	3	117	48.17	3.53	yes	< 6.92	0.08
	M10	**S + RD**	**2**	**117**	**48.66**	**4.02**	**yes**	**< 1.24**	**0.08**
	M1	V + F + R + S + D + RD + B	7	118	49.53	4.89	yes	< 2.54	0.08
	M5	R + S	2	117	49.56	4.92	yes	< 1.05	0.09
	M11	S * RD	3	117	50.6	5.96	yes	< 11.90	0.09
	M2	V + F + R + S + D	5	116	54.2	9.56	yes	< 1.69	0.09
	M14	S * B	3	117	57.45	12.81	yes	< 13.13	0.09
	M13	S + B	2	117	60.1	15.46	yes	< 1.99	0.09
	M6	S	1	117	61.69	17.05	yes	1	0.10
	M4	F * S	3	117	61.92	17.28	yes	< 86.1	0.09
	M3	F + S	2	117	63.66	19.02	yes	< 1.04	0.10
	M12	B	1	117	131.36	86.72	yes	1	0.17
	M7	R	1	117	147.97	103.33	no	1	0.20

Where: F: fragment/area size (ha); V: vegetation type (FED, FOD, FOM); R: region (tropical or subtropical); S: richness; D: average distance of each area in relation to all others; RD: richness of distribution restricted or locomotion via brachiation; B: community biomass (sum of body size of species co-occurrence); k: number of parameters of model; df: degrees of freedom; VIF: values of variance inflation; O: model overdispersal. The best model according to best AIC value, residual validation, values of variance inflation (VIF≤ 2) and best model overdispersal in bold (M10).

Changes in species richness over spatial and temporal scales provide a basis for predicting and evaluating community responses to management and natural disturbance, and to changes in factors such as community composition (Nichols et al., 1998) and evolutionary processes (Melo et al., 2009). Nestedness is another phenomenon that influenced the beta diversity (Koleff et al., 2003a, 2003b; Baselga, 2010a, 2010b, 2012), which was 20% greater than expected at random. In this case, the dissimilarity among sites is related to the difference in specific richness and occurs even in the absence of a real turnover of species (Baselga, 2010a, 2010b, 2012). Nested patterns also suggest predictable sequences of species loss (Patterson, 1990). This is something that we found partially in the bipartite network and nestedness analysis where there was a moderate nestedness among mammal communities of the Atlantic Forest. Furthermore, “true diversity” represented 63.5% of the overall species richness for the TotWgt. This metric is more informative than species richness because it is an estimate that considers the number of species under equal abundances (Jost, 2007). Although sometimes measurements used to determine equivalent numbers are mathematically or conceptually very different (Hoffmann and Hoffmann, 2008). Thus, the “true diversity” obtained reflects the presence of some rare (and/or endemic) species in some of the evaluated mammal communities and in our different theoretical approach, while the calculations for entropy are focused on the dominant species (Hill, 1973; Jost, 2007; Chao and Jost, 2015), generally with large distributions.

The degree of habitat specialization is an important determinant of species vulnerability to landscape changes (e.g., fragmentation and habitat loss), can bias the dispersal ability and, thus, the degree of isolation of populations (Püttker et al., 2013). Therefore, it is unlikely that there is direct dispersal among the 118 mammal communities, except for neighboring areas or, over time, for species with high vagility, especially those with large home ranges (Bowman et al., 2002). However, the presence of stepping stones along the Atlantic Forest may be maintaining the landscape's functional connectivity for these species (Andrén, 1994; Uezu et al., 2008). Even though we analyzed an area covering < 6.8% of the Atlantic Forest fragments (based on Ribeiro et al., 2009), we believe that there is high connectivity among areas located in the highland region (Ribeiro et al., 2009) that functions as a large biological corridor at medium to long-term (Ribeiro et al., 2009). Conversely, additional factors that limit dispersal, such as the type of locomotion (e.g., brachiation) and matrix permeability, can reduce the connection between local communities and their surrounding communities (Schmidt, 2011; Caryl et al., 2013). These factors have implicit effects on the species probability obtained (independent of the scenario).

Among species with the largest presence probabilities in all scenarios, most are generalists (e.g., *Nasua nasua* and *Cerdocyon thous*). Generalists are flexible in the face of disturbances and have higher matrix tolerance because of their diet and body size (Canale et al., 2012; Bogoni et al., 2016a). Thus, the generalist species contribute to reducing the beta diversity and increasing the probability of metacommunity formation. In contrast, the species showing the lowest occurrence probabilities are specialists, endemic, under threat of extinction, and have a large body size and/or are naturally rare, thus occurring in few localities (Jorge et al., 2013; Dirzo et al., 2014) and contributing to an increase in beta diversity. Moreover, the species detection probability, which is dependent on the sampling method (Lyra-Jorge et al., 2008), can affect the results with an increase in beta diversity induced by pseudo-absences. Yet, for the Local metacommunity approaches, we found low beta diversity (approaching the minimal value of 1 for the index). This pattern can be explained because at smaller spatial scales the environment is likely homogeneous and the short distances can allow species flow (Legendre et al., 2005; Melo et al., 2009).

Additionally, our data transformation can introduce bias. Although difficult to obtain and standardize, measures that consider presence probability and species body size (e.g., *Priodontes maximus*, *Ozotoceros bezoarticus* and *Tapirus terrestris* [low frequency and large-bodied species] and *Cerdocyon thous*, *Dasypus novemcinctus* and *Nasua nasua* [high frequency and medium-bodied species] have distinct probabilities than that they would have in a binary scenario) can represent the most accurate pattern. This is because of the ecological implications of body size, since there is an increase in locomotion capacity with an increase in species body size (Peters, 1983), and a higher demand for local persistence, home range and habitat quantity and quality (Canale et al., 2012). Our results could also be biased due to distinct sampling methods in the studies that composed the dataset, because of the positive relationship between species richness and fragment size (e.g. Canale et al., 2012; Magioli et al., 2015), or differences between studies conducted in different years, because the temporal dynamic is constantly changing (Ricklefs, 2006).

The overall direction of our results may contribute to better understanding medium- to large-bodied mammal diversity patterns and variations in the Atlantic Forest from a neutral perspective. Connectivity between large geographical areas depends on the expansion and contraction of the geographical distribution of populations of each species, which is the result of long-term ecological and evolutionary processes (Holt, 2003). Individual dispersion occurs in a shorter time span and at a smaller spatial scale (Vangestel et al., 2013). Both of these issues are related to home ranges (Bowman et al., 2002). We conclude that the diversity of medium- to large-bodied mammals along the Atlantic Forest is composed of a nested summary of local to regional diversities. The tropical region was very important to the composition of the overall diversity. There is a gain in beta diversity due to the difference among communities that is not observed when looking only at the alpha diversities. The neutral process is an important tool from a metacommunity perspective, but species diversity is a complex result of dispersal abilities (mainly in a fragmented environment), environmental filters and competitive abilities, such as stochastic processes at several scales. The prospects about metacommunity paradigms on mammals diversity highlight that are an ambiguity between niche effects and neutral effects, and more studies can be performed to evaluate these processes. Conservation strategies should consider all scales of the Atlantic Forest, because the diversity of mammals is dependent both the local and regional pool of mammals to create high diversity at a biogeographic scale. The pool in each scale serves as a source to the nearest fragment within a region, even without connecting large geographic areas, mainly because of locally endemic or rare species. Some of the most important standing issues are to find out whether dispersal across regional landscapes occurs for most species and, if it does, to ensure that this is maintained or increased, to maintain species diversity and ecological processes.

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Supporting Information

Supporting Information S1. Secondary metadata of medium to large-bodied mammals communities obtained in search engines along Atlantic Forest. FS: fragment/area size; S: mammals richness; CS: carnivore richness; HS: herbivores richness; OS: omnivores richness; AS: arboreal species richness; TS: terrestrial species richness; SS: semi-aquatic species richness.

Reference	Journal	ID	W	S	FS	S	CS	HS	OS	AS	TS	SS
Abreu-Júnior and Kohler 2009	Biota.Neotrop	A1	-52.53	-29.38	221	12	2	3	7	2	8	2
Alves et al. 2012	Iheringia.S.Zool.	A2	-48.44	-22.79	1152	12	2	4	6	0	11	1
Bogoni et al. 2013	ISRN.Forestry	A3	-52.17	-27.03	55	7	1	0	6	0	7	0
	ISRN.Forestry	A4	-52.17	-27.04	47	6	1	0	5	1	5	0
	ISRN.Forestry	A5	-52.18	-27.09	51	6	1	0	5	1	5	0
Bogoni et al. 2016a	J.Mammal	A6	-52.58	-26.46	612	19	4	6	9	2	14	3
	J.Mammal	A7	-48.81	-27.74	5000	10	2	1	7	1	9	0
	J.Mammal	A8	-48.85	-27.90	5000	13	4	2	7	0	12	1
	J.Mammal	A9	-48.86	-27.44	4436	15	4	3	8	0	14	1
	J.Mammal	A10	-48.88	-27.10	509	14	4	2	8	1	11	2
	J.Mammal	A11	-49.60	-28.55	7672	10	3	1	6	0	10	0
	J.Mammal	A12	-49.37	-28.00	126.5	14	4	3	7	0	13	1
	J.Mammal	A13	-49.17	-27.68	10	11	4	2	5	0	10	1
	J.Mammal	A14	-49.88	-27.91	4987	17	4	4	9	1	15	1
Bogoni et al. 2016b	Biod.Cons.	A15	-48.88	-27.63	27	14	2	4	8	1	11	2
Bovendorp and Galetti 2007	Biol.Invasions	A16	-45.03	-23.45	3000	14	0	6	8	3	9	2
Brocardo and Cândido Jr. 2012	Rev.Arv	A17	-53.25	-25.15	520	28	6	9	13	3	22	3
	Rev.Arv	A18	-53.25	-25.17	405	26	5	8	13	3	22	1
	Rev.Arv	A19	-53.28	-25.00	135	19	4	4	11	2	16	1
Carvalho et al. 2013	Biosci.J.	A20	-46.84	-23.24	2300	20	4	6	10	2	16	2

Carvalho et al. 2014	Biota.Neotrop	A21	-42.71	-22.37	7300	22	4	7	11	6	15	1
Cassano et al. 2012	Biotropica	A22	-39.25	-15.13	6000	25	5	10	10	5	18	2
Chagas et al. 2012	Rev.Nordestina.Bio	A23	-37.23	-11.20	4000	12	1	7	4	4	7	1
Cherem and Perez 1996	Biotemas	A24	-51.50	-26.50	3500	22	5	5	12	4	16	2
Cherem et al. 2011	Biotemas	A25	-49.82	-27.67	5000	13	3	3	7	1	9	3
Chiarello et al. 1999	Biol.Cons.	A26	-39.83	-18.20	20000	31	7	11	13	6	24	1
	Biol.Cons.	A27	-40.08	-19.08	20000	28	6	11	11	6	21	1
	Biol.Cons.	A28	-40.25	-19.80	2000	22	4	8	10	5	17	0
Cullen et al. 2001	Oryx	A29	-49.75	-22.47	2000	6	0	2	4	2	4	0
Cunha 2010	J.Nat.Conserv.	A30	-43.09	-22.52	60	5	0	1	4	2	3	0
Cunha and Rajao 2007	Bol.Mus.Biol.Mello	A31	-44.38	-22.88	2106	10	0	4	6	3	7	0
Delciellos et al. 2012	Check.List	A32	-44.73	-23.00	104000	15	2	5	8	3	12	0
Di Bitetti et al. 2014	Mastozool.Neotrop.	A33	-53.75	-26.10	4900	15	5	5	5	1	14	0
Dias et al. 2012	Multiciência	A34	-47.94	-21.95	90	13	3	3	7	1	12	0
Dotta and Verdade 2011	Mammalia	A35	-47.79	-22.38	6200	17	3	5	9	2	14	1
Druprat and Andriolo 2011	Rev.Bras.Zoocienc.	A36	-43.13	-21.46	11900	17	1	7	9	5	11	1
Eduardo 2011	Rev.Bras.Biosci.	A37	-45.97	-22.22	700	19	6	6	7	3	14	2
	Rev.Bras.Biosci.	A38	-45.74	-22.20	300	11	1	4	6	2	9	0
Espartosa et al. 2011	Biod.Cons.	A39	-48.85	-25.77	10000	12	1	3	8	1	10	1
Falcão et al. 2012	Check.List	A40	-39.20	-16.35	6069	27	5	9	12	6	19	2
Flesher and Laufer 2013	Trop.Cons.Scien.	A41	-39.17	-13.83	550	15	1	5	9	4	11	0
	Trop.Cons.Scien.	A42	-38.83	-12.83	190	12	1	5	6	3	9	0
	Trop.Cons.Scien.	A43	-38.50	-12.00	170	10	0	4	5	3	7	0
	Trop.Cons.Scien.	A44	-39.17	-13.00	140	7	0	4	3	1	6	0
Fornitano et al. 2015	Oecol.Australis	A45	-48.13	-21.16	166.2	8	0	3	5	3	5	0
	Oecol.Australis	A46	-48.12	-21.16	55.1	10	1	3	6	3	7	0
	Oecol.Australis	A47	-48.08	-21.16	189.2	10	1	3	6	3	7	0
	Oecol.Australis	A48	-48.07	-21.15	128.5	11	1	4	6	4	6	1
	Oecol.Australis	A49	-48.05	-21.16	163.8	8	1	3	4	2	6	0
Gatti et al. 2014	Natureza.on.line	A50	-40.56	-19.91	4000	28	6	11	11	7	19	2

Geise et al. 2004	Braz.J.Biol.	A51	-44.63	-22.37	28000	31	8	8	15	7	22	2
Giacomini and Galetti 2013	Biol.Cons.	A52	-52.28	-22.53	6200	9	0	4	5	2	6	1
	Biol.Cons.	A53	-49.71	-22.42	4600	6	0	1	5	1	5	0
	Biol.Cons.	A54	-51.05	-22.48	2100	6	0	3	3	2	4	0
	Biol.Cons.	A55	-51.52	-22.67	4700	7	0	3	4	2	5	0
	Biol.Cons.	A56	-40.13	-18.76	650	8	0	5	3	4	4	0
	Biol.Cons.	A57	-40.20	-18.42	670	10	0	4	6	3	6	1
	Biol.Cons.	A58	-40.14	-19.43	460	6	0	3	3	4	1	1
	Biol.Cons.	A59	-40.17	-19.43	490	4	0	1	3	3	1	0
Gomes-Albuquerque et al. 2013	Check.List	A60	-41.87	-21.48	1000	5	0	1	4	0	5	0
Graipel et al. 2001	Biotemas	A61	-48.50	-27.58	45100	13	1	2	10	2	9	2
Hendges et al. 2015	Biotemas	A62	-52.11	-27.29	476	19	4	5	10	2	14	3
	Biotemas	A63	-52.15	-27.30	265	4	0	2	2	0	3	1
	Biotemas	A64	-52.13	-27.27	700	14	3	2	9	1	11	2
Junges and Cademartori 2012	Mouseion	A65	-50.37	-29.57	550	12	3	3	6	2	9	1
Juraszek et al. 2014	Acta.Iguazu	A66	-53.07	-25.44	3000	24	6	6	12	3	21	0
Kasper et al. 2007a	Biosciências	A67	-51.76	-29.68	486700	25	6	6	13	3	19	3
Kasper et al. 2007b	Rev.Bras.Zool.	A68	-53.72	-27.17	17491	30	8	10	12	4	24	2
Lima and Pasciani 2014	Rev.Biosciências	A69	-46.62	-21.83	50	11	2	3	6	1	8	2
Maciel and Maciel 2015	REB	A70	-51.22	-26.23	133	12	3	5	4	3	9	0
Magioli et al. 2014	Check.List	A71	-47.13	-22.60	173	16	3	4	9	2	13	1
Marques et al. 2011	Rev.Bras.Biosci.	A72	-50.39	-29.41	1607	28	7	9	12	3	23	2
	Rev.Bras.Biosci.	A73	-50.21	-29.53	4500	16	4	4	8	2	13	1
Mendes et al. 2014	Rev.Bras.Zoosci.	A74	-41.98	-20.10	960	17	5	5	7	5	11	1
Miranda et al. 2008	Biotemas	A75	-51.60	-26.58	1000	23	5	6	12	4	18	1
Modesto et al. 2008	Biota.Neotrop	A76	-41.86	-21.92	22400	19	5	6	8	4	14	1
Morcatty et al. 2013	Ecol.Res.	A77	-44.03	-20.03	4398	18	4	6	8	3	15	0
	Ecol.Res.	A78	-43.88	-20.00	148	20	4	8	8	4	16	0
	Ecol.Res.	A79	-43.67	-20.07	7543	28	6	10	12	6	20	2

	Ecol.Res.	A80	-43.42	-20.06	148	21	5	5	11	3	17	1
	Ecol.Res.	A81	-43.37	-19.92	3941	24	6	7	11	3	20	1
	Ecol.Res.	A82	-43.95	-20.33	148	7	0	3	4	2	5	0
	Ecol.Res.	A83	-43.53	-20.30	10187	23	5	8	10	3	18	2
	Ecol.Res.	A84	-43.52	-20.33	605	13	0	5	8	3	9	1
	Ecol.Res.	A85	-43.92	-19.92	280	7	0	3	4	3	4	0
Negrão, Valladares-Pádua 2006	Biota.Neotrop	A86	-46.98	-23.73	10870	11	0	4	7	2	8	1
Norris et al. 2012	Biota.Neotrop	A87	-45.43	-23.60	49953	16	4	7	5	3	11	2
Nunes et al. 2013	Check.List	A88	-42.67	-20.55	14984	11	3	2	6	0	11	0
Oliveira et al. 2012	Arq.Ciênc.Vet.Zoo.	A89	-53.26	-24.16	382	6	0	2	4	2	4	0
Oliveira et al. 2013	Check.List	A90	-41.00	-20.55	10755	13	2	4	7	4	9	0
Paglia et al. 2005	Lundiana	A91	-43.37	-19.90	605	6	0	2	4	2	4	0
Passamani et al. 2005	Biotemas	A92	-40.59	-20.78	390	9	1	1	7	1	7	1
Passamani et al. 2000	Bol.Mus.Biol.Mello	A93	-40.53	-19.95	440	23	4	10	9	6	15	2
Penido and Zanzini. 2012	Check.List	A94	-44.61	-20.45	1563	17	3	3	11	1	15	1
Penter et al. 2008	Rev.Bras.Biosci.	A95	-51.11	-30.04	1000	7	0	1	6	2	4	1
Percequillo et al. 2007	Bio.Geral.Exper.	A96	-34.85	-7.14	515	5	1	1	3	1	3	1
	Bio.Geral.Exper.	A97	-34.84	-7.14	34.5	4	0	3	1	2	2	0
Pereira et al. 2012	Biosci.J.	A98	-44.08	-22.46	211	21	4	5	12	2	17	2
Peters et al. 2010	Biotemas	A99	-53.03	-28.00	3110	13	0	4	9	1	10	2
	Biotemas	A100	-53.12	-27.67	820	14	2	4	8	1	12	1
	Biotemas	A101	-53.27	-27.18	3310	9	1	3	5	1	7	1
Pires and Cademartori 2012	Biota.Neotrop	A102	-51.03	-30.27	142	14	3	4	7	3	8	3
Portela and Flynn 2012	Rev.Inter.	A103	-47.87	-24.98	18923	6	2	0	4	0	5	1
Prado et al. 2008	Rev.Arv	A104	-42.85	-22.30	385	17	2	7	8	4	12	1
Prado et al. 2014	J.Ethnob.Ethnomed.	A105	-48.70	-24.92	16800	10	0	3	7	0	10	0
Reale et al. 2014	Check.List	A106	-48.52	-22.30	190	22	5	6	11	3	16	3
Rocha et al. 2015	Check.List	A107	-48.77	-18.21	938	23	3	6	14	2	20	1
Rocha-Mendes et al. 2005	Rev.Bras.Zool.	A108	-51.97	-23.90	22400	29	7	6	16	3	23	3
Rossaneis 2014	Semina	A109	-51.21	-22.43	10.5	7	0	2	5	1	5	1

	Semina	A110	-51.26	-22.46	5.4	8	2	1	5	0	8	0
	Semina	A111	-51.29	-22.40	6	8	0	2	6	0	7	1
	Semina	A112	-51.31	-22.48	15	8	1	3	4	0	7	1
Sousa and Gonçalves 2004	Rev.Biol.Ciênc.Ter.	A113	-35.50	-7.50	5200	18	6	4	8	1	15	2
Spezia et al. 2013	Unoesc.Ciência	A114	-53.41	-26.75	78	18	4	4	10	2	14	2
Stallings et al. 1991	Rev.Bras.Zool.	A115	-42.56	-19.59	35000	21	4	9	8	6	14	1
Tortato et al. 2014	Biotemas	A116	-49.67	-26.70	3682	29	7	9	13	4	22	3
Wallauer et al. 2000	Biotemas	A117	-50.21	-26.21	2012	16	3	6	7	3	12	1
Wolfart et al. 2013	Biotemas	A118	-53.56	-26.11	220	12	3	3	6	1	10	1

Supporting Information S2. References of database obtained in search engines along Atlantic Forest.

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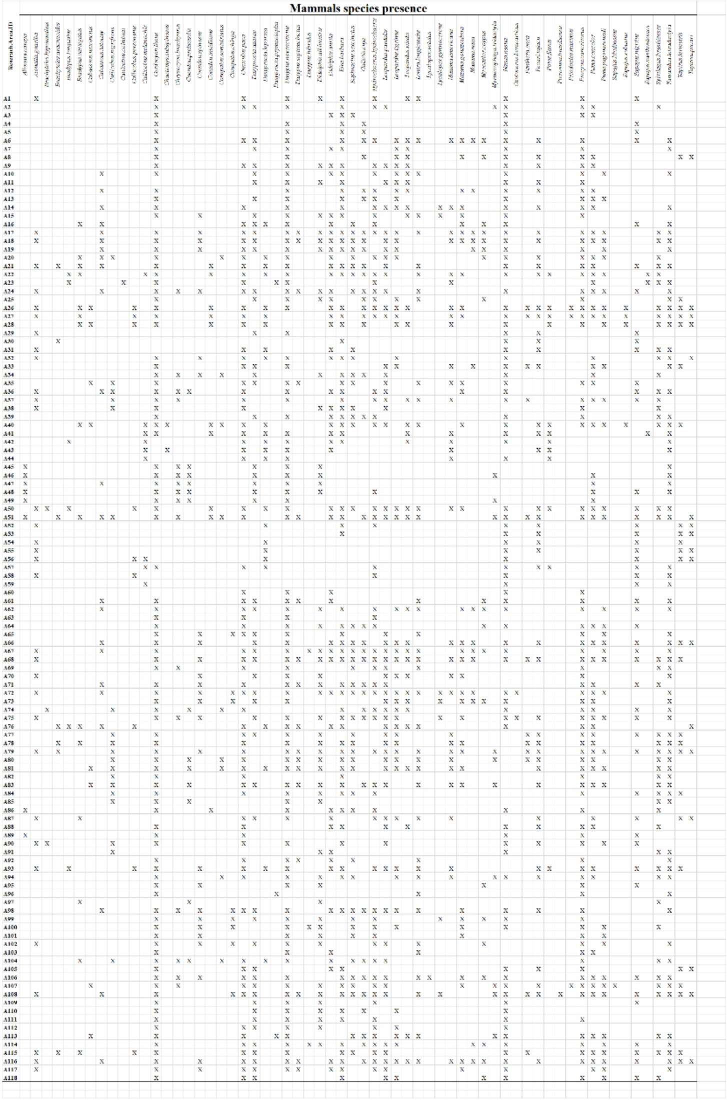
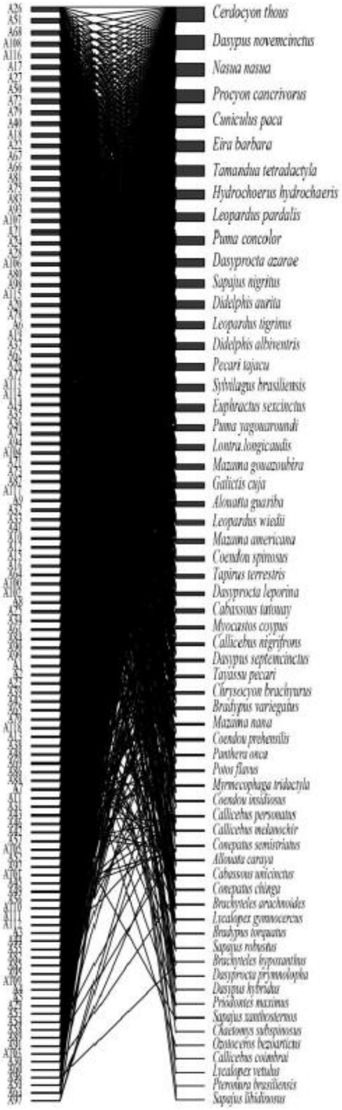
Supporting Information S3. Secondary data obtained in search engines of 118 communities (presence-absence) of medium- to large-bodied mammals along Atlantic Forest.



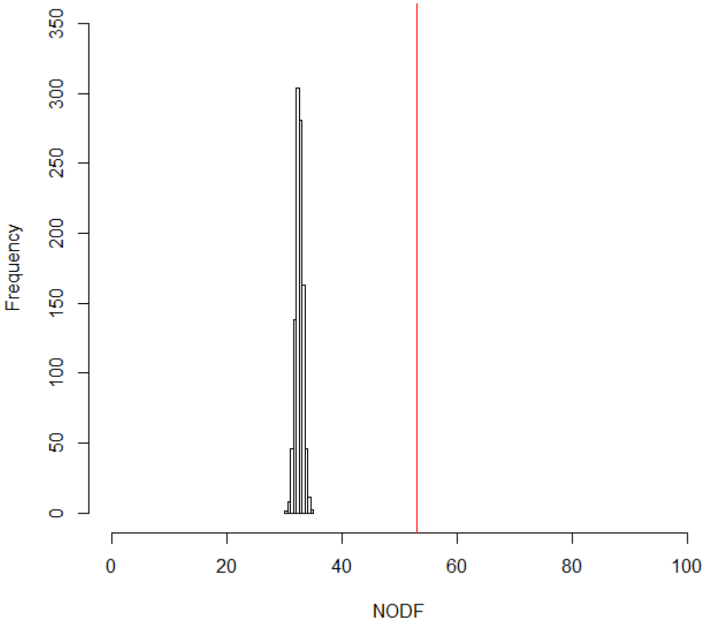
Mammals species presence

Research.Area.ID

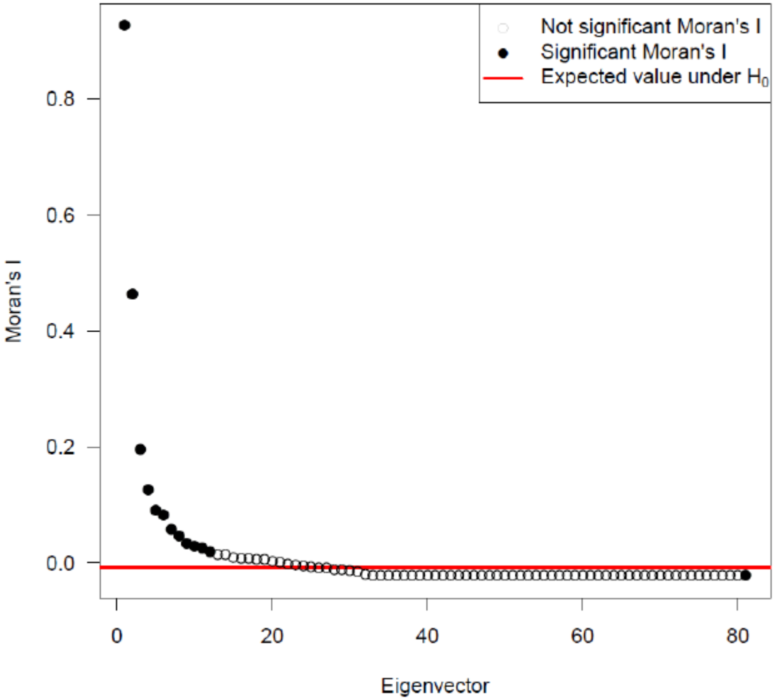
Supporting Information S4. Binary network bipartite by localities, organized by species degrees, of secondary data of mammals communities obtained in search engines along Atlantic Forest.



Supporting Information S5. Nestedness (NODF) real (red) of medium- to large-bodied mammals communities at entire Atlantic Forest vs. Nestedness (NODF) of 1000 null models (bars).



Supporting Information S6. Moran index and eigenvectors generated via principal coordinate analysis of neighborhood matrices (PCNM) to determine significant spatial components obtained from the truncated distance matrix among mammals communities along Atlantic Forest.



Supporting Information S7. Species presence probabilities at "Total Weighted metacommunity" approach.

Species	Calculed probability
Cerdocyon thous	0.065295816
Nasua nasua	0.055572185
Dasypus novemcinctus	0.054191953
Procyon cancrivorus	0.045917382
Tamandua tetradactyla	0.044346464
Cuniculus paca	0.044030001
Eira barbara	0.040398103
Sapajus nigritus	0.037910263
Didelphis aurita	0.031008604
Dasyprocta azarae	0.029679546
Hydrochoerus hydrochaeris	0.02951941
Pecari tajacu	0.029430791
Euphractus sexcinctus	0.029084961
Puma concolor	0.028725362
Leopardus pardalis	0.027457369
Alouatta guariba	0.024802138
Didelphis albiventris	0.023941677
Sylvilagus brasilienses	0.023247897
Leopardus tigrinus	0.019969305
Puma yagouaroundi	0.018893661
Callicebus nigrifrons	0.01830735
Mazama gouazoubira	0.017910476
Galictis cuja	0.017468731
Lontra longicaudis	0.017170093
Coendou spinosus	0.016132776
Leopardus wiedii	0.015902935
Myocastor coypus	0.015670979
Mazama americana	0.014563427
Tayassu pecari	0.013591421
Tapirus terrestris	0.013295318

Dasyprocta leporina	0.013099518
Cabassous tatouay	0.011734069
Dasypus septemcinctus	0.010778936
Bradypus variegatus	0.009713957
Coendou prehensilis	0.008064911
Callicebus personatus	0.00778949
Mazama nana	0.006974521
Chrysocyon brachyurus	0.005688213
Panthera onca	0.005390339
Callicebus melanochir	0.005319513
Myrmecophaga tridactyla	0.005193798
Cabassous unicinctus	0.005089997
Bradypus torquatus	0.00469502
Lycalopex gymnocercus	0.00460805
Conepatus semistriatus	0.004500721
Conepatus chinga	0.004165402
Brachyteles arachnoides	0.003780481
Potos flavus	0.003679633
Allouata caraya	0.003286021
Sapajus xanthosternos	0.002284923
Coendou insidiosus	0.002187959
Dasypus hibridus	0.001649103
Dasyprocta prymnolopha	0.001382365
Priodontes maximus	0.001109008
Sapajus robustus	0.001033129
Callicebus coimbrai	0.000835425
Brachyteles hypoxanthus	0.000825689
Ozotoceros berzoarticus	0.000471877
Sapajus libidinosus	0.000418025
Lycalopex vetulus	0.00041366
Pteronura brasiliensis	0.000246074
Chaetomys subspinosus	0.000153778

Supporting Information S8. Local metacommunities mammals (distance ≤ 14.4 km) metadata description. V: vegetation type; FS: fragment size; M: methods employed; S: mammals richness; FED: Deciduous (or semi) Seasonal Forest; FOD: Dense Ombrophilous Forest; CT: camera trap; AS: active search; ET: interviews; LI: literature; CZ: zoological collections data.

Metaco mmunity	Reference	Journal	ID	W	S	Locality	State	V	FS	M	S
Local1	Bogoni et al. 2013	ISRN Forestry	A3	-52.166	-27.028	Linha Salgado	SC	FED	55	CT, AS	7
			A4	-52.166	-27.039	Linha Três Marias			47		6
			A5	-52.175	-27.086	Linha Varanal			51		6
Local2	Hendges et al. 2015	Biotemas	A62	-52.111	-27.293	Parque Estadual Fritz Plaumann	SC	FED	476	CT, AS, ET	19
			A63	-52.154	-27.300	Parque Estadual Fritz Plaumann (Insular pluvial)			265		4
			A64	-52.133	-27.269	Parque Estadual Fritz Plaumann (Adjacent area)			700		14
Local3	Rossaneis 2014	Semina	A109	-51.207	-22.430	Horto Florestal UEL	PR	FED	10.5	AS	7
			A110	-51.258	-22.458	Sítio Santana			5.4		8
			A111	-51.292	-22.400	Parque Municipal Histórico			6		8
			A112	-51.308	-22.476	Sítio Casado			15		8
Local4	Cullen et al. 2001	Oryx	A29	-49.749	-22.473	Fazenda Tucano	SP	FED	2000	AS	6
	Giacomini and Galetti 2013	Biol Cons	A53	-49.708	-22.417	Reserva Caetetus			4600	AS	6
Local5	Fornitano et al. 2015	Oecol Australis	A45	-48.133	-21.160	ReBio Augusto Ruschi, Sertãozinho-F1	SP	FED	166.2	CT	8
			A46	-48.122	-21.156	ReBio Augusto Ruschi, Sertãozinho-F2			55.1		10
			A47	-48.081	-21.164	ReBio Augusto Ruschi, Sertãozinho-F3			189.2		10
			A48	-48.074	-21.150	ReBio Augusto Ruschi, Sertãozinho-F4			128.5		11
			A49	-48.050	-21.160	ReBio Augusto Ruschi, Sertãozinho-F5			163.8		8
Local6	Morcatty et al. 2013	Ecol Res	A78	-43.883	-20.000	SG	MG	FOD	148	CT, AS, ET	20
			A85	-43.917	-19.917	PMM			280		7
Local7	Morcatty et al. 2013	Ecol Res	A83	-43.533	-20.300	Caraça	MG	FOD	10187	CT, AS, ET	23
			A84	-43.517	-20.333	Peti			605		13
Local8	Gatti et al. 2014	Natureza on line	A50	-40.562	-19.906	ReBio Augusto Ruschi, Santa Teresa	ES	FOD	4000	AS, CT, LI	28
	Passamani et al. 2000	Bol Mus Biol Mello Leitão	A93	-40.533	-19.950	Estação Biológica Santa Lucia			440	AS, CT, LI, CZ	23
Local9	Giacomini and Galetti 2013	Biol Cons	A58	-40.142	-19.425	M7	ES	FOD	460	AS	6
			A59	-40.167	-19.425	Putiri			490		4
Local10	Percequillo et al. 2007	Bio Geral Exper	A96	-34.845	-7.138	Jardim Botânico Benjamim Maranhão	PB	FOD	515	CZ	5
			A97	-34.843	-7.141	Campus UFP			34.5	CZ	4

CAPÍTULO 2

The ecological footprint of *Acca sellowiana* domestication maintain the residual vertebrate diversity in threatened highlands of Atlantic Forest

(A domesticação da *Acca sellowiana* mantém a diversidade residual de vertebrados em terras altas ameaçadas da Mata Atlântica)

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Eira barbara (Linnaeus, 1758) [irara] registrada removendo frutos de *Acca sellowiana* em 22 de março de 2015 na Reserva Particular do Patrimônio Natural Leão da Montanha, Urubici, Santa Catarina, Brasil (28°00’12” S; 49°22’23” O; 1.035 m.a.s.l.). Foto: Bogoni 2015.

The ecological footprint of *Acca sellowiana* domestication maintain the residual vertebrate diversity in threatened highlands of Atlantic Forest

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Abstract

Past and contemporary human actions are causing numerous changes in patterns and processes at various ecosystem scales and trophic levels, including unintended downstream changes, such as species interactions. In its native range *Acca sellowiana* (Feijoa) combines some characteristics of human interactions: incipient domestication, restricted to subtropical Atlantic Forest highlands, associated with the threatened conifer *Araucaria angustifolia* (Araucaria), within a domesticated landscape with anthropogenic forest patches, and provides fruit at a time of resource shortage (Araucaria seeds - *pinhão*). We quantify the trophic relationships between Feijoa and vertebrates, and evaluate the influences on interactions caused by environmental variations, Feijoa domestication evidences, spatial distance and fruit availability. In four sites within protected areas, we selected 28 focal individuals of Feijoa (seven/site) and collected three temporal replicas between 2015 and 2016, when we measured productivity and frugivory via 45-second videos taken with camera traps. Using ecological network, rarefaction curves and variation partitioning analyses, we evaluate the frugivory network topology, the spatiotemporal structure of communities in relation to fruit availability and the influence of predictive variables on frugivory. We found a large spatiotemporal variation in productivity of Feijoa and that 20 species consumed Feijoa fruits, with a species degree of 2.8 (±5.7) and average Feijoa degree of 14.4 (±10.1), in a modular network with intermediary connectance. Rarefaction curves showed that richness and the independent records are congruent with the fruit amount. Variation partitioning showed that, for the focal individuals, canopy area, green coverage, patch size and distance to water influenced frugivory, and the Feijoa domestication influenced significantly the mammalian frugivory. Feijoa is an important resource that provides food during the time of year when *Pinhão* is absent, and attracts frugivores; maintain the residual diversity of vertebrates contributing to the structure of communities in highlands. Our insights allowed us to evaluate the magnitude of the interactions between vertebrates and an incipient domesticated tree, in a cultural landscape and highly threatened environment, under a basal foodweb approach with implications for bottom-up and top-down forces. The results contribute to understanding animal-plant relationships, including concepts that can be replicated for other sessile prey and mobile predators in any region or habitat under different gradients of

management. Thus, this work shows how human actions can change not only patterns of distribution and abundance but also the diversity and direction of interspecific interactions among species.

Introduction

Ecological systems are complex, dynamic, self-organized, with emergent properties, and feedbacks [1]. In addition, past changes and the persistent feedbacks generated by human ecosystem engineers in coconstructed landscapes with nature have important implications for current diversity patterns and ecological processes [2-3]. Yet, contemporaneous disruptions can promote numerous changes and move ecosystems from one stable state to another stable alternative: a process known as phase shifts [4]. One of these disorders is “Anthropocene Defaunation”: a process of extinction caused by human impacts [5-6]. The main human-driven causes of defaunation and compositional changes are habitat loss, fragmentation, hunting and forest conversion [7-8]. Compositional changes and selective species loss in communities can produce strong side-effect impacts on ecosystem function, promoting cascade effects at several scales [9]. These effects include evolutionary changes (e.g., decreasing seed size) and affect population dynamics and community structure (e.g., changes in the detritivore foodweb, seed dispersal and trophic webs, and rearrangements of top-down and bottom-up forces) [9-11].

The top-down model of community regulation predicts that organisms can be limiting resources, both as predator or prey, depending on their position in the food web [12]. The effectiveness of top-down vs. bottom-up forces in the chain depends in part, on how many efficient consumers exploit their prey [12]. The chain dynamic models of food webs are often unpredictable because different assumptions about mechanisms (e.g. co-limitation by predators and resources) lead to different predictions (e.g., consumer efficiency at a multi-trophic level) [13]. Among various processes that fit these premises, frugivory is an ideal candidate for these ecological and evolutionary analyses [14-16]. Patterns and processes of predation/dispersal of seeds are highly structured and coevolved spatiotemporally [14], with potential alterations promoted both by past human drivers [2] and current disturbances [9]. Plant-animal interactions within a community should consider the energy used at the individual level [14, 17].

Mammals and birds disperse about 90% of the woody plant species that produce fruits in Neotropical environments, generating an important feedback to plant fitness and forest regeneration [15, 18]. In the Atlantic Forest of South America, the family Myrtaceae is an important group of woody species and resource provider for a range of vertebrate taxa [19-20]. Myrtaceae species are the main components of lower altitude rainforests, where there can be over 50 species in a relatively small space [~1 ha] [21-22]. In subtropical Atlantic Forest, Myrtaceae in general are closely associated with the threatened conifer *Araucaria angustifolia* (Araucaria), which form Ombrophilous Mixed Forest (FOM) [23]. Forests dominated by Araucarias have been used as a proxy for conservation strategies [24]. Within FOM there is a vegetation mosaic of highlands (e.g., upper montane forest, swamps, and native grassland) that is spatially restricted and highly endangered mainly due to climate change [24-26]. In interspersed forest patches in this mosaic, Araucarias dominate the upper stratum, while Myrtaceae and Lauraceae are the main families that form the middle and lower strata [27-28].

A few Myrtaceae species dominate the flora in highlands, which are usually characterized by small fruits (< 1 cm of diameter) [29-30]. An exception to this is *Acca sellowiana* [Berg] Burret (Feijoa). Feijoa is a tree native to Southern Brazil and northern Uruguay that is restricted to areas in Southern Brazil over 800 meters above sea level (m.a.s.l.) associated with FOM [23, 31]. Feijoa is pollinated by birds and bees [32-33], and produces large fruits (20 to 250 g) with small seeds (~3 mm) [29]. Like Araucaria in local landscapes, Feijoa has been subjected to historical anthropogenic influence promoting a certain level of domestication of some populations *in situ*, which has resulted in increased fruit size and productivity by human selection [23, 34-36]. Nowadays, within FOM, Feijoa is used in several ways (circa 14) by local people that manage the species via pruning, transplanting, propagation by seeds and vegetative propagation [23]. Its domestication is incipient [23], a process that exhibits phenotypic variation within the range normally found in wild populations [37, 109, 110]. Moreover, the expansion of FOM by pre-Columbian people (i.e., indigenous Xokleng and Kaingang) favored the expansion of Feijoa and other associated Myrtaceae [23, 35]. In addition, the past and contemporaneous management of Feijoa and Araucaria increased the availability of resources in FOM [23, 35].

Plant and animal domestication is the most important development of human history since 13,000 years ago, and changed the course of humanity [38]. Since Darwin (1859), domesticated systems have played a critical role in the development and testing of evolutionary theory [39]. Management of native fruits *in situ*, both by indigenous populations and by local farmers, is a recognized conservation practice that contributes to genetic diversity and several ecological processes through downstream propagation within biological networks [40-43]. Another outstanding characteristic of local landscape domestication – human intervention in the landscape components resulting in changes in evolution, ecology, interactions and species demography [3, 37] – is the presence of *Bos taurus* (cattle) and its impacts [36]. Cattle is an allochthone element that has been managed for a long time (> 100 years) by local small-scale landowners in highlands of subtropical Atlantic Forest [36]. Understanding the complex ecological legacy of management in past landscapes and their use components is important when debates are raging about the future of forests in relation to new human colonization dynamics, climate change, contemporaneous political conflict and defaunation [2, 44].

Currently, primary dispersion of Feijoa is barochoric [45], because the distribution region of Feijoa overlap areas under a constant defaunation of large-bodied vertebrates [8], remaining only a residual diversity reduced to a pale shadow of the once amazing biota of the Atlantic Forest. Yet, Feijoa still has a *posthoc* association with frugivores [29]. The functional loss of large fruit-eating vertebrates can decrease Feijoa fitness near conspecific adults [16, 46], disrupts the natural regeneration dynamics of plants, and changes the main components of the dispersal process [16, 47]. There is little empirical information on the interaction of Feijoa with its associated fauna, although there may be many species that feed on its fruits, as found for other Myrtaceae species, resulting in feedback that helps maintain ecosystem processes [13].

Therefore, as a temporary alternative during the austral summer-autumn with scarce resources (mainly the absence of *pinhão*), Feijoa can act as an attractor, contributing to the structure of animal communities and can maintain the residual diversity of vertebrates in Southern Brazil highlands. The aim of this study was to provide a scenario of the trophic relations between Feijoa (a species under incipient domestication and an alternative resource in threatened highlands) and local wildlife (which has experienced defaunation effects in a landscape influenced by historical management), to evaluate the space-time congruence between diversity patterns and resource productivity.

Additionally, we aimed to evaluate the influence of the environment, the spatial distance among sites, the Feijoa domestication evidence, and the resource offer on the intensity of frugivory. We posed three hypotheses: (1) mammals and birds that remove fruits of *Acca sellowiana* – assuming *a priori* defaunated sites – are small- to medium-bodied frugivores-herbivore-omnivores and the cattle; (2) the seasonal Feijoa fruit structures the vertebrate fauna in space and time, increasing the diversity patterns in congruence with fruit offer. The productivity is linked with the incipient domestication process, and the positive effect of fruit offer include species that do not eat fruits, an implication of bottom-up control with historical influences; and (3) the number of interactions are related to environmental patterns, spatial distances, Feijoa domestication evidence and resource productivity. Both this factors directly or indirectly reflects local landscape domestication as a whole.

Material and Methods

Ethics Statement

Data collection was authorized based on license number 47255 from Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). Within private land (Reserva Particular do Patrimônio Natural [RPPNs]) we confirm that the owner of the land gave permission to conduct the study on this site. We confirm that the field studies did not involve manipulation of endangered or protected species, only species records via camera-trap. Vertebrate records were performed with non-invasive sampling (i.e. camera-trap). The work was not submitted to an Institutional Animal Care and Use Committee (IACUC) or equivalent animal ethics committee, because the data were collected only with camera-trap. Sampling procedures and/or experimental manipulations were reviewed or specifically approved as part of obtaining the field permit by the license number 47255 from Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

Research areas and design

We selected four sites in protected areas of subtropical Atlantic Forest highlands, in southern Brazil: within São Joaquim National Park (S1 and S2), surroundings of Reserva Particular do Patrimônio Natural (RPPN) Grande Floresta das Araucárias (S3), and within RPPN Leão da Montanha (S4) (Fig 1; S1 Table). All areas fall within the humid subtropics (Cfa: Köppen-Geiger classification, [48]), and are unequal in age and terms of protection, but share similarities in management and historical exploitation [36, 49]. Sites lie within a radius of circa 40 km and – based on previous studies and unpublished data – has a similar composition and richness of fauna, including defaunation indexes, and presumably a similar biota at pre-Columbian era [6; Bogoni et al. unpublished data]. The areas feature elements of cultural landscapes, which include anthropogenic forests with different intensities of past and present use [35-36] and regeneration stages, formed by Araucaria Forest (FOM), cloud forest, and native grassland [50]. These areas represent a mosaic of forest patches and high-altitude grassland composed by old rural proprieties destined to cattle breeding, logging and *Pinhão* extraction. These old proprieties were abandoned for more than 10 years, and are characterized for the presence of rock structures to retain the cattle (*taipas*), the foundation of old-houses (*taperas*), and other structures linked to past livestock activities. An exception is in S3 that remain with intensive livestock activity. Moreover, in the sites S1, S2 and S4 have the presence of Feijoa trees typically maintained with management (e.g. traces of pruning, producing largest fruits and located near to old proprieties foundations [23, 37]). These changes in species traits starting from wild ancestors (e.g. changes on the morphology of aerial vegetative parts and selection of fruits size and quality) are classical syndromes of domestication in food crops [112].

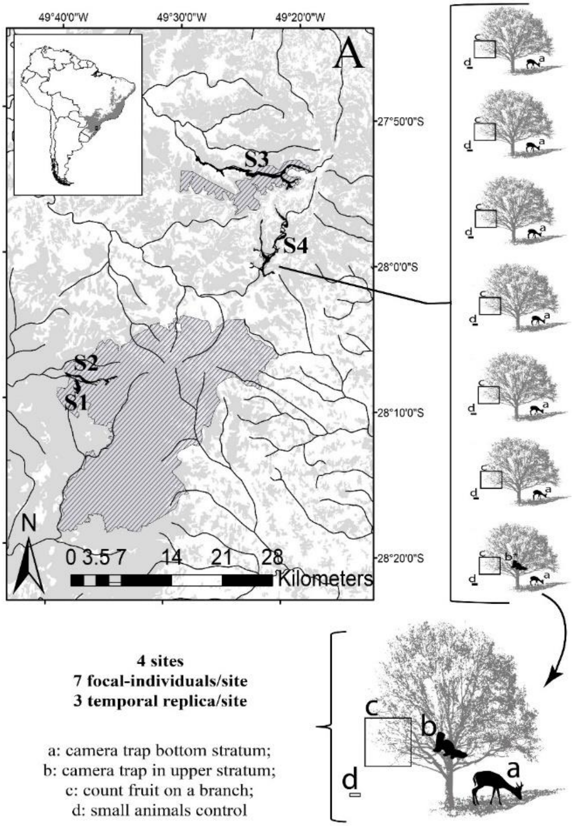

Fig 1. Research areas (political size dotted), sites and sample design to evaluate the removal of *Acca sellowiana* fruit by vertebrate fauna (mammals and birds) in highlands of subtropical Atlantic Forest, Brazil. In black: polygon of the site (based on lowland area or fragment size); in gray: the remnant of Atlantic Forest in years 2008-2010; lines in black: rivers. S1 and S2: São Joaquim National Park; S3: surrounding of RPPN Grande Floresta das Araucárias; and S4: RPPN Leão da Montanha.

At each site, due to the supply of equipment, we chose seven focal individuals of Feijoa based on fruit presence and, as a secondary factor, the distance among them larger than 300 m. For each focal individual, we recorded the fauna in the lower stratum (~30 cm from the ground) using a camera trap (*Bushnell* ®: Trophy Cam HD, Model: 119537c, Bushnell Outdoor Products Canada, Ontario, Canada), including three temporal replicas during 2015–2016 (autumn in the beginning of 2015 [TR1], middle of spring of 2015 [without fruits] [TR2] and autumn in the beginning of 2016 [TR3]). For the focal individuals 1, 4 and 7 of each site, we installed camera traps at ≥ 1.7 m high (upper stratum) and attached five fruits on each tree with nails. Since is technically impossible attach fruit in locations that they would occur naturally (e.g. tips of branches), Feijoa fruits were attached in a trunk capable of receiving the small nails (12 x 12 mm) and that it was possible to install the camera trap immediately ahead of these attached fruits. Due to the number of available camera traps, in TR2 and TR3 we only used one camera trap in the upper stratum that was installed on focal individual one. This reduction in camera traps within upper stratum was chosen because according to the TR1 the main frugivory activity was performed on lower stratum. Thus, we can keep the equal number of focal individual (seven) in each temporal replica.

We left the camera traps active in each site for at least 30 days or for 60 days in sites where available fruits exceeded 30 days; in these cases, after 30 days we inspected the equipment. Thus, a total of 40 (or 32) camera traps were used, programmed to record footage for 45 seconds, with an interval of 45 seconds between recordings, totaling 4,470 traps/day (Fig 1). In both strata and temporal replica, we analyzed the independence of interactions according to fruits consumed, with sequential videos of the same species, where consuming the same fruit was considered a single interaction record. We established the spectrum of fruit removal by the following criteria: (1) sinzoochory, the quantity of whole fruits taken and transported away from the location; and (2) endozoochory, fruits consumed locally [45]. Additionally, we counted fruit removal by small animals at each focal individual in TR1, using 3-inch pipes stuck to the ground, which contained 5 Feijoa fruits (prohibiting the access of medium to large animals) (Fig 1).

Resource availability, environmental and spatial data

For each temporal replica with fruits (TR1 and TR3), at the time of camera trap installation (t0), we counted the number of fruits available on the ground below the canopy of the focal individual. We estimated the productivity of every tree by the number fruits on the main branch (or entire tree when possible) multiplied by the number of equal-sized branches on the focal individual (modified from Clark et al. 2005 [51]). At intervals of 30 days (t1) and 60 days (t2), we returned to count the amount of fruit on the tree and quantified fruit availability during camera trapping. In t0, t1 and t2, we weighed five fruits from each individual with a manual precision balance, and calculated the biomass for each time. Furthermore, in TR1 we: (1) calculated the fruit decomposition time using 20 fruits chosen randomly at a single moment, left under conditions similar to the sites; and (2) counted the number of seeds in 15 fruits.

In the first year of the study, we recorded the focal-individual canopy area and the distance of the focal individual to the closest Feijoa adult (with reproductive signals or circumference at breast height [CBH] ≥ 15 cm [52]). To characterize the site habitats, we measured environmental features using an adapted point quadrant (S2 Fig.) method [53]. For each focal individual, we measured the canopy cover percentage (from photographs taken 1.5 m above the ground, at four points [N, S, E and W] five meters from each individual), diameter, height and distance to the nearest tree and shrub. We also estimated the percentage of ground cover (litterfall and herbaceous green cover within 1 m² delimited on the ground), slope, orientation, intensity of use of the area by livestock (ordinal: 0 [absence] to 4 [high]) and actual human presence (binary: 0 [low] and 1 [moderate]).

We also noted the presence of evidences of management in the focal individuals of Feijoa (e.g. traces of pruning, tree and fruit size, fruit variety [e.g. thin bark, more appreciated for local people consumes] and proximity of places with past human activities), that can indicate the continuity of domestication process [23, 37, 112] (S2 Fig). We supported this aforementioned information with semi-structured questionaries' applied to local people (Bogoni et al. unpublished data). Thus, we obtained a proportion of domesticated Feijoas within sites based on qualitative data. For this, we considered presence Feijoas with management evidence (domesticated Feijoas) and absent for individuals of Feijoa ("under-domesticated" Feijoas) with inconspicuous domestication evidences, although it may present at a lower level [e.g. molecular]) [37, 112].

Moreover, we delimited one plot of 1,600 m² in each site to determine the demographic characteristics (account of adults) of Feijoa within the sites (c). We measured landscape characteristics of the sites and the distance between focal individuals and sites through georeferenced data. Using GPS, satellite images and QGis software [54], we measured the linear distance from the focal individual to the closest water course, to the nearest open area and to the nearest fragment of native forest [55]. Additionally, we obtained the size (as a polygon) of the forest fragment or lowland (i.e., *várzea* or flat areas of river banks, an environment where Feijoa often occurs) based on *in situ* personal observations and Santos et al. (2009) [23].

Data analysis

We performed a principal component analysis (PCA) of correlation to evaluate the ordination sampling sites acrossenvironmental and landscape parameters, including the proportion of managed Feijoa trees within sites [56-57]. Descriptively, we explored the spatial distance, demography, and fruit productivity of Feijoas per site and temporal replicates (TR1 and TR3), using central tendency and variation measures. We analyzed the structure of the communities using diversity descriptors (i.e., species richness and rarefaction curves with confidence intervals of 95% for each replica) [58-59]. For each site, we only used independent video recordings, excluding records of the same species at the same focal individual for time intervals shorter than 1 hour [60], adjusted by site sampling effort, and assuming spatial dependence among focal individuals for mammals and birds.

We analyze the topology of weighted two-mode frugivory networks per site for each temporal replicate and per focal individual [61-62], in which a set of nodes representing frugivore species is connected to another set of nodes representing sampling sites or focal individual where they were recorded consuming Feijoa fruits. We calculed one quantitative metric: (a) modularity, and three qualitative (binary) metrics: (b) average degree (c) connectance and (d) nestedness [63-64]. Degree is the number of interactions each node has. Modularity (M) quantifies the tendency of the nodes to cluster into cohesive groups that are more connected among themselves than with the rest of the network [63]. Connectance is the proportion of realized links, which is the ratio between the number of interactions observed in relation to the possible interactions [64]. Nestedness (N) measures the degree by which the nested network, showing a possible hierarchical pattern [65]. In case of nestedness, one or more sites can be a subset of other sites with largest species richness or largest interaction number. For modularity, we used Newman's metric [61] and compared its empirical value with a benchmark distribution of modularity values calculated to an ensemble of 1000 theoretical matrices created by a null model, in which species degree ranges between zero and the mean of the degree of the real network. Significance ($p \leq 0.05$) was based on the ratio at which larger or equal to the observed M value occurred in the null model [66]. For nestedness, we used the NODF metric [65]. NODF ranges from zero, when the matrix is perfectly non-nested, to 100, when the matrix is perfectly nested [67]. We also compared the NODF value of empirical network with a benchmark distribution generated by 1000 theoretical matrices generated by a null based on a probability matrix (null model 2 of Bascompte et al. 2003 [66]) and adopting the same aforementioned criterion for M significance [66]. Additionally, to show resource sharing graphically, we build the network with the deconstructed interactions per temporal replica in: (1) disperser groups (mammals and birds); (2) dispersal syndromes (endozoochory and sinzoochory); (3) vertical strata (upper and lower); (4) time (t0 to t1 and t1 to t2); and (5) circadian condition (day and night).

We performed a variation partitioning analysis to assess the environmental (including Feijoa domestication evidence), spatial distanceand productivity variation effects on interactions [56-57] at the focal individual scale, considering the two groups (native mammals and birds) separated. However, *a priori*, we conducted a principal component analysis of neighboring arrays (PCNM) to determine significant spatial components obtained by the array of distance between focal individuals. The PCNMs represent the spatial relationship between sampling sites and can be used as predictors of variation. Only positive PCNMs were selected according to spatial autocorrelation obtained by Moran's index [56-57].

To partition the variation, we used the forward selection method (to reduce the likelihood of a type I error; [68]) to select a subset of significant predictor variables based on the non-multicollinear data (tested *a priori* via the variance inflation factors; [69]). Variation partitioning performs RDAs for all predictors, and individually for each set of predictors, removing effects of other predictors (e.g., RDA for the environment removes effects of spatial distance). The proportions explained by predictors were represented by Ezekiel-adjusted R^2 [70]. For the variation partitioning, we corrected the asymmetry in the interaction number using Hellinger transformation. The asymmetry of the environment and landscape features (numerical magnitudes) was transformed by standardization, and the resource availability (total biomass) was logarithmized [57]. We based the significance of variation partitioning tests ($p \leq 0.05$) on 999 permutations. For other analyses, used the original, untransformed datasets. We performed all analyses in R [71] with the sna [72], bipartite [73], vegan [74] and Packfor [75] packages.

Results

Environment, spatial distances and demographic features

Environment and landscape features, analyzed via PCA, explained 85.4% of total data variation among sites, with 52.7% of the explanation related to axis one (linked mainly to slope and lowland/fragment size) and 32.7% of explanation related to axis two (linked to tree height and distance to nearest fragment). The sites are distinct in the following aspects: S1 is the furthest from a watercourse (340 m); S2 has higher adult density (each one by 5.5 m apart); S3, besides the intense presence of cattle, is characterized by the greater area (697 ha) of "*várzea*"; and S4 is the furthest from an open area (105 m) (S3 Fig.). Although not the main factor in the ordination analysis, at different intensities or replications, there was a real or virtual presence of cattle in all sites. The average distance between sites is 23.7 km (±11.3; 1.6 to 34.3 km). The distance among focal individuals is 261.5 m (±182.4; 11.3 to 496.5 m) in S1, 446.7 m (±320.9; 11.2 to 1000 m) in S2, 346.4 m (±246.7; 7.7 to 716 m) in S3, and 584.9 m (±356.4; 88 to 1167 m) in S4. Considering all sites, and based on the distance among Feijoa trees and demographic plots, there is an average of 48.8 (±39.8) Feijoa adults per hectare. The proportion of Feijoa trees (focal individuals) with clear evidence of past management (i.e. domestication) was 85.7% (6 in 7) in S1, 57% (4 in 7) in S2 and S4 and 0% in S3 (Table 1).

Productivity and interactions

Spatially, the productivity among sites varied from dozens to more than 2,500 fruits (average 746.9; SD ±838.1; totaling 5,975 fruits), and the biomass was also highly variable (3.03 ±5.98 kg per individual; 28.6 ±40.2 per site) (S4 Fig.). These values, extrapolated for the density of adults per hectare, maintained high spatial variation (4,120.9 ±3782.4

fruits/ha^{-1} and 153.8 ±162.8 kg/ha^{-1}) with major productivity in S1 and S4. Temporally, we also found high variation in the number of fruits and biomass, with a 67.6% decrease in fruit availability between TR3 with TR1 (Table 1). The fruits rotted in nine (±2.4) days and the average number of seeds per fruit was 61.9 (±36.4).

Table 1. Density, domestication evidence, and productivity of *Acca sellowiana* at four sites and two temporal replicas with fruits in subtropical Atlantic Forest highlands, Brazil. S1 and S2: São Joaquim National Park; S3: surrounding of RPPN Grande Floresta das Araucárias; and S4: RPPN Leão da Montanha; A: adults.

Replica		**Density**	**Domestication evidence**	**Fruits**		**Biomass**		
Spatial	**Temporal**	**Ind/ha (A)**	**N in 7 focal individuals (%)**	**N total/Site (±SD)**	**N total/ha (±SD)**	**Average (g/fruit [±SD])**	**Kg/Site**	**Kg/ha**
S1	TR1	-		2,661	14,255.3	46.2 (16.5)	123.7	662.7
	TR3	-		924	4,950	24.2 (12.1)	22.4	120.0
	Mean	**37.5**	**6/7 (85.7%)**	**1,792.5 (1,228.2)**	**9,602.7 (6,580)**	**35.2 (15.6)**	**73.1 (71.3)**	**391.4 (383)**
S2	TR1	-		844	1,700.1	30.6 (7.9)	25.8	52.0
	TR3	-		72	145.1	27.4 (15.1)	1.9	3.8
	Mean	**14.1**	**4/7 (57%)**	**458 (545.9)**	**922.6 (1,100)**	**29.0 (2.3)**	**13.9 (16.9)**	**27.9 (34)**
S3	TR1	-		313	4,753.2	28.1 (14.4)	8.8	133.6
	TR3	-		96	1,457.8	12.8 (6.2)	1.2	18.2
	Mean	**106.3**	**0/7 (0%)**	**204.5 (153.4)**	**3,105.5 (2,330)**	**20.5 (10.8)**	**5.0 (5.4)**	**75.9 (82)**
S4	TR1	-		696	3728.6	39.8 (15.8)	34.8	186.4
	TR3	-		369	1976.8	27.2 (11.9)	10.0	53.6
	Mean	**37.5**	**4/7 (57%)**	**532.5 (231.2)**	**2,852.7 (1,239)**	**33.5 (9.0)**	**22.4 (17.5)**	**120.0 (94)**
Average		**48.8 (39.8)**	**50 (36)**	**746.9 (838.1)**	**4,120.9 (3,782.4)**	**29.6 (10.0)**	**28.6 (40.2)**	**153.8 (162.8)**

Camera traps recorded a total of 1,948 videos (1,461 minutes), including 470 independent interactions and 1,141 independent records according to both our criteria, with 37 native species recorded when considering Cricetidae as a unique species (S5 Table). Rarefaction curves considering all the native species recorded (independently of interaction with Feijoa) showed there was a significant temporal difference in species richness, i.e., between presence (TR1 and TR3) and absence (TR2) of the resource when comparing a minimum of independent records (S1: 72; disregarding S3 due low richness). However, among sites, there was no significant difference in richness, with confidence intervals overlapping, except for S3 (Fig 2A). This pattern was maintained when the temporal replicas were separate (Fig 2B; S6 Fig.).

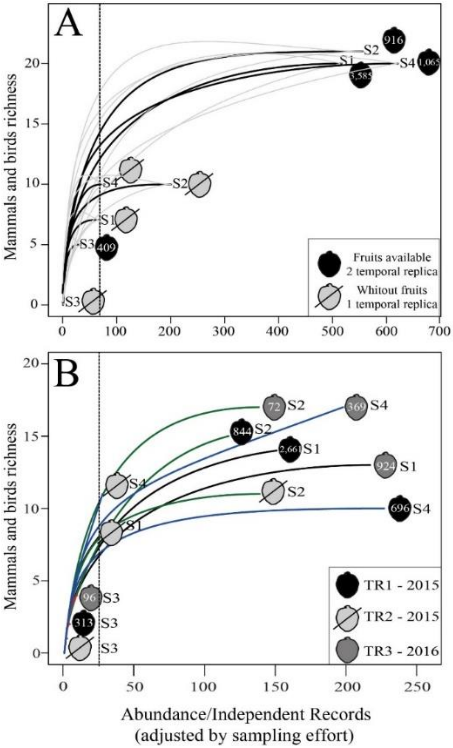

Fig 2. (A) Rarefaction curve (with a confidence interval of 95% in gray) for all independent records (considering two replicas with fruit

and one without fruits) of mammal and bird species (except exotic) during evaluation of fruit removal from *Acca sellowiana* in four sites in subtropical Atlantic Forest highlands, Brazil; (B) Rarefaction by spatial and temporal replicas for all independent records of mammals and birds species (except exotic species) during evaluation of fruit removal from *Acca sellowiana* in four sites in subtropical Atlantic Forest highlands, Brazil. Independent records were adjusted by sampling effort (camera-trap/day/replica). S1 and S2: São Joaquim National Park; S3: surrounding of RPPN Grande Floresta das Araucárias; and S4: RPPN Leão da Montanha.

During the two years of sampling, 20 species (including cattle and Cricetidae: S7 Fig. and S8 Movie File) interacted with Feijoa, with an average sites degree of 14.41 (±10.1), a Feijoa fruit removal of 9.6% representing 572 fruits removed and more than 35,400 seeds. Among sites, when both temporal replicas were combined the removal proportion were 3.35% for S1, 27.84% for S2, 13.70% for S3 and 12.77% for S4. In TR1, the average removal was 14.39% (3.2% to 28.1% among sites, with the same pattern as the total average) made by 19 species: 2.83% by 10 native mammals (including Cricetidae), 7.28% by eight native birds, and 4.29% by cattle. In TR3, the average removal was 13.41% (3.57 to 25.0% among sites) made by 13 species: 7.80% by eight native mammals, 2.75% by four native birds and 2.86% by cattle (Fig 3). Among native mammals, Cricetidae (species degree of 6.09), *Eira barbara* (1.91), *Cerdocyon thous* (1.88), *Nasua nasua* (1.66) and *Didelphis aurita* (1.05) are the main species that remove fruits. *Aramides saracura* (22.76), *Penelope obscura* (2.05), *Pyrrhura frontalis* (1.50), *Turdus rufiventris* (0.78) and *Cyanocorax caeruleus* (0.77) are the main bird species that remove fruits (Fig 3; S9 Fig.).

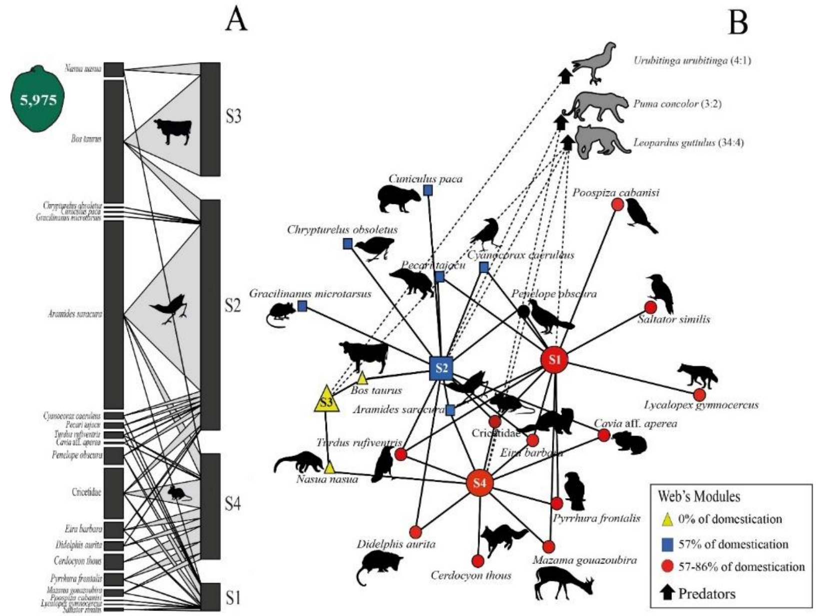

Fig 3. Topology of the total network by the site for years 2015 and 2016 to evaluate the removal of *Acca sellowiana* fruit by vertebrate fauna (mammals and birds) in the subtropical Atlantic Forest highlands, Brazil. (A) Two-mode network (bipartite) network considering two years of research; and (B) Two-mode network showing the modularity of different groups. S1 and S2: São Joaquim National Park; S3: surrounding of RPPN Grande Floresta das Araucárias; and S4: RPPN Leão da Montanha. Figure in high resolution, for details, apply zoom. In (A) the left column and their thickness represents the species that performed frugivory and the frugivory intensity (species degree); the right column represent and their thickness represents the sites and the intensity of frugivory in each one; transverse lines represents the links between species and sites. In (B) each minor point represents the species and larger points represents the sites; the lines linking the nodes (species and sites) represents the interaction among them; dotted links represent the presence of each predator in each site.

Total connectance of the network was high, with 0.46 for two years, 0.41 for TR1 and 0.38 for TR3. Total modularity of the network was statistically higher thannull expectancy [$M^{Total}_{obs} = 0.42$; $M^{Total}_{null} = 0.14$; $p < 0.01$] and identified three different modules containing S1 and S4, S2 alone, and S3 alone (Fig 3). In TR1, modularity [$M^{TR1}_{obs} = 0.36$; $M^{TR1}_{null} = 0.14$; $p < 0.01$] identified two modules, and in TR3 each site was identified as one module and the modularity was significantly higher than null expectancy [$M^{TR3}_{obs} = 0.45$; $M^{TR3}_{null} = 0.16$; $p < 0.01$]. The total spatial nestedness was intermediary and did not differ from the null expectancy ($N^{Total}_{obs} = 51.4$; $N^{Total}_{null} = 47.3$; $p = 0.19$), as in TR1 and TR3 ($N^{TR1}_{obs} = 46.7$; $N^{TR1}_{null} = 40.6$; $p = 0.08$; $N^{TR3}_{obs} = 35.7$; $N^{TR3}_{null} = 39.0$; $p = 0.26$). The network, in all sites and temporal replicas, showed higher variations in removal types, vertical stratum, fruit duration and circadian period (S10 Fig.). The removal of small animals (including invertebrates) using three-inch control pipes was 31.56%. Additionally, we made 49 independent records of medium- to large-bodied carnivores (*Puma concolor, Leopardus guttulus, Leopardus wiedii, Parabuteo leucorrhous* and *Urubitinga urubitinga*), 79.6% (39) of each during replicas with fruits (TR1 and TR3) (Fig 3).

Network analysis per focal individual jointing all temporal replica with Feijoa fruit presence sowed a focal individual degree of 16.6 (±21.8). Considering Feijoas with signals of domestication the focal individual degree was 10.8 (±19), while Feijoas without domestication evidence ("under-domesticated") was a degree of 22.6 (±23.6). Whereas Feijoas domesticated that, has interaction with vertebrates summed 4,607 fruits produced (329.1 [±292.3] fruits per tree representing circa four times more than "under-domesticated" Feijoas) and the frugivory was ~45% larger than in "under-domesticated" Feijoas. Moreover, among the Feijoas domesticated 16 species (mammals and birds) performed frugivory, representing four more species than in "under-domesticated" Feijoas (Fig 4). In this condition, the network connectance was 0.15, the modularity and nestedness of were statistically higher than null expectancy [$M^{Focal\_ind}_{obs} = 0.12$; $M^{Focal\_ind}_{null} = 0.07$; $p < 0.01$; and $N^{Focal\_ind}_{obs} = 27.8$; $N^{Focal\_ind}_{null} = 20.9$; $p < 0.01$]. The main species that performed frugivory at focal individual scale were the same observed when the data was jointed at site scale (e.g. *Aramides saracura*, *Bos taurus,* Cricetidae, *Cerdocyon thous, Eira barbara*, *Penelope obscura* and *Didelphis aurita*) (Fig 4).

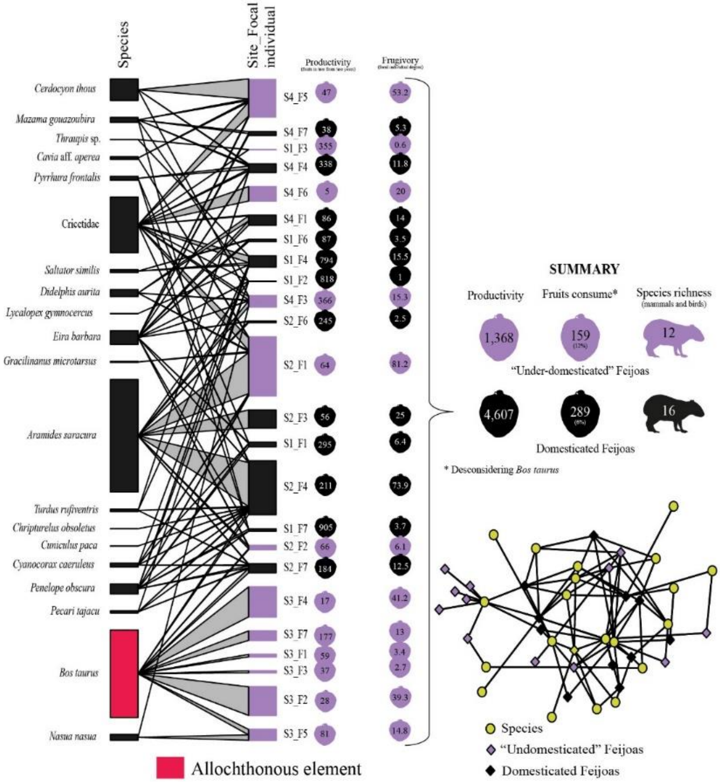

Fig 4. Topology of the total network by focal individual (Feijoas trees) for years 2015 and 2016 to evaluate the removal of *Acca sellowiana* fruit by vertebrate fauna (mammals and birds) in the subtropical Atlantic Forest highlands, Brazil. Bipartite network considering two years of research. S1 and S2: São Joaquim National Park; S3: surrounding of RPPN Grande Floresta das Araucárias; and S4: RPPN Leão da Montanha. Figure in high resolution, for details, apply zoom. The graphic representation is the same contained in the Figure 3(A).

Trends in influence of environment, spatial distance, temporal replicas and resource availability on frugivory

Numerically, the mammal and bird interactions for different focal individuals in each site are influenced only by habitat structure, represented by canopy area, percentage of herbaceous coverage, fragment/lowland area and distance to water body/drain trench (only for birds). Thus, the variation partitioning analysis for all interactions over two years showed that the habitat explained 27% [$r^2adj = 0.27$; $F = 4.39$; $p < 0.01$] of the interaction variation of mammals and 23% [$r^2adj = 0.23$; $F = 3.08$; $p < 0.01$] of the interactions of birds with Feijoa fruits (Fig 4). Moreover, the proportion of domesticated trees within the sites were responsible for the 6% of variation of interaction between Feijoa fruits and mammals [$r^2adj = 0.06$; $F = 2.96$; $p = 0.03$]. For birds, an additional explanation (8%) was attributed to the combination of environment and distance among focal individual [$r^2adj = 0.08$; $F = 3.01$; $p = 0.02$] (Fig 5).

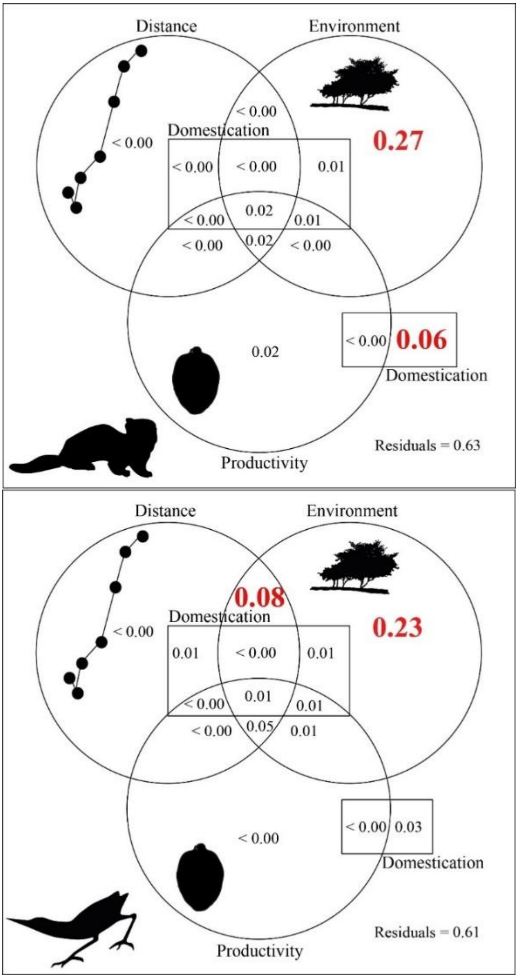

Fig 5. Variation partitioning by focal individuals of *Acca sellowiana* and their interaction with vertebrate fauna (mammals [above] and birds [below]) in four sites in subtropical Atlantic Forest highlands, Brazil. The value in red was statistically significant at $p \leq 0.05$ based on 999 permutations.

Discussion

The identification of the selective forces on plant dispersal engenders theoretical and empirical issues [15]. The game of seed and fruit removal is played by mobile predators in search of sessile prey; discharge by a single dispersal move, seed chemistry, parental morphology and behavior, evolutionary change [14] and this game are influenced by human actions [2, 16]. Accordingly, our main findings show that Feijoa acts as an attractor of fauna and so contributes to the community structuring of mammals and birds. The diversity of fauna had a seasonal diversity increase – especially in terms of number of independent records – in congruence with spatiotemporal fruit offer, and the incipient domestication of Feijoa continues to favor the associated fauna, with a maintenance of local residual diversity, supplying food during the seasonal absence of *pinhão*. For example, a recent study in the Atlantic Forest of South America performed in 118 areas at a neutral perspective – generally without the presence of Feijoa – showed an alpha diversity of medium- to large-bodied mammalian of 9.86 species [111]. This average is numerically lesser than the richness recorded in this study (i.e. 12 medium- to large-bodied mammals species within a stressful environment due to the high altitude). An ambiguity of several contingency and determinism processes are able to determine the diversity pattern in a specific place [111]. Yet, the pattern showed in our result may be directly related with the seasonal resources of FOM (e.g. Feijoa and *pinhão* in alternation) that are able to maintain the residual richness of species that once was larger and nowadays range from nine to 16 species of medium- to large-bodied mammals [8]. Moreover, the process of landscape domestication, containing managed trees in anthropogenic forests, transcends the limits of natural distribution and abundance patterns, causing the dynamic of species interactions (e.g., seed removal) to be influenced by accumulated past and present human actions [2].

Whereby Feijoa domestication evidence – that was performed via management of trees near to local people houses [23, 112] – observed in this study was responsible for the 6% of the variation in interactions between mammals and Feijoa fruits. Besides, the sites with more Feijoa trees under these aforementioned conditions (e.g. S1) showed the largest diversity of vertebrates, presumably a cascade-effect of past human activities. At focal individual scale, this relationship also was highlighted because: (1) the fruit removal on Feijoa domesticated was circa 45% more than observed in Feijoas without evidence of domestication; (2) no Feijoa tree had 100% of fruit removal, suggesting that the removal in both conditions could be larger than observed; and (3) the number of species that performed frugivory in domesticated Feijoas was 25% larger than in "under-domesticated" trees. Furthermore, domestication activities ensure the genetic diversity of Feijoa that is maintained *in situ* (native forests) and/or on farms [109, 112]. Feijoa presents a low effect of endogamy, large genetic divergence among the populations and high incidence of rare and exclusive alleles among some populations within the highlands (including our sites S1 and S2) of subtropical Atlantic Forest [110], a strong indicative of the anthropic activities of management on species and local landscapes [23, 109, 110, 112].

Excluding *Homo sapiens* and their past influences on forest composition [3, 35], information about dispersal agents of Brazilian Myrtaceae and the success of plant establishment after the dispersal process remains unknown [29]. The fauna ecologically associated with Feijoa can enhance the fitness and natural regeneration of this tree, as for other plants [14-16], ensuring the maintenance of forest diversity [76]. How groups of frugivores disperse plant seeds needs to be studied by evaluating: (1) the speed and the percentage of germination; (2) seed deposition pattern, influenced by the number of seeds and species combination in the deposition; and (3) plant establishment success within the community [77]. Thus, for example, if only 0.5% of the seeds removed (a very low number compared to other Myrtaceae that pass through animal guts [e.g., 78-80]) successfully germinate; we predict that Feijoa frugivory can generate ~178 new Feijoa seedling in two years. For animals, mainly because of more than 18 native species consume fruits, the Feijoa is an alternative resource during the season when food is scarce in highland areas that can contribute to maintaining diversity and populations [81]. Feijoa promoted well-structured trophic relationships [13, 82], due to the spatiotemporal increase in the quantity of medium- to large-bodied predators, congruent with fruit availability (e.g., 83), an example of bottom-up forces in community structuring [13].

The array of frugivores can influence productivity, fruit and seed size, and demographic variations from both short- and long-term evolutionary scales, because evolutionary changes are underway for some plant species at sites without large fruit-eating species [16]. In the short-term, the productivity of Feijoa is related to pollination, dependent directly on birds and bees and indirectly on the environment and climatic variables [84]. Thus, in the long-term the sites can be subject to evolutionary changes in interaction patterns (e.g., reduction in fruit size) due to the absence of large native fruit-eating species (e.g., 16). Therefore, decompensation is expected due to incipient domestication efforts aimed at increasing fruit size, quality and productivity of Feijoa [23]. However, Feijoa may be maintained by the presence of cattle in sites where they recently occurred, another remarkable human impact in a landscape [36] that favors large Feijoa fruits. Cattle presence and biomass were determinant factors for fruit removal, as well as the displacement of native fauna, evidenced by the low native richness in the site (S3) where the presence of cattle was outstanding. The contribution of cattle to Feijoa fruit removal was high, as found in other studies for seed and fruit removal in the presence of cattle [85-86], which can compromise seed viability [87]. Human activities can favor Feijoa fitness, and although past management maintained the diversity of interacting species that promoted propagation throughout the entire local network [41-42], some activities paradoxically displaced the native fauna, especially livestock farming at large scales [44].

Many areas of Atlantic Forest have suffered from defaunation [8, 88-89]. The absence of animals that mainly remove seeds in all of the sites (*Tapirus terrestris* and *Tayassu pecari*: [90-91]) can promote an increase in seed predation, due high interactions with small rodents [91]. Our results agree with this pattern, since theCricetidae was an important removal group that has the potential to significantly compromise the seed dispersal network [18, 89]. The connectance of the fruit-removal network was intermediary, indicating that Feijoa can driveinteractions with the fauna in the sites and that it is partially compromised by defaunation (Vidal et al. 2013). Modularity was higher than expected indicating weak groups of sites linked by some species in common (e.g., Cricetidae, *Aramides saracura* and *Eira barbara*), but with modules (e.g., S1 and S4, the most productive sites) internally stronger with a large variation between temporal replicas, showing an unstable dynamic in the removal of Feijoa fruits. Modularity increased with the link specificity, being stronger in insect herbivory networks than in pollination and seed-dispersal networks, characterized by low interaction specificity [63, 92]. Yet, the nestedness was intermediate and not statistically different from expected by chance. This reflects in the degree animals influence on the network [93] and is congruent with the connectance pattern of the network.

Among the main species in the networks, mammals with great plasticity and tolerance to environmental changes were notable (e.g., *Eira barbara*, *Cerdocyon thous*, *Nasua nasua* and *Didelphis aurita*). Studies about the diets of these mammals showed that home range and a large spectrum of food items, including many fruits (e.g., 94-98), can result in spreading seeds from 3 km² to 20 km² [99]. Among birds, the main species have the largest body size in the sites, supposedly have a variable diet of food items, including fruits [100-101], and can disperse seeds over long distances [102-103]; although, there is a decrease in the number of seeds as the distance increases [104]. However, due to high variability in local relief and the restriction on the establishment and productivity of Feijoa at altitudes lower than 800 meters [23], the potential dispersal home range can be further reduced, which confirms the importance of conservation efforts to preserve the highlands and their environmental components. These environmental characteristics of the sites exerted significant influence on the interaction number at the focal-individual scale (based on variation partitioning). The relationship between species distribution and environmental characteristics is a major goal of ecology, and such relationships are likely to be important predictors of community structure [70].

The network partitioning showeda tendency of resource sharing and functional redundancy among species [105], not only for taxonomic groups but also in removal syndromes, vertical stratum, beginning and end of fruiting and activity time (day and night). Sites spatially closer to each other can be linked by Feijoa frugivores over the short- and medium-term, mainly because the distance is not significantly important to the amount of fruit removal and the main interactors can disperse seeds between sites over the short-term. Among sessile organisms, with seeds that represent the predominant mobile stage, dispersal is the primary spatial demographic process [106]. Yet, it also serves as a template for subsequent processes, such as predation, competition and mating [106], and evaluations of habitat loss, disturbances and landscape connectivity [89, 107].

Overall the patterns we found could be present in other fruit-eating and seed dispersal networks in different ecosystems, especially in neotropical regions where the gaps are even greater [89, 108]. Thus, we can conclude that our hypotheses were totally or partially corroborated because Feijoa was ecologically related to small- to medium-bodied herbivore-omnivores, was the resource structuring the vertebrate fauna in space and time, was increasing the diversity patterns seasonally in congruence with the fruit offer, and the ecological relationships were related to environmental characteristics and Feijoa domestication (for mammals). Sequential years with lower productivity of Feijoa probably not would cause a local extinction, but can lead to a decrease in vertebrate population sizes. Long-term experimental studies can be developed to corroborate if this seasonal increase in diversity is propagating at long-term, reinforcing the importance of Feijoa in an environment with low productivity and high seasonality. Our insights allowed us to evaluate the magnitude of interactions between vertebrates and an incipient domesticated tree, in a cultural landscape and highly threatened environment (Atlantic Forest highlands), under a basal foodweb approach with implications for bottom-up and top-down forces. We contributeunderstanding the relationship between mammals, birds, and fruit trees with concepts and results that can be replicated for other relationships between a sessile prey and mobile predators in any region or habitat under different gradients of human actions, environmental management, and historical ecology. This study shows how human actions can change not only the distribution patterns and abundance of species, but also the diversity and direction of interspecific interactions. The human footprint on forest composition can modify the ecological components of a landscape in a continuous cascading effect.

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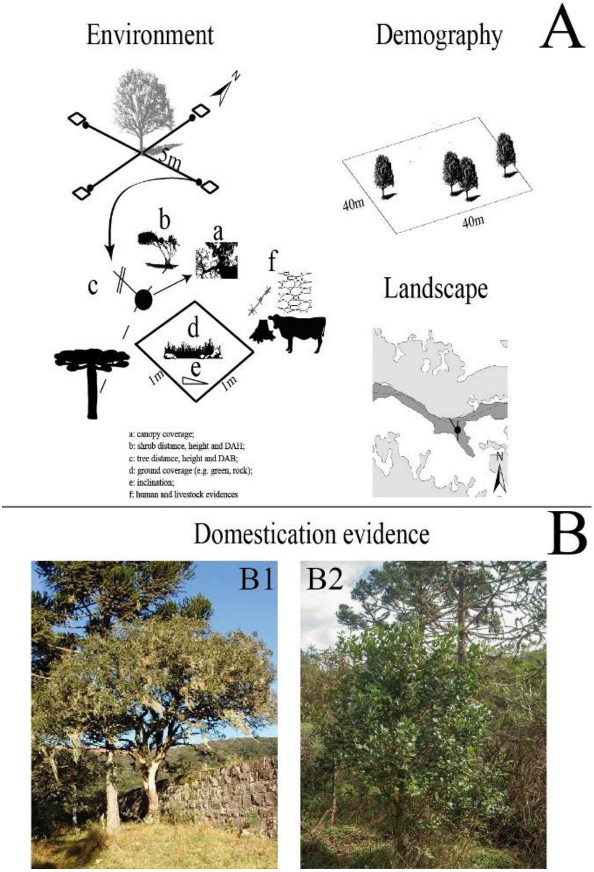
Supporting Information

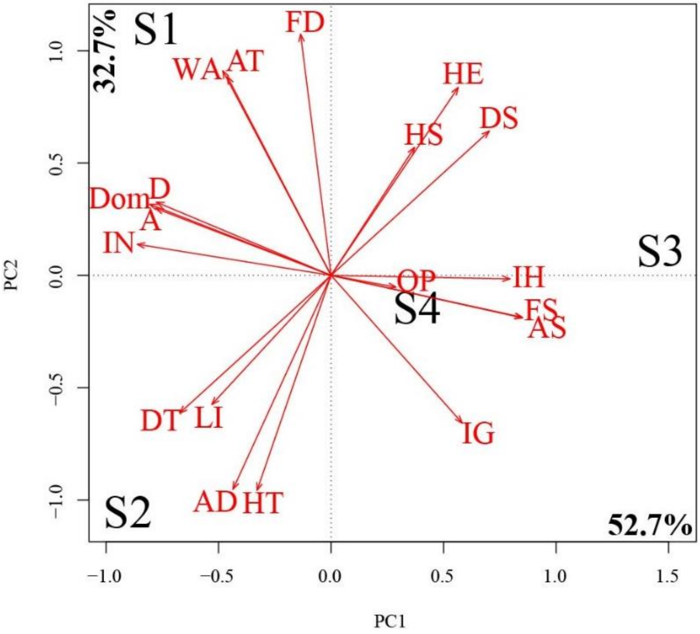
S1 Table. Characteristic of research areas and sampling sites used to evaluate the removal of *Acca sellowiana* fruit by vertebrate fauna (mammals and birds) in the subtropical Atlantic Forest highlands, Brazil. PSA: São Joaquim National Park; RGF: Reserva Particular do Patrimônio Natural (RPPN) Grande Floresta das Araucárias; RLM: RPPN Leão da Montanha; FOM: Mixed Ombrophilous Forest; UM: upper montane; AL: alluvial; m.a.s.l.: meters above sea level; SE: sampling effort (days); TR1: Temporal replica one (2015); TR2: Temporal replica two (2015, without fruit); TR3: Temporal replica three (2016).

Area	**Political Size (ha)**	**Year of creation**	**Vegetation type**	**Sites**	**Latitude (S)**	**Longitude (O)**	**Altitude (m.a.s.l.)**	**TR1 - 2015**	**SE**	**TR2 - 2015**	**SE**	**TR3 - 2016**	**SE**
PSA	12,841	1961	FOM-UM	S1	28°09'	49°38'	1,578	02/21 - 04/22	60	10/03 - 11/04	30	03/06 - 05/07	60
			FOM-AL	S2	28°08'	49°37'	1,378	02/21 - 04/22	60	10/03 - 11/04	30	03/06 - 04/07	30
RGF	4,018.8	2011	FOM-AL	S3	27°53	49°26'	952	03/15 - 04/16	30	10/03 - 11/04	30	04/06 - 05/05	60
RLM	126.5	2008	FOM-AL	S4	28°00'	49°22'	1,052	03/15 - 04/16	60	10/03 - 11/04	30	03/06 - 05/07	60

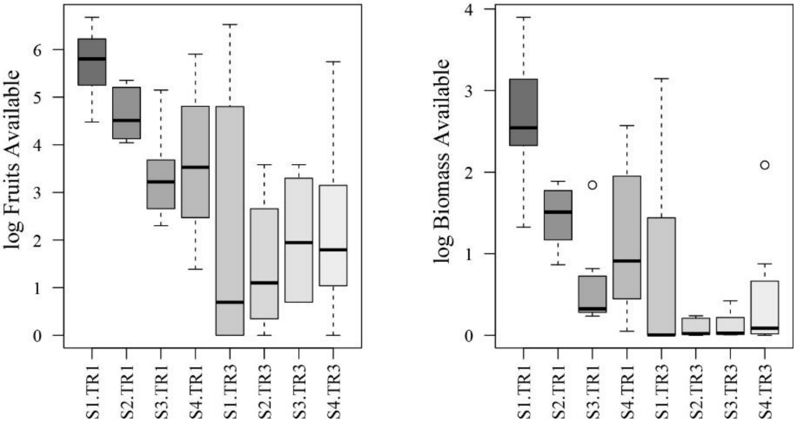
S2 Fig. (A) Sampling design to evaluate the environment, demographic and landscape features at sites used to evaluate the removal of *Acca sellowiana* fruit by vertebrate fauna (mammals and birds) in the subtropical Atlantic Forest highlands, Brazil; and (B) Evidences of *Acca sellowiana* domestication via management within sites: Where: (B1) Tree with signals of pruning near to old rural propriety (S1); and (B2) Trees without signals of domestication (native) within the site S4.



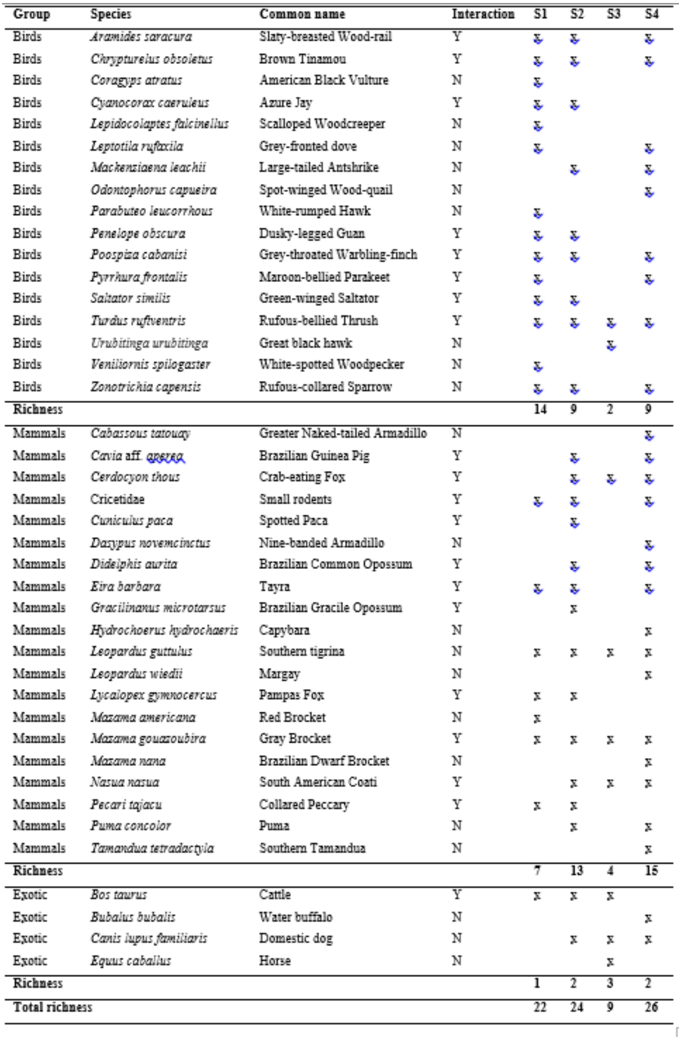
S3 Fig. PCA analysis to environmental, landscape, anthropization and *Acca sellowiana* density in four sites in the subtropical Atlantic Forest highlands, Brazil. Where: A: altitude (m.a.s.l.); AD: distance from nearest adult Feijoa (m); AC: focal-individual canopy area (m²); WA: distance from water bodies (m); OP: distance from open area (m); FD: distance from nearest fragment (m); FS: fragment/lowland size (ha); DO: canopy coverage (%); DT: diameter of nearest tree (m); HT: height of nearest tree (m); AT: distance from nearest tree (m); DS: diameter of nearest shrub (m); HS: height of nearest shrub (m); AS: distance of nearest shrub; LI: litterfall coverage (%); HE: herbaceous coverage (%); IN: inclination (°); IH: human presence intensity; IG: cattle intensity; Dom.: proportion of Feijoa trees with evidence of domestication within sites



S4 Fig. ***Acca sellowiana*** **productivity (N and biomass) into four sampling sites and two temporal replicas in the subtropical Atlantic Forest highlands, Brazil.**

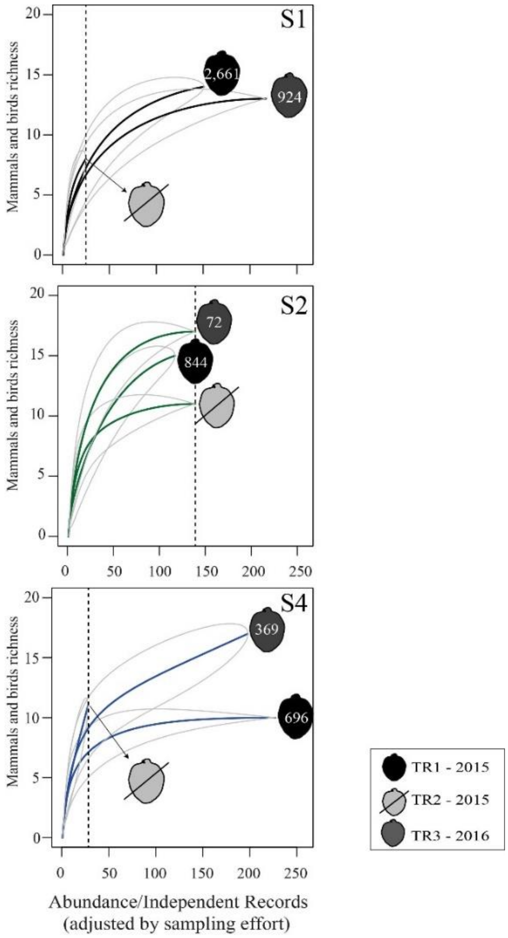


S5 Table. Birds, mammals and exotic species recorded into four sampling sites used to evaluate the removal of Acca sellowiana fruit by vertebrates in the subtropical Atlantic Forest highlands.



Group	Species	Common name	Interaction	S1	S2	S3	S4
Birds	*Aramides saracura*	Slaty-breasted Wood-rail	Y	x	x		x
Birds	*Chrypturelus obsoletus*	Brown Tinamou	Y	x	x		x
Birds	*Coragyps atratus*	American Black Vulture	N	x			
Birds	*Cyanocorax caeruleus*	Azure Jay	Y	x	x		
Birds	*Lepidocolaptes falcinellus*	Scalloped Woodcreeper	N	x			
Birds	*Leptotila rufaxila*	Grey-fronted dove	N	x			x
Birds	*Mackenziaena leachii*	Large-tailed Antshrike	N		x		x
Birds	*Odontophorus capueira*	Spot-winged Wood-quail	N				x
Birds	*Parabuteo leucorrhous*	White-rumped Hawk	N	x			
Birds	*Penelope obscura*	Dusky-legged Guan	Y	x	x		
Birds	*Poospiza cabanisi*	Grey-throated Warbling-finch	Y	x	x		x
Birds	*Pyrrhura frontalis*	Maroon-bellied Parakeet	Y	x			x
Birds	*Saltator similis*	Green-winged Saltator	Y	x	x		
Birds	*Turdus rufiventris*	Rufous-bellied Thrush	Y	x	x	x	x
Birds	*Urubitinga urubitinga*	Great black hawk	N			x	
Birds	*Veniliornis spilogaster*	White-spotted Woodpecker	N	x			
Birds	*Zonotrichia capensis*	Rufous-collared Sparrow	N	x	x		x
Richness				**14**	**9**	**2**	**9**
Mammals	*Cabassous tatouay*	Greater Naked-tailed Armadillo	N				x
Mammals	*Cavia* aff. *aperea*	Brazilian Guinea Pig	Y		x		x
Mammals	*Cerdocyon thous*	Crab-eating Fox	Y		x	x	x
Mammals	Cricetidae	Small rodents	Y	x	x		x
Mammals	*Cuniculus paca*	Spotted Paca	Y		x		
Mammals	*Dasypus novemcinctus*	Nine-banded Armadillo	N				x
Mammals	*Didelphis aurita*	Brazilian Common Opossum	Y		x		x
Mammals	*Eira barbara*	Tayra	Y	x	x		x
Mammals	*Gracilinanus microtarsus*	Brazilian Gracile Opossum	Y		x		
Mammals	*Hydrochoerus hydrochaeris*	Capybara	N				x
Mammals	*Leopardus guttulus*	Southern tigrina	N	x	x	x	x
Mammals	*Leopardus wiedii*	Margay	N				x
Mammals	*Lycalopex gymnocercus*	Pampas Fox	Y	x	x		
Mammals	*Mazama americana*	Red Brocket	N	x			
Mammals	*Mazama gouazoubira*	Gray Brocket	Y	x	x	x	x
Mammals	*Mazama nana*	Brazilian Dwarf Brocket	N				x
Mammals	*Nasua nasua*	South American Coati	Y		x	x	x
Mammals	*Pecari tajacu*	Collared Peccary	Y	x	x		
Mammals	*Puma concolor*	Puma	N		x		x
Mammals	*Tamandua tetradactyla*	Southern Tamandua	N				x
Richness				**7**	**13**	**4**	**15**
Exotic	*Bos taurus*	Cattle	Y	x	x	x	
Exotic	*Bubalus bubalis*	Water buffalo	N				x
Exotic	*Canis lupus familiaris*	Domestic dog	N		x	x	x
Exotic	*Equus caballus*	Horse	N			x	
Richness				**1**	**2**	**3**	**2**
Total richness				**22**	**24**	**9**	**26**

S6 Fig. Rarefaction curve (with a confidence interval of 95% in gray) for all independent records of mammals and birds species (except exotic) during evaluation of fruit removal from *Acca sellowiana* in three sites in subtropical Atlantic Forest highlands, Brazil. Independent records were adjusted by sampling effort (camera-trap/day/replica). S1 and S2: São Joaquim National Park; and S4: RPPN Leão da Montanha.

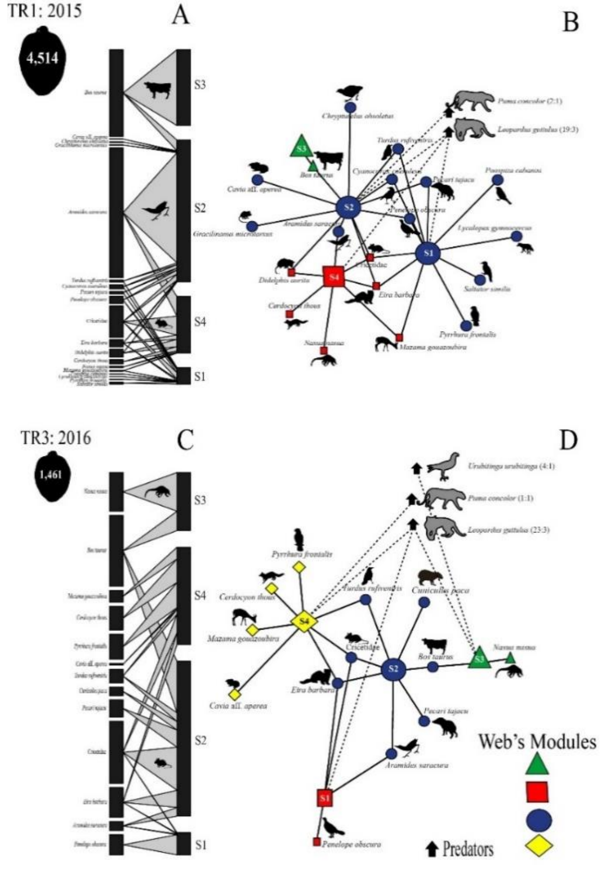


S7 Fig. (Left) Interaction between Cricetidae, *Eira barbara*, *Cerdocyon thous*, *Nasua nasua* and *Didelphis aurita* with *Acca sellowiana* fruits. (Right) Interaction between *Aramides saracura*, *Penelope obscura*, *Pyrrhura frontalis*, *Turdus rufiventris* and *Cyanocorax caeruleus* with Feijoa fruits in the subtropical Atlantic Forest highlands, Brazil.

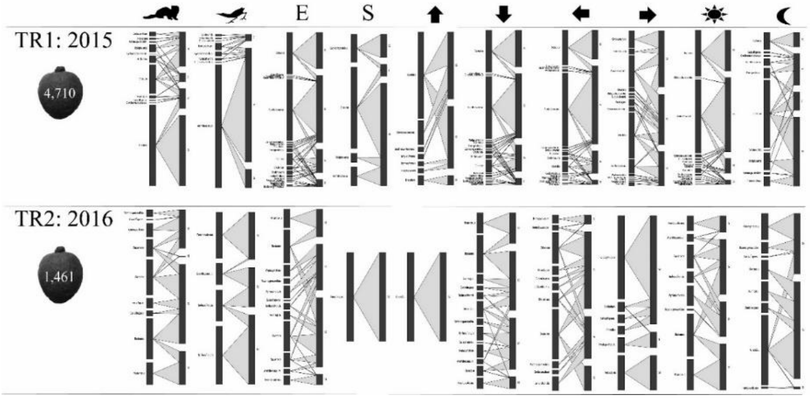
S8 Movie File. Compiled video of frugivory in *Acca sellowiana* in the subtropical Atlantic Forest highlands, Brazil.

Available online.

S9 Fig. Topology of the total network by the site for years 2015 (above) and 2016 (below) to evaluate the removal of *Acca sellowiana* fruit by vertebrate fauna (mammals and birds) in the subtropical Atlantic Forest highlands, Brazil. A: bipartite network considering 2015; B: modular network considering 2015; C: bipartite network considering 2016; D: modular network considering 2016. S1 and S2: São Joaquim National Park; S3: surrounding of RPPN Grande Floresta das Araucárias; and S4: RPPN Leão da Montanha.



S10 Fig. (A) Network by groups, behavior, stratum, time and circadian period in TR1 (2015); and (B) Network by groups, behavior, stratum, time and circadian period in TR3 (2016) obtained in four sampling sites used to evaluate the removal of *Acca sellowiana* fruit by vertebrates in the subtropical Atlantic Forest highlands, Brazil. In this order: mammals, birds, endozoochory, sinzoochory, upper stratum, bottom stratum, early fruiting (< 30 days), end of fruiting (> 30 days), day and night.



CAPÍTULO 3

Spatio-temporal congruence between resources availability and mammals diversity in threatened Brazilian highlands

(Congruência espaço-temporal entre a variação dos recursos e a diversidade de mamíferos nas ameaçadas terras altas brasileiras)

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Puma concolor (Linnaeus, 1771) [puma, leão-baio] registrado em 17 de agosto de 2014 no Parque Nacional de São Joaquim, localidade do Morro da Igreja (28°05’15.7” S; 49°30’15.1” O, 1.605 m.a.s.l.). Foto: Bogoni, 2014.

Spatio-temporal congruence between resources availability and mammals diversity in threatened Brazilian highlands

RH: **Congruence between resource and mammals**

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Abstract

Understanding the spatiotemporal patterns of species distribution, abundance, interactions, and their determinants is one of the main goals in ecology. We explore the relationships between mammals and two main tree resources (*Araucaria angustifolia*: Araucaria seeds and *Acca sellowiana*: Feijoa fruits) in Mixed Ombrophilous Forest (FOM). We studied seven highland areas of FOM within the subtropical Atlantic Forest of South America, collecting mammal and tree data through spatial image analysis, climatic databases, demographic plots, productivity accounts within transects and via camera traps. We analyzed the data via Morisita index, regression models, rarefaction curves, diversity partitioning and ordination analysis to understand the resource productivity and diversity variation among areas and temporal replicas. Our results showed that the landscape, environment, tree demography and productivity are highly variable along the gradient of subtropical Atlantic Forest. Mammalian diversity is partially positively related to resources productivity in space and time. The demography and productivity of trees and their co-occurrence are mainly related to climatic and environmental features and mammals feedback on tree demography and forest composition. We suggest that the integrity of elements in highlands is fundamental to the maintanance of ecological process. From a conservation ecology viewpoint, developing integrative conservation strategies is necessary to maintain the Araucaria and Feijoa population viabilities, encourage the sustainable use of resources and promote the mammalian fauna conservation.

Key-words: mammals, Araucaria, Feijoa, interactions, communities structure, diversity, domestication, Atlantic Forest, highlands

Introduction

Understanding spatiotemporal patterns of distribution, species abundance, species interactions, and their determinants are one of the main goals in ecology (Ricklefs 2004; Jiménez-Alfaro et al. 2016). Several ecological theories have been developed to tackle this question relying on neutral and niche paradigms (Hubbel 2001; Leibold et al. 2004). Regional species composition is a response to long-term regional-scale environmental modification or evolutionary change among interacting populations, since species production and extinction to connections from local to regional processes (Hubbel 2001; Ricklefs 2004). Moreover, the biota responds to historical processes that can be evolutionary discontinuous or punctual, for example can be linked to human intervention (e.g. artificial selection *sensu* Darwin 1859). Community structure has recently been reevaluated and reinterpreted within a metacommunity framework, such as a set of local communities connected by the dispersal of many species that are potentially interacting (Leibold et al. 2004). The paradigms of metacommunity theory (i.e., patch dynamics, species sorting, mass effects and neutral model) depend on spatial scale, extent, or spatial distances between areas (Declerck et al. 2011; Chase 2014).

Another theoretical framework to evaluate patterns in species distribution and abundance is the communities structuring via bottom-up and top-down forces (Power 1992). It contains their indirect effects propagating across ecosystem scales (Raimondi et al. 2000; Estes et al. 2011), based on primary productivity derived from plants (Daskin and Pringle 2016). Generally, plant communities are also controlled by abiotic factors (e.g. climatic niche) or vegetation structure, and plant composition influences animal diversity and distribution (Jiménez-Alfaro et al. 2016). The complexity of the relationships between plant-animal induces to a conceptual difficulty, because is difficult to disentangle the role of plant communities as a causal driver of animal diversity or as a coexisting counterpart controlled by abiotic niche (Jiménez-Alfaro et al. 2016).

The theoretical duality of niche concept provides a means for analyzing the biogeographic distribution in relation to the environmental patterns (Brown 1995). Classical niche theory predicts that all dimensions of the niche are responsible for the probability of species persistence (Hutchinson 1957). However, these niche dimensions change; there can be displacement over evolutionary or spatial history, lessening the competition for resources and/or promoting direct consequences on dispersion patterns and communities structure, including their mechanisms (Pulliam 2000). Several other processes can change the structure of the ecosystem. Among them, human historical influences and the persistent feedbacks generated by human ecosystem engineers in co-constructed landscapes with nature or niche construction, has important implications for current biodiversity patterns and ecological process (McKey et al. 2010; Zeder 2016). Modern human impacts can promote cascade effects at several scales (Redford 19992; Dirzo et al. 2014; Bogoni 2016a; 2016b). All these patterns and process (i.e. climatic niche and human impact influencing the plant composition, and plant composition structuring animal distribution) feedback on forest regeneration and in communities structure (Roemer et al. 2009; Galetti and Dirzo 2013; Bogoni et al. 2016b), especially via predation/dispersal of seeds, that are highly structured and coevolved spatiotemporally (Janzen 1971; Peres 2000; Peres and Palacios 2007). Among animals groups, mammals and birds disperse about 90% of woody crop plant species in tropical environments (Howe and Smallwood 1982; Gentry 1988; Vidal et al. 2014).

In the tropical region, the Atlantic Forest of South America is one of the five most important biodiversity and endemism in the world (Myers et al. 2000) and have almost 318 mammal species, with 90 endemism (Paglia et al. 2012; Graipel et al. 2016). Atlantic Forest is extremely threatened by several factors, such as defaunation, biological invasions, habitat loss, fragmentation and isolation and landscape changes (Galetti et al. 2009; Ribeiro et al. 2009; Canale et al. 2012; Bogoni et al. 2016a). Within the subtropical province of the Atlantic Forest at highlands areas, the main vegetation formation is Mixed Ombrophilous Forest (FOM or Araucaria Forest), characterized by the outstanding and key presence of critically endangered *Araucaria angustifolia* (Bertol.) Kuntze (Araucaria) (Rambo 1951; Mattos 2011; IUCN 2016). The Araucaria Forest has Pre-Columbian Anthropogenic management indicators and has been transformed since the mid-Holocene (Reis et al. 2014; Bitencourt and

Krauspenhar 2006). Currently being substantially threatened due to logging, deforestation and expansion of urban areas (Ribeiro et al. 2009; Mattos 2011).

Within FOM, Araucarias trees dominate the upper forest stratum, whereas Myrtaceae and Lauraceae are the main families forming the middle and lower strata (Rambo 1951; Souza 2007). A few Myrtaceae species dominate the flora in the highlands, usually those characterized by small-sized fruits (i.e. < 20 g) (Mazine and Souza 2008). An exception is *Acca sellowiana* [Berg] Burret (Feijoa), a tree native to southern Brazil and northern Uruguay, which produce large-sized fruits (> 50 g) and a large quantity of small seeds (< 2 mm) (Gressler et al. 2006; Santos et al. 2009). Feijoa is distributed mainly in riparian areas within the Araucaria Forest and within the Pampa ecoregion (Santos et al. 2009). Feijoa, as Araucaria and local landscapes, also have received historical anthropogenic influence promoting a certain level of domestication *in situ*, favoring large-sized fruits and more productive trees (Santos et al. 2009).

Both tree species – Araucaria and Feijoa – produce resources for wildlife, for livestock and for humans (Iob and Vieira 2008; Paludo et al. 2009; Bogoni et al. submitted), and especially Araucaria seeds – *Pinhão* – is an important source of income for local residents (Mello and Peroni 2015). Araucaria tree is a dioecious conifer with different varieties (Mattos 2011; Adan et al., 2016). The female strobilus – *Pinhas*: composed of viable seeds (*Pinhão*), non-viable seeds (*Chochos*) and sterile scales (*Falhados*) – are mature approximately four years after via-wind pollination and the peak of *Pinha* maturing occurring from April to June (Shimoya 1962; Mattos 2011). *Pinhão* is highly energetic because is mainly starch (Mattos 2001). Feijoa is a monoicous tree whose pollinators are relatively unknown, with fruit maturation from February to May (Gressler et al. 2006), thus an alternative to the time (summer/autumn) of scarce resources (i.e. in absence of *Pinhão*) acting as attractor and communities structuring (Bogoni et al. submitted). Yet, different of the *Pinhão*, Feijoa fruits have lower energetic levels for being composed mainly by carbohydrates (i.e. fructose) and fibers (Gressler et al. 2006; Santos et al. 2009). Spatial patterns of these trees species and the mammals communities are scale-dependent, associated to landscape characteristics, such as the forest cover, fragment size, open areas and matrix connectivity (Paludo et al. 2009; Mello and Peroni 2015; Bogoni et al. 2016a; Lacerda 2016; Bogoni et al. 2017). Landscape features are able to promote changes in spatial distribution patterns of trees (Turner et al. 2004) and lead to a nonrandom shift in mammals communities (Bogoni et al. 2016a).

Using a holistic approach, we generated a database from several ecological features that influencing the Araucaria, Feijoa and mammal abundance and distribution. We obtained landscape characteristics, tree demographic patterns, tree resource productivity, species niche features and variation in spatiotemporal diversity of mammals to fill several gaps in the knowledge of Araucaria and Feijoa distribution and their relationship with fauna. We aimed to understand: (1) the climate, the environment and the landscape cover in areas of Araucaria Forest; (2) the pattern and the influence of climate, environment, and landscape on the distribution of trees (Araucaria and Feijoa), their co-occurrence and spatio-temporal productivity of fruits; (3) the spatiotemporal patterns of trees productivity influencing the mammal diversity; and (4) the feedback from the abundance of mammals within functional groups (e.g. body size and trophic level) to the trees patterns and to the richness of other woody plants within forest patches. We hypothesize that: (1) among the areas the climate is conspicuous variable, yet the environment and the landscapes vary greatly according to the different management regimes; (2) the distribution of trees within their ontogenetic classes are from random to aggregate due the modern reduction of mammalian dispersers, the trees co-occurrence is marked by environmental factors and the main influencer of the productivity of trees is the climate; (3) the diversity of mammals are influenced by the trees productivity, with soften and eventually delayed impacts due their diversity homogeneity across the subtropical Atlantic Forest; and (4) the mammals – according to the abundance within the trophic level and body-size guilds – provide feedbacks to trees patterns and richness of plants, increasing the richness of woody plants, the non-aggregation via dispersal and highest rates of regeneration of trees.

Material and Methods

Research areas and landscape cover

We carried out the research in seven areas of FOM, within subtropical Atlantic Forest of South America (26°30’ - 28°10’S; 52°00’ - 49°30’W). These areas are linearly distant one each other by 148.3 km

(±118.4; ranging from 4.8 to 290 km), with altitude reaching from an average of 887 meters above sea level (m.a.s.l.) to an average 1,549 m.a.s.l. The areas are located within four protected areas: two within National Park of Araucarias (PAA and PAB); two within National Park of São Joaquim (PSA and PSB); one in the Reserva Particular do Patrimônio Natural (RPPN) Leão da Montanha (RLM); one in the RPPN Grande Floresta das Araucárias (RGF); and one in a particular area: Lages, SC, Coxilha Rica (CXR). The study region falls within the humid subtropics (Cfa according to the Köppen-Geiger classification), with seasons are well-defined, rainfall well-distributed throughout the year and high variation on temperatures during the year (Monteiro 2001; Peel et al. 2007). The areas feature elements of cultural landscapes; visually constituted by anthropogenic forests with different intensity of past and present use (Mello and Peroni 2015; Reis et al. 2014) and regeneration stages, formed mainly by Araucaria Forest (alluvial, montane and upper-montane) and grasslands (Veloso et al. 1991). The areas differ in the period of time with protected status (except CXR) and time affected by human exploitation (Eduardo 1974; Bogoni et al. 2016a) (Figure 1A; Supporting Information S1).

We obtained the landscape cover in each area using an automatic classification using the *MultiSpec Software* (Biehl and Landgrebe 2002). The spatial images were obtained in Geographic Information System of Santa Catarina (http://sigsc.sc.gov.br/sigserver/SIGSC/wms) at scale 1:85,000 cm and coordinates expressed as a UTM projection (Datum WGS 84), with a buffer of 10 km radius from the central point of each area, totalizing 31,400 ha. We classified the landscape cover in Mixed Ombrophilous Forest (FOM), Dense Ombrophilous Forest (FOD), silviculture of exotic species (SIL: *Pinus* spp. and *Eucalyptus* spp.), water bodies (WAT) and open areas (GRA: native and non-native grasslands) using a likelihood approach (similar to Bogoni et al. 2016a).

Plants demography and resource productivity

We collected data on tree demography (Araucaria and Feijoa) within four plots (except for PAA, in eight plots) per area. The plots had dimensions of 40 m x 40 m (1,600 m²) each. These samples plots had a ratio of sampling area in relation to areas size of 0.11 (±0.17; ranging from 0.002 to 0.379) – numerically higher than Floristic-Forest Inventory of Santa Catarina State, with a ratio of 0.001 (Vibrans et al. 2010)

(Supporting Information S2). The plots were spatially equidistant (approximately 500 m) and attending to two criteria: (1) at least 25% of total plots with trees co-occurrence; and (2) one plot in each area had not any of these two tree species.

In total, we positioned 32 plots and counted the individuals in ontogenetic stages for Araucarias as follow: (1) seedling: individuals with height ≤ 1.5 m; (2) juveniles: individual without reproductive signal with height ≥ 1.5m; (3) adults (male and female): individuals with reproductive signals; and (4) undefined: individuals with adults' configuration, but without visual reproductive signals. Ontogenetic classes of Feijoa were: (1) seedling: individuals without reproductive signals with a circumference at breast height (CBH) ≤ 15 cm; and (2) adults: with reproductive signals or CBH ≥ 15 cm (Lorenzini 2006; Paludo et al. 2009; 2011). The seedling of both tree species were sampled within 2 subplots of 5 x 5 meters (totaling 50m²) delimited at the southest and northeast vertices of each plot (similar to Vibrans et al. 2010). In addition, within subplots we recorded richness of shrubby-arboreal species, identified by a botanic specialist *in loco*. For each individual of Araucaria and Feijoa in plots and subplots, we measured height, canopy diameter, basal area, vertical position (emergent, canopy, sub-canopy and understory), canopy format (only for Araucaria: in pyramidal, intermediate and umbel) and habit (only for Feijoa: in opening, lying down, erect and semi-erect) (Lorenzini 2006; Paludo et al. 2009; 2011). We performed the Araucarias sexing in several opportunities within each plot, because the reproductive structures of males are difficult to visualize.

We estimate Araucaria seed productivity in each area by counting the number of *Pinhas* in Araucaria trees during one linear transect (with size ranging from ~500 to ~3500 m according to the size of each area), during two years (TR1: 2014 for PAA and PAB; 2015 to the other areas; and TR2: 2016), totaling 245 females (ranging from 17 to 40 per area). We select the Araucarias trees for productivity evaluation at random, adopting as unique criterium the *Pinha* presence in first inventory (Schüssler 2014). We account and classified the *Pinhas* in Araucarias according to visual estimative in small, medium or large (Batista 2015). At random, we obtained in all studied sub-regions (via collect or direct acquisition with local extractors) 64 *Pinhas* (2015: 25 and 2016: 39) ranging among the different *Pinha*-size. We measured the *Pinhas* volume (vertical, horizontal and deepness axis), accounted the number of viable seeds (*Pinhões*) and obtained the biomass via *Pinhão* weighing from dozen in dozen (Schüssler 2014). Feijoa productivity was estimated at two years in 28 focal-individuals distributed within three areas (PSB, RGF and RLM). The Feijoa fruit account occurred on a main (control) branch and multiplied by the number of equal-sized branches in the tree (Bogoni et al. submitted) summed to the quantity of fruits on the ground. We obtained the biomass via weighing of ≤ 15 Feijoa fruits per tree and temporal replica, choosing at random (Bogoni et al. submitted) (Supporting Information S2).

Environmental characteristics and climate features

Within each plot vertices and in the center of plot, we obtained some niche dimensions based on point-quadrant method (Brower 1998) and georeferenced data. Niche dimensions were defined *a priori* as follow: (1) canopy cover: through canopy convex densiometer; (2) altitude: via GPS; (3) cover and height of litterfall: cover within 1 m² delimited on the ground and defined at classes of 0-5, 6-25, 26-50, 51-75, 76-95 e 96-100%; and height in five random measures within 1 m²; (4) green cover, exposed soil and rock outcrop: equal to the litterfall cover; (5) declivity and orientation: using a clinometer. Completely, we classified the plots according to: (i) past livestock presence/absence: by signals visualization (e.g. fences and rocky walls); (ii) actual livestock: intensity by visual classification (ordinal: from 0 [absence] to 2 [high]); (iii) waterlogged: presence or absence; (iv) selective cutting: by presence of visual signals; (v); fire: by presence of visual signals; and (vi) climatic variables: variations (amplitudes and average) monthly and annually of temperature and precipitation obtained at *WordClim: Global Climate Data* (http://www.worldclim.org/download), generated by climatic interpolated data from 1950 to 2000 (Hijmans et al. 2005).

Mammals inventories

We obtained the medium- to large-bodied mammals records via camera traps (*Bushnell* ®) in seven, four or two temporal replicas in each area (Supporting Information S3), during the end-2013 to beginning-2017 – intentionally coinciding with the harvest of Araucaria (for all areas), Feijoa (only for PSB and RLM) and without both these resources for all areas. In each area, we installed from nine to 10 camera traps attached in trees or posts at circa 30 cm on the ground, without baits (except per natural availability of *Pinhões* or Feijoa fruits), intentionally placed on trails and paths naturally used by mammals (Bogoni et al. 2016a). We distributed the camera traps along areas in points with different environments structure (e.g. riparian areas, grasslands, swamp, upper-montane, montane and alluvial Araucaria Forest). In total, we sampled 102 points with sampling duration at each point ranged from 30 to 61 days. Thus, our total sampling effort was 11,956 camera-trap-days. The distance between camera-traps varied according to the political size of areas, however, we concern to keep a minimum distance of 360 m between pairs of camera-trap, except for replica in Feijoa fruit season due the trees aggregation (Bogoni et al. submitted). This distance (360 m) was obtained taking into account the average living area of probable mammals be recorded (which had information in literature: see Parera 2002; Oliveira and Cassaro 2005; Reis et al. 2006), multiplied by 3 (Maffei and Noss 2008). Thus, camera traps were placed at an average distance of 3,287 m (±2,025: ranging to 403.9 to 7,328.5 m), with a density of approximately 0.021 (±0.035) camera traps per hectare. The camera-traps were programed to perform photographic and video records at each 15 from 30 seconds, depending on the temporal replica. However, we used only independent records by area and temporal replica, excluding records of the same species at the same point at intervals shorter than 1 hour and weighted the number of independent records by the sampling effort of each area and temporal replica (camera-trap-day-temporal replica) (Bogoni et al. 2016a). We also include the records of small rodents as a group (within Cricetidae family) from the dataset because is a group strongly associated with both tree species (Bogoni et al. 2016a; Bogoni et al. submitted).

Data analysis

Araucaria and Feijoa: spatial patterns, productivity and niche influences

We use descriptive statistics to explore demographic population structure of Araucaria and Feijoa per hectare and per area based on landscape cover. Based on central and variation tendency measures in plots we obtained the values standardized to hectares and hectares/FOM/area, including the productivity. To evaluate the pattern of spatial distribution, we used the Standardized Morisita Index (SMI)

(Morisita 1959; Smith-Gill 1975) and create 1000 null models – with values into trees classes ranging from minimum to maximum observed in all classes – to compare de observed values at each trees classes with the random (Gotelli and Ulrich 2012). SMI range from -1 to 1 and is expected a uniform pattern next to -1, random pattern next to 0 and aggregate pattern next to 1 (Smith-Gill 1975). Significance ($p \leq 0.05$) of SMI in relation to the null models was based on the ratio at which larger/lesser or equal to the observed SMI in each class occur in the null models (Bascompte et al. 2003).

SMI in each class per tree species became used as response variable in generalized regression models (*glm*). The models were made containing three predictors groups (i.e. climate niche, environmental niche and landscape cover), to evaluate the spatial patterns of distribution in relation to this predictors set. We utilized Gaussian distribution due to the characteristic of values of SMI (decimal numbers with values ranging from -1 to 1 and with non-normal verified *a priori*) (Dobson 1990; Johnson and Omland 2004). Still, through *glm* we evaluate the patterns of productivity of trees in relation to SMI, to the climate and environmental niche and to the landscape cover, utilizing Gamma distribution (Dobson 1990; Johnson and Omland 2004). For both *glm* performing, we use the *a priori* an analysis of variance inflation (VIF) to evaluate the multicollinearity of predictive variables, keeping only the variables with VIF ≤ 10 (Fox and Monette 1992; Legendre and Legendre 1998). The best predictive model was based on AIC criterion, and in overdispersal (OD) and a posteriori VIF values (Dobson 1990; Johnson and Omland 2004).The trees co-occurrence was evaluated via principal components analysis (PCA) of correlation with data from climate and environmental niche and landscape cover separately (Legendre and Legendre 1998).

Feedbacks: mammals such as response and mammals such as predictor

Initially we explored the mammals numbers via diversity descriptors (richness and independent records) by area and temporal replica per area (Magurran 2004). We use rarefaction curves with 95% confidence intervals to evaluate the spatiotemporal diversity patterns in mammals in relation to the resources (*Pinhão*, Feijoa fruits and in absence of both resources) productivity (i.e. feedback from plants) (Colwell et al. 2012). We used metacommunity theoretical models based on species-neutral diversity (Hubbell 2001; Hu et al. 2007) in a multiplicative framework (Ellison 2010; Veech and Crist 2010; Chao et al. 2012) to compare the diversity of the mammal communities in relation to the resources amount in space and time. We based the analysis on the number of independent records of medium- to large-bodied native mammals and including Cricetidae, *Cavia* aff. *aperea*, *Gracilinanus microtarsus* and *Philander frenatus* due to their presumed relationship with the resources. The diversity partition of metacommunity metrics was summarized into average alpha, beta and gamma diversity (Jost 2007; Marcon et al. 2012; 2014). Due the number of replicas with the resources are dissimilar (N = 12 with *Pinhão*; N = 4 with Feijoa, and N = 14 without both resources), we compared the alpha, beta and gamma diversity proportionally, dividing the values of diversity by the number of replicas. Additionally, we compared the observed values of alpha and beta diversity in relation to 1000 null models of communities based in the distribution and abundance of mammals among replicas, adopting as the p-value (significance at $p < 0.05$) the ratio of how many times the observed beta diversity was lager/lesser than or equal to the alpha and beta diversity values in the null models, divided by the number of null models (i.e., 1000).

We use a redundancy analysis (RDA) (Legendre and Legendre 1998) to evaluate the proportion explained by the mammals abundance within trophic level, body-size and interactors and non-interactors with Araucaria and Feijoa (according Paglia et al. 2012, Iob and Vieira 2008 and Bogoni et al. submitted) on variation of the average richness of woody plant species, the average SMI to tree species, the sum of trees species basal area and the ratio between seedling and adult of each tree species (regeneration rates) among areas. The trees patterns and plants richness data asymmetry as corrected by standardization and the mammals data asymmetry by Hellinger correction (Legendre and Legendre 1998). To perform the analysis, we use the program R (R Core Team 2017) and the packages vegan (Oksanen et al. 2013), ade4 (Dray and Dufour 2007), HH (Heiberger 2013), spatstat (Baddeley and Turner 2005), and entropart (Marcon and Hérault 2015).

Results

Landscape cover, demographic patterns, resource productivity and niche measures

Among the studied areas, within the 219,800 ha of landscape sampled and classified, we obtained a cover of FOM ranging from 5,966 ha (19%) to 23,550 ha (75%), an average of 13,906 (±6,120) ha of FOM. Among others types of cover, predominate the open areas (28.8% in average) (Figure 1B; Supporting Information S4). We sampled along 51,200 m² within the seven areas, 951 individuals of Araucaria and 67 individuals of Feijoa. Standardizing the demography per hectare, we found an average of 32.1 (±13.9; from 9.4 to 49.6) female of Araucaria by hectare, and a ratio of regeneration of 9.6 (±9.7) individual per adult. Other ontogenetic classes of Araucaria ranged from zero to 229.2 individuals per hectare. We found Feijoa only into four areas (CXR, PSB, RGF and RLM), with an average of 29.2 (±13.9) adult per hectare and 8.0 (±6.1) seedling per adult. Individual sizes of trees by ontogenetic classes also have a large variation spatial among areas and in spatial distribution within the plots of each area (Supporting Information S5). The general spatial pattern of Araucaria and Feijoa was random to aggregate, especially to juvenile and seedling. Yet, some classes in some areas where exceptions. SMI showed a random pattern in adult Araucarias in PAA and PAB, and *quasi*-uniform in RLM, both statistically minor [$p < 0.01$] that expected at null models. For the undefined class of Araucaria, in PAA and PAB it is expected a pattern more aggregate, as the juvenile at PSA and Araucaria seedling in PSA and PSB. Feijoa seedling in all areas had a *quasi*-random distribution, different from expected in null models, i.e. more aggregate (Figure 2A).

Resource productivity varied from zero to 44 *Pinhas* in all size classes per Araucaria female between the two years, with a median of four *Pinhas* per individual. Large *Pinhas* had an average volume of 5,801 (±1,632) cm³, medium-sized *Pinhas* 3,523 (±1,635) cm³ and small 2,300 (±1,566) cm³. In 64 *Pinhas* we found 4,203 *Pinhões*, with an average of 71.5 (±39.5; ranging from 0 to 147) *Pinhões*, resulting in an average of 500.6 (±632.1) *Pinhões* per female sampling. The average biomass of each seed (*Pinhão*) was 6.2 (±2.7) g, a biomass of 3.4 (±4.5) kg per female. The biomass of *Pinhões* per hectare was on average 106.6 kg/ha^{-1}. However, we found a large spatiotemporal variation, with biomass per hectare decreasing 68.7% in TR2 when compared to TR1, especially in PSA, RGF and RLM areas (Summary in Figure 1A; Variation in Figure 2B). Feijoa productivity also was extremely variable spatiotemporally, from zero to up to 700 fruits per individual sampled along the two years. On average, we found 106.7 (±175.6) fruit per adult. Based on 99 fruits, the average biomass was 33.25 (±19.4) g, resulting in a biomass of 120.8 kg/ha^{-1}, decreasing 79.3% from TR2 to TR1 and with a large variation among areas (Figure 1A; Figure 2B). Climate niche in each area (nested by demographic plots) were poorly variable, except by the average precipitation (142.1 ±11.2 mm) and precipitation amplitude (75.0 ±15.1). Yet, environmental characteristics are highly variable among areas and plots, especially the canopy cover (61.2% ±38.8), litterfall cover (38.8% ±37.4) and green cover (74.3% ±29.6) varying further in relation to plots with trees occurrence, co-occurrence, and absence.

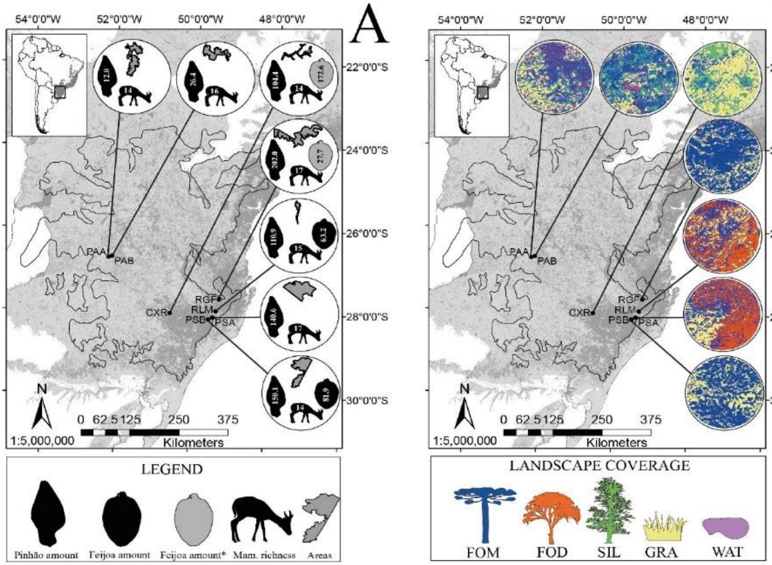

Figure 1. (A) Spatial localization of seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil. Light gray corresponds to the original distribution of Brazilian Atlantic Forest, dark gray is the Atlantic Forest remnants in the study area in 2011-2012 (according to the foundation SOS Mata Atlântica: http://mapas.sosma.org.br/). The black line delimits the FOM domain

according to The Nature Conservancy Organization (http://maps.tnc.org/gis_data.html). Within the circles: The *Pinhão* silhouette (left) and the number represented the average of biomass (kg/ha) based on 2 years of sampling. The Feijoa fruit silhouette (right) and the number represented the average of biomass (kg/ha) based in 2 years of sampling (* gray silhouette of Feijoa representing areas without replicas for fauna considered in the analysis). The brocket silhouette (below) and the number represent the mammals species richness in each area. The map (above) is the political delimitation of each area; and (B) Landscape characteristics of seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil. Codes and maps are PAA: National Park of Araucárias, west portion; PAB: National Park of Araucárias (eastern portion); CXR: Coxilha Rica region, Municipality of Lages; PSA: National Park of São Joaquim (Morro da Igreja); PSB: National Park of São Joaquim (Santa Bárbara); RLM: Reserva Particular do Patrimônio Natural (RPPN) Leão da Montanha; RGF: RPPN Grande Floresta das Araucárias; FOM: Misted Ombrophilous Forest; FOD: Dense Ombrophilous Forest; GRA: grasslands/open areas; SIL: silviculture; WAT: water bodies.

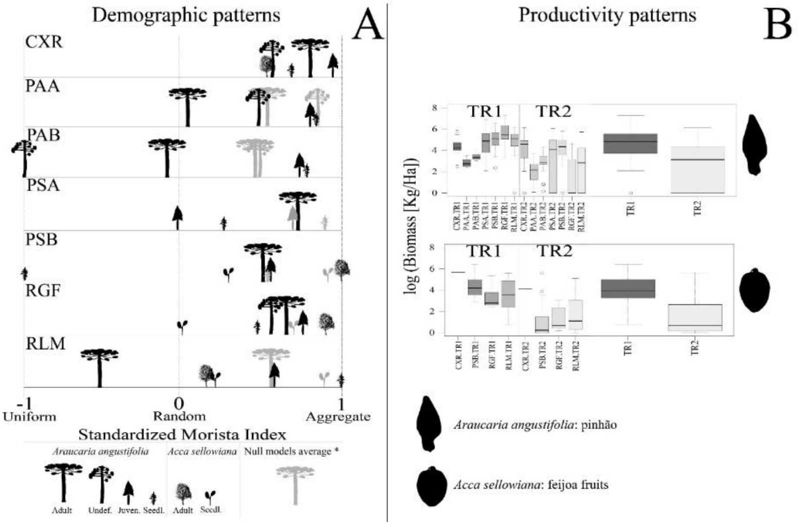

Figure 2. (A) Standardized Morisita Index (SMI) showing the spatial distribution of *Araucaria angustifolia* (Araucaria) and *Acca sellowiana* (Feijoa) classes within seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands. (B) Resource productivity within seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil. The cold period is represented by biomass of Araucaria seeds (*Pinhões*) per hectare; the Warm period is represented by biomass of Feijoa fruits per hectare (only in four areas where the species is present). TR1 (Cold): 2014 to PAA and PAB; 2015 to other areas; TR2 (Warm): 2016 for all areas. Areas codes in Figure 1.

Niche influences in Araucaria and Feijoa patterns

The main non-inflationed niche features that influenced the SMI of Araucaria was minimal temperature minimal (TMM) and canopy cover (CC) [AIC = 27.6; OD = 0.23], both positively increasing the aggregation in relation to the increase of TMM and CC. The tendency of aggregation of Feijoa was influenced negatively by CC [AIC = 8.0; OD = 0.11]. The productivity of Araucarias is related negatively to the increase in average precipitation (PA) [AIC = 81.2; OD = 0.58] and the Feijoa productivity positively affected by the increase in minimum temperature minimal (TMM) [AIC = 9.1; OD = 0.12] (Table 1). Tree co-occurrence was explained 91% by the climate niche, mainly by the average minimum temperature that increases the co-occurrence in coldest places. The co-occurrence of tree also was explained by environmental characteristics (54.5%), mainly by litterfall (positive effect) and green cover (negative effect), selective logging (positive effect) and outcrop rock (positive effect). Still, landscape features explain 73.5% of co-occurrence, this relation is positively associated with the extent of FOM cover (Supporting Information S6).

Table 1. Multiple regression analysis to evaluate de Standardized Morisita Index (SMI) and productivity patterns of *Araucaria angustifolia* (Araucaria) and *Acca sellowiana* (Feijoa) distributed along seven highland areas into subtropical Atlantic Forest in relation to the climate niche, environmental niche and landscape features. Where: OD: overdispersion model; PA: Precipitation average; TMM: Minimal Temperature; CC: Canopy cover; FOM: Mixed Ombrophilous Forest cover at the landscape scale. The best model is based on AIC values, OD and VIF. These best models are highlighted in bold.

Response variable	**Model**	**Description**	**K**	**AIC**	**Δ AIC**	**OD**	**VIF**
SMI Araucaria	**M11**	**TMM + CC**	**2**	**27.58**	**0**	**0.23**	**< 3**
	M10	PA + CC	2	27.62	0.04	0.23	< 2
	M12	CC	1	28.62	1.04	0.25	-
	M4	TMM + CC + FOM	3	29.04	1.46	0.24	< 3
	M3	PA + CC + FOM	3	29.61	2.03	0.24	< 3
	M5	CC + FOM	2	30.43	2.85	0.27	< 2
	M1	PA + TMM + CC + FOM	4	30.94	3.36	0.26	< 8
	M14	TMM	1	39.22	11.64	0.24	-
	M7	TMM + FOM	2	40.71	13.13	0.25	< 2
	M9	PA + TMM	2	41.07	13.49	0.25	< 3
	M13	PA	1	41.15	13.57	0.26	-

	M8	FOM	1	42.24	14.66	0.27	-
	M6	PA + FOM	2	42.56	14.98	0.27	< 2
	M2	PA + TMM + FOM	3	42.59	15.01	0.26	< 3
SMI Feijoa	**M12**	**CC**	**1**	**8.05**	**0**	**0.11**	**-**
	M14	TMM	1	8.94	0.89	0.13	-
	M5	CC + FOM	2	9.12	1.07	0.12	< 4
	M8	FOM	1	9.76	1.71	0.14	-
	M11	TMM + CC	2	9.87	1.82	0.14	< 2
	M10	PA + CC	2	10.02	1.97	0.14	< 2
	M13	PA	1	10.05	2	0.15	-
	M9	PA + TMM	2	10.21	2.16	0.14	< 4
	M7	TMM + FOM	2	10.78	2.73	0.15	< 2
	M1	PA + TMM + CC + FOM	4	11.11	3.06	0.16	> 10
	M2	PA + TMM + FOM	3	11.11	3.06	0.16	< 5
	M3	PA + CC + FOM	3	11.11	3.06	0.16	< 4
	M4	TMM + CC + FOM	3	11.11	3.06	0.16	< 6
	M6	PA + FOM	2	11.73	3.68	0.17	< 2

Produc. Araucaria	**M6**	**PA**	**1**	**81.22**	**0**	**0.58**	**-**
	M4	TMM + PA	2	81.92	0.7	0.61	< 3
	M7	SMI	1	82.91	1.69	0.73	-
	M3	SMI + PA	2	83.04	1.82	0.71	< 2
	M5	TMM	1	83.55	2.33	0.79	-
	M1	SMI + TMM + PA	3	83.87	2.65	0.81	< 4
	M2	SMI + TMM	2	84.42	3.2	0.85	< 2
Productivity Feijoa	**M5**	**TMM**	**1**	**9.13**	**0**	**0.12**	**-**
	M4	TMM + PA	2	11.11	1.98	0.16	< 2
	M6	PA	1	11.74	2.61	0.17	-
	M7	SMI	1	47.93	38.8	0.79	-
	M3	SMI + PA	2	48.09	38.96	1.02	< 2
	M2	SMI + TMM	2	49.92	40.79	1.57	< 2
	M1	SMI + TMM + PA	3	-98.62	-107.75	> 10	< 5

Mammals diversity and relationship with resources

We obtained 2,299 independent records of native mammals (including Cricetidae, *Cavia* aff. *aperea*, *Gracilinanus microtarsus* and *Philander frenatus*) including 31 native species, 27 out of them were medium- to large-bodied. Moreover, we recorded six exotic species (*Bos taurus*, *Bubalus bubalis*, *Canis l. familiaris*, *Equus caballus*, *Lepus europaeus* and *Sus scrofa*). Among areas, the richness of native mammals ranged from five to 16 species. Among the replicas with resources presence, mammal richness ranged from five to 16 (*Pinhão* presence), nine from 11 (Feijoa fruit presence), and from seven to 13 (without both resources).

Rarefaction curves did not show a clear pattern of increase of richness and independent records in relation to the resources available. Yet, some areas (e.g. PSB, RLM, PAB) showed that de richness and independent records increased with the presence of *Pinhão* and Feijoa fruits, and for CXR and RGF this relationship are partial (Figure 3). Temporally, we observed a reduction in mammal diversity in CXR, PSA and RLM congruent with the decreasing of *Pinhão* availability and in PSB the same pattern in relation to the Feijoa fruits availability (Figure 3). Diversity partitioning showed a marginal increase of the patterns of alpha and beta diversity with the presence of resources when compared with the absence of both resources (Figure 4). However, comparing the values of diversity proportionally at the number of replicas (mammal communities in space and time) we observed that the alpha, beta and gamma diversity of mammals are numerically larger than the replicas without both resources (Figure 4). Temporally, analyzing only the areas with temporal replicas in sequence, we found lower alpha diversity than the expected by chance and larger beta diversity than random when in the presence of *Pinhão* followed by their immediate absence. The same pattern was found with Feijoa such as conditioning, however the beta diversity was lower than expected in 2015 and larger in 2016 (Supporting Information S7).

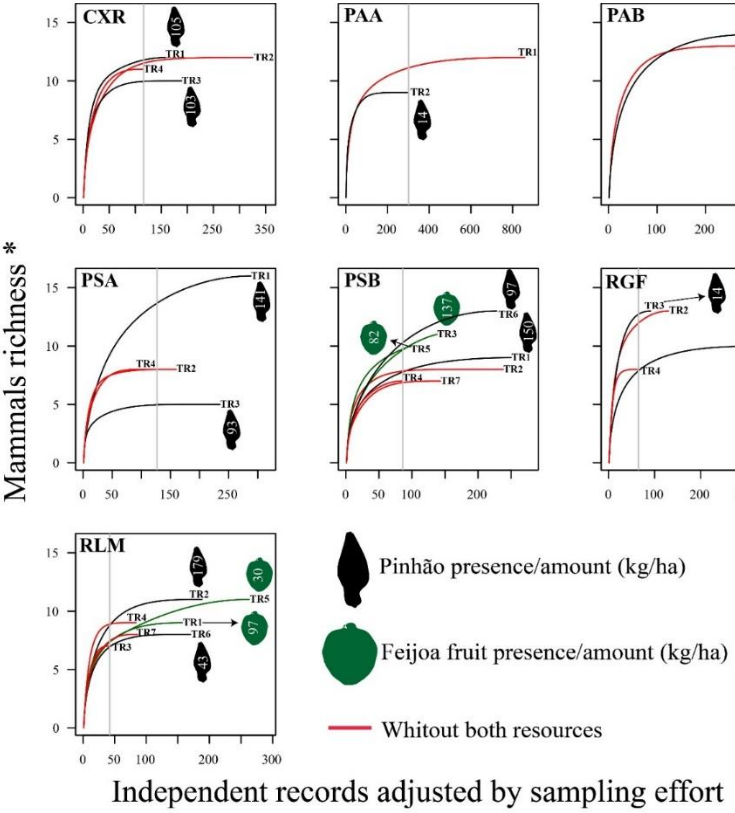

Figure 3. Rarefaction curves to mammals diversity per area and temporal replicas (with resources [*Pinhão* and Feijoa] and without resources) among seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil.

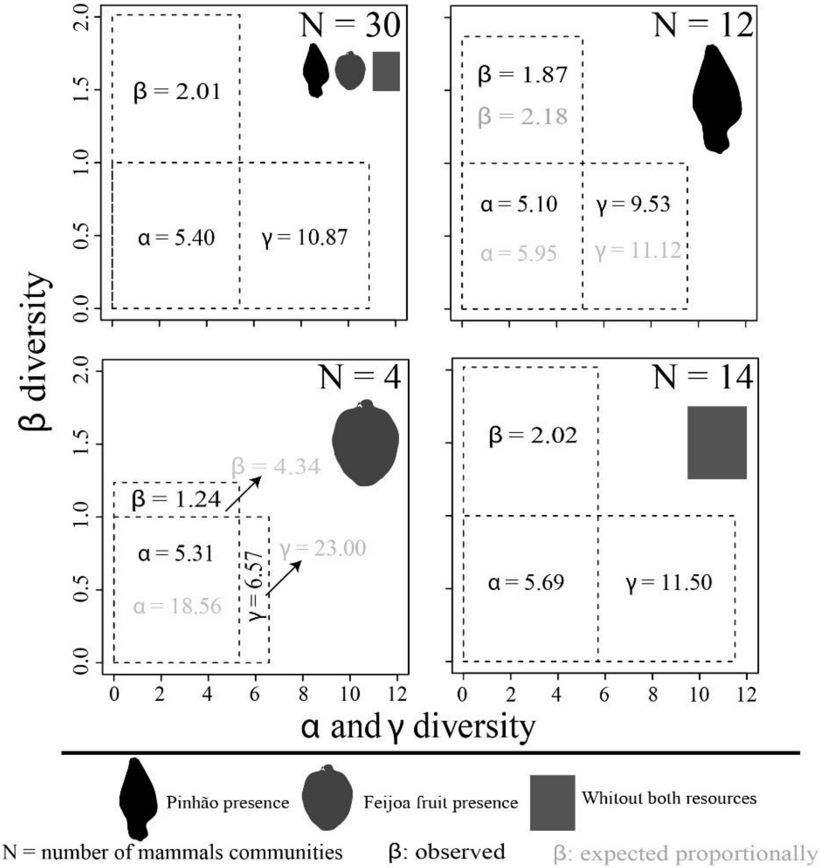

Figure 4. Spatiotemporal mammal diversity partitioning to in relation to the presence and absence of resources within seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil.

Plants response to mammal abundance into functional groups

Besides the trees (Araucaria and Feijoa), we recorded the richness of shrubby-arboreal species ranging from zero to 12 within subplots, and among area an average richness of 4.53 (±1.03). Whereby the demographic pattern aforementioned, we found a large variation in the individual's measures of tree species. The sum of the basal area of Araucarias (all classes) ranged from 3.8 to 5.92 m² and Feijoa ranged from 0.41 to 0.65 m² (Supporting Information S5). The RDA explained 88.8% of tree demography and morphometry variation. The first axis of ordination (RDA1) explained 55.8% of variation, and the negative portion of RDA1 showed a linking between the BA of Feijoas. The SMI of Araucarias classes and Araucaria regeneration were explained manly by medium-bodied abundance, numerically showing an increase in these metrics in relation to the increase in abundance of medium-bodied mammals. Yet, the positive portion of RDA1 showed a relationship between the SMI of Feijoa, BA of Araucarias and Feijoa regeneration with the small-bodied mammals abundance, also numerically increasing congruently with the increase of small mammal abundance. The second axis (RDA2) explained 33.0% of data variation and their negative portion showed a relationship between SMI of Feijoas, Araucaria regeneration, BA of Araucarias and SMI of Araucaria with the large-bodied mammals abundance, both indices increase with the increase of large mammal abundance. The positive portion of RDA2 showed a relation between plants richness and small-bodied mammals abundance, that also is a relationship numerically positive (Figure 5).

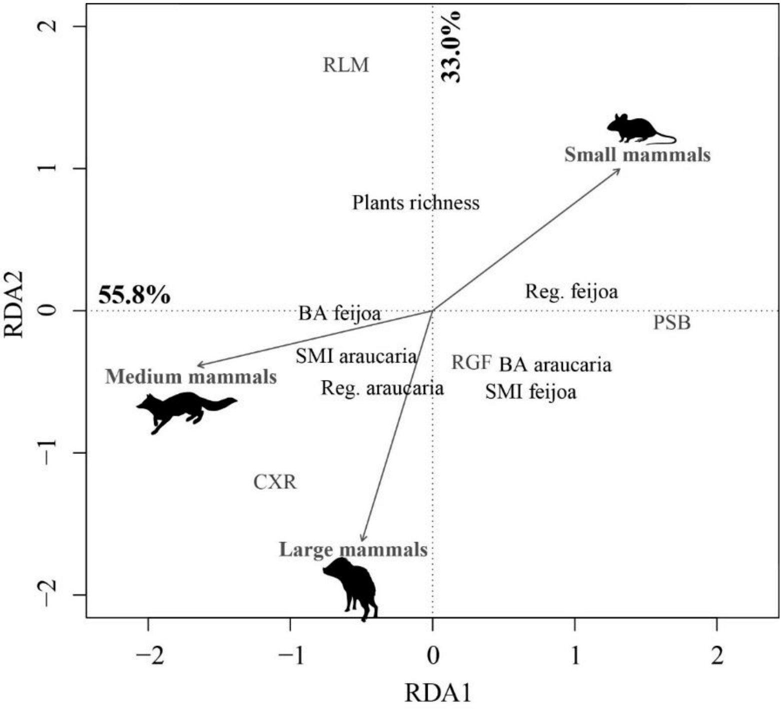

Figure 5. Redundancy analysis (RDA) to evaluate the proportion explained by the mammal abundance into functional groups (trophic level, body size and interacting or not with the Araucaria and Feijoa resources) on variation of the average richness of plants (shrubby-arboreal) species, the average SMI to tree species, the sum of trees species basal area and the ratio between seedling and adult of each tree species among seven areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil. Where: BA: basal area; SMI: Standardized Morisita Index; Reg.: regeneration.

Discussion

Several processes can modulate the population and community patterns along spatial and temporal scales, even at a continuous ecological gradient (Hutchinson 1957; May 1976; Agrawal et al. 2007; Bogoni et al. 2017). Our main results showed that – except for climatic conditions – the landscape, environment, trees demography and productivity are highly variable along the gradient of subtropical Atlantic Forest. Still, the mammal diversity is positively related, at least partially, to trees resources productivity in space and time. The demography and productivity of trees and their co-occurrence are mainly related to climatic and environmental features and mammals promote feedbacks on demography and forest composition. Thus, we identified a cycle of a biotic and abiotic process affecting ecological patterns – which also become processes into this ecological cycle, likely an emergent propriety. All these findings provide an idea of the high-complexity of ecological systems, the legacy of landscape and their elements domestication resulting in a niche construction. There is growing interest in the complexity of ecological systems, mainly through the concepts of non-linear dynamics, self-organization and emergent proprieties (Milne 1998; Cadenasso et al. 2006). However, the applicability of these concepts is abstrat to empirical ecologists (Anselin and Cho 2002). In this study, we reveal some of the processes (e.g. niche influences and community structuring) influencing patterns (e.g. diversity and demographic patterns). We showed that the diversity and ecological processes maintaining are a complex result of additive factors and cumulative cascade effects, which in historical terms spread since the end of the Pleistocene to modern times.

Lower minimal temperatures and larger canopy cover influence the demography of Araucaria, when lower canopy cover influences the Feijoa demography. The increase in Araucaria productivity among areas had a relationship with minor precipitation volumes and the Feijoa fruits productivity are related to colder areas. Climatic and environmental conditions *in loco* are factors that influence the Araucaria and Feijoa establishment (demography) and productivity (Gressler et al. 2006; Mattos 2011), at several niche dimensions. However, the patterns of demography in trees are mainly related with seeds availability, seed predation, patterns and movement of dispersion (i.e. where the seed was deposited), and other biotic interactions (e.g. competition and facilitation) (Janzen 1971; Duarte et al. 2007; Traveset et al. 2007). In relation to the productivity, Araucaria productivity is an exception, because it is dependent on climatic conditions (e.g. wind velocity), when Feijoa depends on a combination between pollinators and climatic variables (Gressler et al. 2006; Mattos 2011).

Tree productivity and demography are directly and indirectly affected by climatic niche, environment and their interactions with the mammal diversity (Moore et al. 2016). The richness and the number of independent records of mammals had an increase among spatial and temporal replicas when the resources are ascending, and showed a temporal delay. Fruit production generally enhance mammal diversity and biomass along several regions (Stevenson 2001; Mourthé 2014; Moore et al. 2016; Bogoni et al. submitted). Mammals and birds disperse large part of crop species in Neotropical environments, generating an important feedback to plants fitness and forest regeneration (Howe and Smallwood 1982; Vidal et al. 2014). As presumed, within a site in years when fruit abundance is low, frugivores populations can decline, due to lack of suitable food and in years when fruit abundance is high is expected a corresponding increase in frugivores' reproduction, survival, and so increasing population (Peres 2000; Milton et al. 2005). Many decades of studies have shown the same pattern, that available energy and primary productivity are highly important to determine the structure of communities (e.g. Hutchinson 1959; Connell and Orians 1964; Brown 1981; Currie 1991; Stevenson 2001).

Contrastingly, our results showed that the mammal become a process that influences forest composition. Araucaria's demography is positively linked with large-bodied mammals abundance, whereas Feijoa's regeneration and plant richness among areas are linked with the small-bodied mammals amount. Mammals play important roles that influence forest regeneration (Galetti and Dirzo 2013). Seed dispersal, seed predation, herbivory and pollination are direct effects of mammals on forest composition and the predation among these animals affects indirectly these dynamics (Peres and Palacios 2007; Peres et al. 2016). The demographic patterns and regeneration of Araucaria not only were related to large mammals, but also negatively with the small-bodied mammals. Large carnivores affect the abundance of their prey (e.g. small- to medium-sized animals) and the defaunation affects this equilibrium increasing the seed predation (Galetti et al. 2015). The Feijoa regeneration and plants richness showed an inverse relationship (i.e. both are related positively to small mammal abundance), because small mammals—

especially Rodents—heavily predate *Pinhão* and presumably this issue affects plants with small seeds at lesser intensity.

Another issue is the historical ecology of area and the historical importance since pré-Columbian people to local small-scale landowners (Reis et al. 2014; Mello and Peroni 2015). The past and current human influences in the local landscape continue a cascading effect on non-target species (Zeder 2016; Levis et al. 2017; Bogoni et al. submitted). Both Araucaria and Feijoa had a domestication and expansion process (Santos et al. 2009; Reis et al. 2014). Domestication exemplify niche construction by altering selection pressures and evolutionary trajectories on other organisms living within the niche constructed (Eriksson 2013; Zeder 2015; 2016). However, the exploitation of Araucaria for wood industry drastically reduced their population and distribution (Lacerda 2016), influencing the fauna. Another factor is the exploitation of *Pinhão,* a long-time practicance performed in subtropical Atlantic Forest areas that reduces the availability of resource to fauna (Souza 2007). Aditionally, local mammals also has suffered a high defaunation, compromising the patterns and process within FOM patches (Bogoni et al. 2016a). Thus, what the late-past promoted (e.g. Araucaria expansion favoring the local biota), the recent-past has withdrawn (e.g. logging and defaunation). The late-past expansion via indigenous people promoted or at least maintained the diversity, while the most recent actions (e.g. Araucaria logging and defaunation) reduced the diversity and integrity of ecological processes.

We conclude that the Araucaria and the Feijoa resources (i.e *Pinhão* and Feijoa fruits) are fundamental to local fauna within a threatened landscape. There are several feedbacks and emergent proprieties from climatic conditions, environmental characteristics, landscape features to trees demography and productivity. Still, these influenced the mammal fauna that which in turn provides feedbacks to forest composition. Our prospects are that the integrity of elements in highlands is paramount to maintaining the ecological process, and thus our hypotheses were corroborated. For conservation, our prospects are that is necessary a development of integrative conservation strategies since maintaining the Araucaria and Feijoa population viabilities, encourage the sustainable use of resources and promotes the mammals fauna conservation. Moreover, both for ecology and conservation issues our results showed how complex the ecosystems are, and extend the directions to understand and apply the issues here assessed in both Realms of environmental science.

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SUPPORTING INFORMATION

Supporting Information S1. Study areas to evaluate de spatial distribution and productivity of *Araucaria angustifolia* (Araucaria) and *Acca sellowiana* (Feijoa) and the implications to the mammals communities structuring and diversity within Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil. Where: M: FOM-Montane; A: FOM-Alluvial; AM: FOM-Alto-Montane; G: native grasslands.

Area	**Code**	**Year of Creation**	**Municipality**	**Latitude (S)**	**Longitude (O)**	**Altitude**	**Political Size (ha)**	**FOM**
PARNA Araucárias - Site West	PAA	2005	Passos Maia	26°47'44"	51°59'05"	887	12,841	M
PARNA Araucárias - Site East	PAB	2005	Ponte Serrada	26°49'36"	51°48'24"	1,122	12,841	M
Particular Area - Coxilha Rica	CXR	-	Lages	28°03'39"	50°17'42"	1,045	143*	A
RPPN Leão da Motanha	RLM	2008	Urubici	27°59'29"	49°22'31"	1,130	127	A
PARNA - Morro da Igreja	PSA	1961	Urubici	28°06'11"	49°29'36"	1,549	49,300	AM, G
PARNA São Joaquim - Santa Bárbara	PSB	1961	Urubici	28°08'40"	49°28'47"	1,539	49,300	AM, G
RPPN Grande Floresta das Araucárias	RGF	2011	Bom Retiro	27°53'57"	49°23'19"	1,000	4,019	A

* Cover by FOM, because there are no politic limits as a Conservation Unit.

Supporting Information S2. Sampling effort to evaluate the demography and spatiotemporal resource productivity of trees (Araucaria and Feijoa) within seven highlands areas of subtropical Atlantic Forest, Brazil. Where: PA/TA: plot area/total area size; Arauc.: Araucaria; A: absent in area; P: presence in the area; TS: transect size; SW: seeds weighted; FW: fruits weighted. Areas code in Supporting Information S1.

	Trees													
	Demography					**Productivity**								
Area	**N plots**	**Ratio**	**Year**	**Araucaria**	**Feijoa**	**TS**[1]	**N Araucaria**	**Year**	**N *Pinhas***[2]	**SW**	**TS**[1]	**N Feijoa**	**Year**	**FW**
PAA	8	0.007	14	P	A	18.5	39*	14-16	0, 14	277	-	-	-	-
PAB	4	0.002	14	P	A	11.3	39*	14-16	0, 14	277	-	-	-	-
CXR	4	0.336	15	P	P	1	17	15-16	4, 6	668	-	-	-	-
RLM	4	0.379	15	P	P	1.8	40	15-16	11, 15	1791	1.15	7	15-16	210
PSA	4	0.003	15	P	A	5.2	30	15-16	11, 15	1791	-	-	-	-
PSB	4	0.003	15	P	P	3.3	40	15-16	11, 15	1791	1.5	14	15-16	420
RGF	4	0.012	15	P	P	3.3	40	15-16	10, 4	1467	0.7	7	15-16	210
Total	**32**	**-**	**14-15**	**-**	**-**	**44.4**	**245**	**14-16**	**64**	**4203**	**3.4**	**28**	**15-16**	**840**

Supporting Information S3. Sampling effort of medium- to large-bodied mammals among seven highlands areas of subtropical Atlantic Forest, Brazil. Where: NCT: number of operant camera-traps; Ndays: number of operant days; CTD: camera-trap-days; Areas code in Supporting Information S1.

Area	**Year**	**Period**	**Temporal (TR)**	**Replica**	**Resource**	**Average Distance**	**NCT**	**Ndays**	**CTD**
PAA	2014	Summer	TR1		NA	7,329 (4,272)	9	34	306
	2014	Winter	TR2		*Pinhão*		5	34	170
PAB	2014	Summer	TR1		NA	8,627 (4,734)	9	30	270
	2014	Winter	TR2		*Pinhão*		10	31	310
CXR	2015	Winter	TR1		*Pinhão*	404 (236)	9	51	459
	2016	Summer	TR2		NA		8	30	240
	2016	Winter	TR3		*Pinhão*		8	34	272
	2017	Summer	TR4		NA		9	36	324
PSA	2015	Winter	TR1		*Pinhão*	2,207 (1,416)	9	47	423
	2016	Summer	TR2		NA		9	36	324
	2016	Winter	TR3		*Pinhão*		6	32	192
	2017	Summer	TR4		NA		5	38	190
RGF	2015	Winter	TR1		*Pinhão*	1,603 (1,920)	8	49	392
	2016	Summer	TR2		NA		8	61	488
	2016	Winter	TR3		*Pinhão*		9	55	495
	2017	Summer	TR4		NA		9	34	306
RLM	2015	Autumn	TR1		Feijoa	938 (559)	10	60	600
	2015	Winter	TR2		*Pinhão*		6	55	330
	2015	Spring	TR3		NA		10	30	300

	2016	Summer	TR4	NA		7	30	210
	2016	Autumn	TR5	Feijoa		10	60	600
	2016	Winter	TR6	*Pinhão*		8	31	248
	2017	Summer	TR7	NA		9	41	369
PSB	2014	Winter	TR1	*Pinhão*	1,904 (1,043)	9	46	414
	2015	Summer	TR2	NA		6	36	216
	2015	Autumn	TR3	Feijoa		20	60	1200
	2015	Spring	TR4	NA		20	30	600
	2016	Autumn	TR5	Feijoa		20	45	900
	2016	Winter	TR6	*Pinhão*		16	31	496
	2017	Summer	TR7	NA		8	39	312
Total	**2014-2017**	**-**	**30**	**-**	**3,287 (3,281)**	**289**	**1,226**	**11,956**

Supporting Information S4. Landscape cover of seven highlands areas of subtropical Atlantic Forest, Brazil. Where: FOM: Mixed Ombrophilous Forest; FOD: Dense Ombrophilous Forest; GRA: grasslands and open areas (including non-native grasslands); SIL: Silviculture (*Pinus* spp. and *Eucalyptus* spp.); WAT: Water bodies. Areas code in Supporting Information S1.

Area	**Percentage**						
	Sampled Area (ha)	**Total**	**FOM**	**FOD**	**GRA**	**SIL**	**WAT**
PAA	31,400	100	33	0	28	17	22
PAB	31,400	100	46	0	19	24	11
CXR	31,400	100	19	0	58	22	1
PSA	31,400	100	36	42	20	1	1
PSB	31,400	100	65	0	33	1	1
RLM	31,400	100	36	41	21	1	1
RGF	31,400	100	75	0	23	1	1

Area	**Area (ha)**						
	Sampled Area (ha)	**Total**	**FOM**	**FOD**	**GRA**	**SIL**	**WAT**
PAA	31,400	31,400	10,362	0	8,792	5,338	6,908
PAB	31,400	31,400	14,444	0	5,966	7,536	3,454
CXR	31,400	31,400	5,966	0	18,212	6,908	314
PSA	31,400	31,400	11,304	13,188	6,280	314	314
PSB	31,400	31,400	20,410	0	10,362	314	314

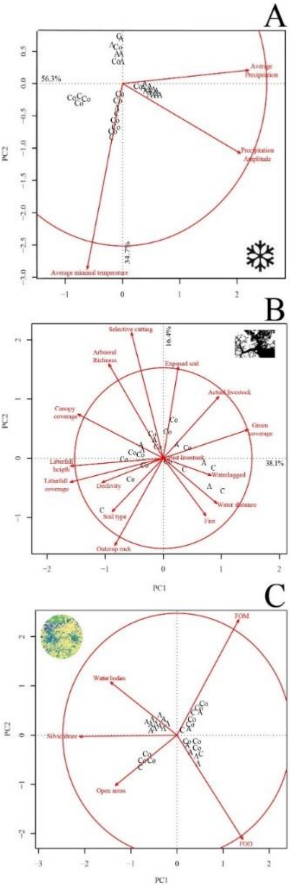
RLM	31,400	31,400	11,304	12,874	6,594	314	314
RGF	31,400	31,400	23,550	0	7,222	314	314

Supporting Information S5. Demographic patterns (ind/ha and female [F]/ha**), height (H) and canopy size (C) by classes of *Araucaria angustifolia* and *Acca sellowiana* within seven highlands areas of subtropical Atlantic Forest, Brazil. Areas code in Supporting Information S1. * All formations within a buffer of 31,400 ha; ** Only to Araucaria

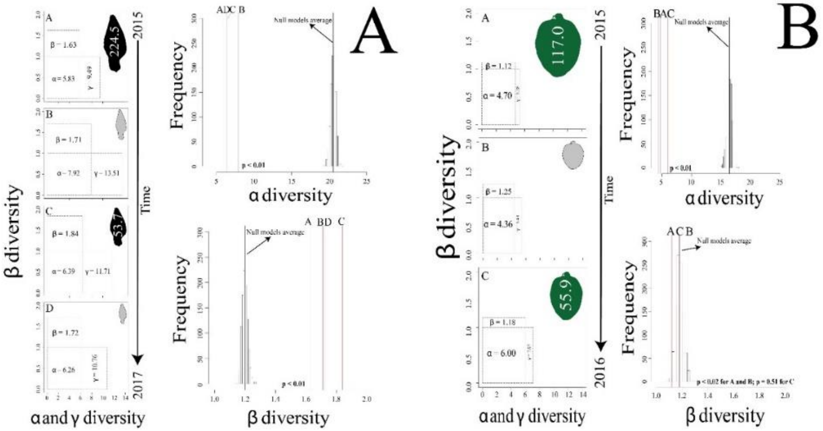
Area	**FOM (ha)***	***Araucaria angustifolia* (Araucaria)**												
		Adult				**Juvenile**			**Seedling**			**Undefined**		
		Ind/ ha	**F/ha**	**H (m±SD)**	**C (m±SD)**	**Ind/ ha**	**H (m±SD)**	**C (m±SD)**	**Ind/ ha**	**H (m±SD)**	**C (m±SD)**	**Ind/ ha**	**H (m±SD)**	**C (m±SD)**
CXR	5,966	79.2	39.6	14.5 (1.5)	11.9 (2.1)	72.9	4.2 (2.3)	2.9 (2)	2200.0	0.3 (0.1)	0.2 (0.1)	50.0	10.4 (1.7)	5.9 (2)
PAA	10,362	18.8	9.4	17.4 (2.9)	-	64.8	8.4 (5.3)	-	97.7	0.6 (0.4)	-	3.9	-	-
PAB	14,444	39.6	19.8	21.6 (6.2)	-	75.0	10.2 (8.9)	-	93.8	0.8 (0.3)	-	6.3	-	-
PSA	11,304	89.6	49.6	12 (2.4)	9.4 (2.8)	29.2	3.6 (1.7)	2.6 (1.7)	466.7	0.7 (0.2)	0.6 (0.2)	2.1	-	-
PSB	20,410	83.3	34.2	12 (4.1)	10.8 (5.8)	104.2	4 (2.2)	2.4 (1.6)	200.0	0.7 (0.6)	0.6 (0.3)	-	-	-
RGF	23,550	89.6	44.8	15.7 (3.8)	12.1 (4.6)	229.2	6.3 (3.4)	3.4 (2.1)	1600.0	0.3 (0.2)	0.2 (0.2)	50.0	10.7 (2.8)	6.3 (3.2)
RLM	11,304	50.0	27.5	17.7 (2.7)	15.6 (3)	191.7	4.8 (2.6)	2.4 (1.5)	333.3	0.9 (0.2)	0.4 (0.2)	-	-	-

Area		***Acca sellowiana* (Feijoa)**												
		Adult				**Juvenile**			**Seedling**			**Undefined**		
		Ind/ ha	**F/ha**	**H (m±SD)**	**C (m±SD)**	**Ind/ ha**	**H (m±SD)**	**C (m±SD)**	**Ind/ha**	**H (m±SD)**	**C (m±SD)**	**Ind/ ha**	**H (m±SD)**	**C (m±SD)**
CXR		41.7	-	6.5 (1)	6.4 (1.9)	-	-	-	66.7	0.55 (0)	1 (0)	-	-	-
PAA		-	-	-	-	-	-	-	-	-	-	-	-	-
PAB		-	-	-	-	-	-	-	-	-	-	-	-	-
PSA		-	-	-	-	-	-	-	-	-	-	-	-	-
PSB		12.5	-	5.6 (0.9)	7.2 (1.1)	-	-	-	200.0	3 (0.2)	2 (0.2)	-	-	-
RGF		39.6	-	5 (1.3)	4.8 (1.1)	-	-	-	333.3	4.1 (1.5)	2.6 (1.3)	-	-	-
RLM		22.9	-	6.3 (1.6)	5.9 (2.5)	-	-	-	133.3	3.1 (0.5)	2.1 (0.1)	-	-	-

Supporting Information S6. (A) Principal components analysis (PCA) of correlation to evaluate the *Araucaria angustifolia* (Araucaria) and *Acca sellowiana* (Feijoa) co-occurrence into seven areas of FOM in Brazilian highlands in relation to their climatic conditions; (B) PCA of correlation to evaluate the Araucaria and Feijoa co-occurrence in relation to environmental conditions; (C) PCA of correlation to evaluate the Araucaria and Feijoa co-occurrence in relation to landscape features. Where: A: plots with only Araucaria presence; Co: trees co-occurrence plots



Supporting Information S7. (A) Spatiotemporal mammals diversity partitioning to in relation to the presence and absence of *Pinhão* within three areas of Mixed Ombrophilous Forest (FOM); and (B) Spatiotemporal mammals diversity partitioning to in relation to the presence and absence of Feijoa fruits within two areas of Mixed Ombrophilous Forest (FOM) in subtropical Atlantic Forest highlands, Brazil. All values of alpha and beta diversity are compared with 1000 null models. The values in *Pinhão* and Feijoa silhouettes are the productivity amount (kg/ha). The red bars in the right graphic are the observed alpha and beta diversity in each temporal replica.



CAPÍTULO 4

The human dimension of Araucaria Forest: resource and landscape uses, niche construction and ethnozoology

(A dimensão humana das Florestas de Araucárias: uso dos recursos e das paisagens, construção de nicho e etnozoologia)

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Pecari tajacu (Linnaeus, 1758) [tatetos] registrada em Mata de Araucária na data de 13 de fevereiro de 2015 no Parque Nacional de São Joaquim, localidade de Campos de Santa Bárbara (28°09’14” S; 49°38’25” O; 1593 m.s.n.m). Foto: Bogoni, 2015.

The human dimension of Araucaria Forest: resource and landscape uses, niche construction and ethnozoology

RH: Araucaria Forest ethnoecology

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Abstract

Local knowledge is useful to understand historical ecology and process, especially in an intensely managed landscape with domesticated trees promoting niche spaces construction. We studied the recent history of Araucaria Forest patches, their resources (Araucaria seeds and Feijoa fruits), landscape use and consequently the niche construction by landscape management within the highlands of subtropical Atlantic Forest of South America. We investigated the local people's perception about native vertebrates and their interactions with tree species by recording the main events that can modify the landscape, applying a semi-structured questionnaire to 36 local informants within the São Joaquim National Park and surroundings, in Southern Brazil highlands. We analyzed the data with descriptive statistics based on percentages of responses, central and variation tendencies measures. We used a network approach to measure the interaction between mammals and the trees species (i.e. Araucarias and Feijoas). Our results showed that that the local management along time maintained the vegetation mosaics across local landscape, the resources productivity and intensity of use are traditionally maintained during longer periods. According to local people, within the local vegetation mosaic the mammalian richness is lower variable. We conclude that the Araucaria and Feijoa are essential to local people, as well as to their domesticated animals and the native fauna. The management maintains the landscapes mosaics within Atlantic Forest highlands. Human footprint on landscape and resources management can construct niche spaces that influences the local diversity patterns and ecological process.

Key-words: mammals, resources, local people, interactions, species distribution, historical ecology, niche construction

Introduction

Traditional societies around the world have developed a sophisticated understanding of their biophysical environment and their practices and knowledge are grounded in ethical, spiritual and cultural values (Berkes and Folke 1998; Berkes 2008). Traditional knowledge is considered the evolving body of knowledge, and practices handed down through generations about the relationships of living beings with one another and with their environment (Berkes and Folke 1998). The local knowledge may flow vertically or horizontally within the human communities, shared extensively or only partially by the local members and be useful for conservation ecology and management of resources and landscapes (Folke 2006; Berkes 2008). The classic idea of ecology dissociated from human beings biased, assuming that peoples interfere directly in ecological and evolutionary processes (Albuquerque et al. 2015). Thus, studies involving peoples and their relation to the environment, and the factors that influence these relationships, can be based on same principles of ecological theories (Begossi 1993).

The interactions among people, resources and landscapes can be considered a niche construction, defined as how and why humans domesticated some species and so have transformed Earth’s biota, landforms, and atmosphere, and shaped the human cultural trajectory and development at multiple scales (Zeder 2016). Local knowledge is a tool for evaluating patterns and process of niche spaces construction, species distribution and abundance within local biological communities (López-Arévalo et al. 2011; Zeder 2016). An increasing number of studies addressed the local ecological knowledge has developed in Brazil in recent decades, especially in Amazonian region (Redford and Robinson 1987; Heckenberger et al. 2007; Iwamura et al. 2016). Within the subtropical Atlantic Forest there are also some studies showing a historical relationship between humans and nature, with species and landscape domestication (Reis et al. 2014; Mello and Peroni 2015). Conceptually, landscape domestication is human intervention in the landscape components resulting in changes in evolution, ecology, interactions and species demography (Clement 1999; Levis et al. 2017). Moreover, the subtropical Atlantic Forest highlands are extremely endangered by climatic changes, thus have been utilized as a proxy for conservation strategies (Lacerda 2016). The species in this mosaic also have relations with local human population, from beneficial (e.g. tree domestication, improvement and expansion of distribution and abundance) to damaging effects (e.g. hunting, defaunation and exotic species introduction) (Santos et al. 2009; Bogoni et al. 2016).

In forest patches, Myrtaceae and Lauraceae are the main families forming the middle and lower strata (Rambo 1951), generally closely associated with the threatened conifer *Araucaria angustifolia* (Araucaria) that is characteristic of the Ombrophilous Mixed Forest (FOM) (Rambo 1951; Reitz and Klein 1966). Within FOM a vegetation mosaic of highlands (e.g. upper montane forest, swamps, and native grassland), spatially restricted and highly endangered are found (Lima et al. 2015; Lacerda 2016; Souza et al. 2016). Flora in highlands, is dominated by a few Myrtaceae species, typically characterized by small fruits (< 1 cm of diameter) (Gressler et al. 2006; Mazine and Souza 2008). *Acca sellowiana* [Berg] Burret (Feijoa) is an execption to this small-sized fruit pattern. Feijoa is a native tree to southern Brazil and northern Uruguay, with occurrence associated to an altitude higher than 800 meters above sea level (m.a.s.l.) and underwent a domestication within subtropical highlands (Santos et al. 2009; Amarante and Santos 2011).

Landscapes, Araucaria and Feijoa has received historical anthropogenic influence, from mid-Holocene to currently, with the cattle presence (an allochthones element managed by > 100 years) promoting a certain level of domestication of landscape and some tree populations *in situ* (Bitencourt and Krauspenhar 2006; Santos et al. 2009; Reis et al. 2014; Mello and Peroni 2015). The Araucaria and Feijoa provide resources (*Pinhão* [Araucaria seeds] and Feijoa fruits) for local fauna and local people (Reitz and Klein 1966; Reis and Ladio 2012; Bogoni unpublished data). Araucaria had its expansion favored by anthropogenic activities. Since 4,000 y.b.p. – leaving from Pleistocene refugia – maintaining a *quasi*-constant expansion performed mainly by Xokleng and Kaingang ethnics groups and Creole farmers (Bitencourt and Krauspenhar 2006; Reis et al. 2014). This expansion was until 100 y.b.p. since then it has suffered logging from 1920s to 1990s (Eduardo 1974; Lacerda 2016). Feijoa also is a species managed by local people; however it is more commercially exploited in other countries (Amarante and Santos 2011). Oftentimes, local people's footprint can be used as a baseline for conservation strategies and environmental protection into a socioecological framework (Folke 2006).

Thus, we aimed to assess the relationships between the people and the landscape components within a Protected Area with land problems (i.e. expropriations, land indemnification and territorial demarcations) to understand the historic of Araucaria Forest patches, the resource and landscape use that results in a niche construction. Moreover, we aimed to understand the local human perception about native vertebrates and their interactions with *Pinhão* and Feijoa fruits, the timeline of main events able to modify the landscape and the futures perspectives under the vision of local peoples. We hypothesize that the Araucaria Forest patches within an area of Atlantic Forest highland had and still has great human influence, creating human-induced niche spaces, and thus this human-maintenance of forest-grassland mosaics increases the diversity and turnover of mammals. Still, local people, native fauna and domestic animals share the resources of FOM (*Pinhão* and Feijoa fruits) influencing the dynamic of forest patches and landscapes as a whole with implications for future perspectives at a conservation ecology approach.

Material and Methods

Study area

We carried our this research in highlands of National Park of São Joaquim (NPSJ) and damping zones, within the municipalities of Urubici and Bom Jardim da Serra, Santa Catarina highlands (Figure 1). The region of study is dominated by Mixed Ombrophilous Forest (Araucaria Forest; FOM), falls within the humid subtropics (Cfa according to the Köppen-Geiger classification) (Veloso et al. 1991; Peel et al. 2007). In general, the seasons are well-defined and rainfall is evenly distributed throughout the year with an annual average of 1,700 mm. Temperatures vary greatly during the year, ranging between -10°C and 40°C with an annual average between 11ºC and 19° C (Monteiro 2001; Peel et al. 2007). The area of NPSJ is a Protected Area (Brasil 1961; Brasil 2000) with the objective of conservation of Dense Ombrophilous Forests (FOD), Mixed

Ombrophilous Forest (FOM; Araucaria Forests) and high altitude grasslands; also the conservation of samples of biodiversity – especially the threatened conifer Araucaria – of the south of Brazil (Lacerda 2016). The total area of NPSJ is nearly 49,800 ha with a perimeter of 114 km, yet many areas are under litigious or not indemnified due to inaccurate delimitation by Federal Decree n° 50922/1961 (Brasil 1961), which generated a new territorial demarcation by Brazilian Law n° 13273/2016 (Brasil 2016).

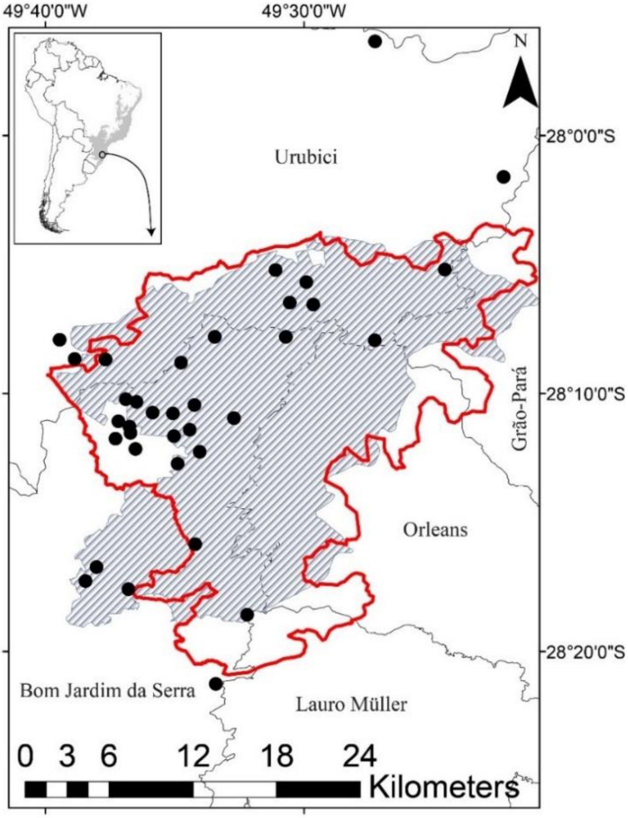

Figure 1. Localization of 36 interview's proprieties (black circles) within the National Park of São Joaquim (NPSJ) and surroundings, municipalities of Urubici and Bom Jardim da Serra, Santa Catarina

highlands. The dashed polygon are the NPSJ area according to Brazilian Decree n° 50.922/1961 and the red polygon are the NPSJ area according to the Brazilian Law n° 13273/2016. The black lines are the municipalities limits, therefore towards the east in the municipalities of Grão-Pará and Orleans the vegetation is Dense Ombrophilous Forest (Atlantic Forest *stricto sensu*) there were no interviewees.

Ethnoecological data

To elaborate a matrix of quantitative and qualitative data, which involving historical land-use aspects, resource use and management both tree species Araucaria, Feijoa and mammals, we use a semi-structured questionnaire (Bernard 1994), containing 42 questions to local people (Supporting Information S1). We used the "snowball technique" to increase the number of informants, with the informants asked to identify others for inclusion in the sample (Bailey 1982; Bernard 1994) until aimed the sample saturation. The main questions blocs are about historical ecology: i.e., aiming to evaluate how, when and for what reasons potentially has expansion or reduction of forest areas across the time, and the perception about possible variations on richness and abundance in local medium- to large-bodied mammals. Yet, the questions address specific issues about the vegetal species, as productivity variations and resource-use and mammals fauna interactions with the two tree species.

To access the traditional knowledge requires an "informed consent" agreement with informants, whereby he agrees to be interviewed (Supporting Information S2) according to current Brazilian legislation. The survive has authorized by Brazilian Institute of Diversity Conservation (ICMBio) on number 47255 (2015-June-01) and opinion sets Ethics Committee in Research with Human (CEPSH) of Federal University of Santa Catarina, and Ministry of Health – National Health Council – National Committee for Ethics in Research (CONEP) on number 1095964 (2015-August-08).

Data analysis

We use descriptive statistics based on percentages of responses, central and variation tendencies measures. To explore the diversity of medium- to large-bodied native mammals – and including Cricetidae and

Cavia aff. *aperea*, due their well-known importance as Araucaria and Feijoa interactors) – we also used used descriptive statistics

We built a network (Newman 2004; Boccaletti et al. 2006) to analyze the general topology of mammals and resource (*Pinhão* and Feijoa fruits) interactions, linking the number of citation of each animal species to the resources they use. We obtained two quantitative network metrics: (1) the mean degree of resources and animals (native mammals, well-known birds [large-bodied, commons and with easy identification], exotic mammals and domestic species); (2) connectivity (Boccaletti et al. 2006; Olesen et al. 2007; Pires et al. 2011). Mean degree is the number of interactions each node has (i.e. resources and animals), connectivity (C) is the proportion between the number of interactions observed in relation to the possible number of interactions (Boccaletti et al. 2006; Pires et al. 2011).

Results

Social and spatial characterization

During November of 2016 and January of 2017, we interviewed 36 informants – two women and 34 men, generally with their families together during the interviews – with an average age of 61.1 (±14.2; from 28 to 91) years old. The informants are resident in local for 43.3 (±20.9) years with the proprieties belonging to their families by 125.4 (±81.4) years on average. This sample represents 36 proprieties and is distributed within Urubici-SC (N = 11; 30.5%) and Bom Jardim da Serra-SC (N = 21; 69.5%) municipalities (Figure 1), southern Brazil, with an amount of 10,898 ha of land. Among the proprieties, circa of ¾ (N = 28) are within the NPSJ limits (considering the last territorial demarcation, Brazilian Law n° 13273/2016 [Brasil 2016]) and only 35.7% (N = 10) of proprieties are indemnified by Brazilian Government, a process that starts in 2007. On average, the properties have a size of 302.7 (±438) ha, located at an average altitude of 1,491 (±126.6) meters above sea level (m.a.s.l.).

History of use and productivity of Araucaria and Feijoa within forest patches

According to the informants, the local Araucaria logging was started in the 1940s with a cut of individuals usually above 30 cm (from 25 to 40 cm) of diameter at breast height (DBH). Before the end of logging (circa the 1980s), the Araucarias trees remnants in local patches have 79.4 (±31.6) years old, ranging from 40 to 200 years. The forest (FOM) cover at > 20 years ago were on average 53.2% and currently it occupies 56.7% of the proprieties, with the remaining territory formed by grasslands. The productivity of *Pinhão* in the past (> 20 years ago) was intermediary (from 70 to 120 kg/ha^{-1}; 50% of informants [N = 18]) and are the same values currently. Actual productivity of *Pinhão* is 107.3 kg/ha^{-1} (±138.5) and only three informants indicated a decrease in productivity, one due to the uncommon phenomena of "*lag snow*" and others two due to the "*absence of cold in right season*". One informant reported that the productivity is increased due the input of new productive females (i.e. seedling of past) in the Araucarias populations. Circa 20% (N = 5) of informants related that was planted Araucarias in proprieties, on average at 33 years ago. Feijoa productivity was predominantly high (>10 kg/per tree; 39% of informants [N = 14]) and currently was maintained in this condition (i.e. high). Feijoa fruitification occurs during February to April and produce 13.4 (±8.7) kg/per individual. Yet for both resource, all informants related that are productivities cycles (during 3 to 5 years, varying from high to low productivity).

The establishment of Araucarias trees are linked mainly to slopes areas and fertile soil, 58.3% (N = 21) and 13.9% (N = 5) respectively, others 22.2% (N = 8) recognized that no have a specific condition to Araucaria establishment, yet are *quasi*-unanimous that Araucaria are unable to established in the current grasslands areas. For Feijoa establishment 39.4% (N = 13) of informants recognized that no have a specific condition, others informed that are linked to rivers borders (15.1%; N = 5) Araucarias presence (12.1%; N = 4) and region (12.1%; N = 4).

The *Pinhão* use is common in all proprieties, begin used an average of 125.4 (±102.2) kg/harvest, and the Feijoa consume is low, representing 8.7 (±9.4) kg/harvest only in 75% (N=27) of proprieties, but in 100% of which Feijoa is present. The *Pinhão* sale is 1,298 kg (±1,134) per harvest in each propriety and remaining in the forest in average 67.2%

(±35.1) of total production. Asked about Araucaria and Feijoa seedling, the majority no manipulated the individuals; however, three informants cut the Araucaria seedlings, when four people prune the Araucaria seedlings to obtain the best development. The time of use the landscape with cattle breeding 126 (±82.6) years, farming is 164.6 (±95.1) years, *Pinhão* extractions are 128.3 (±82.7) years and Feijoa extraction by 146.7 (±80.5) years. The landscape management is characterized by the use of fire (2 in 2 years, generally) and scouring (4 in 4 years, generally) to maintain the grassland areas, throughout the time that the properties belong to the families. Moreover, the density of adult cattle along the time is on average 0.436 (±0.14) individuals per hectare.

Vertebrates and interactions

Jointing the information from all interviewed, we recorded 32 medium- to large-bodied mammals, including two exotic species (*Lepus europaeus* [lebre] and *Sus scrofa* [javali]). *Didelphis* and *Leopardus* (except *L. pardalis* [jaguatirica]) was included at genera level, together with Cricetidae and *Cavia* aff. *apera* summed 34 species (Supporting Information S3 and S4). Yet, the richness informed are variable ranging from seven to 24 mammals species (including Cricetidae and exotic species). The main sighted species are *Nasua nasua* (quati) (27.7%; N = 10), lebre (27.7%, N = 10), *Lycalopex gymnocercus* (graxaim-do-campo) (13.9%; N = 5) and *Mazama gouazoubira* (13.9%; N = 5) mainly due abundance, dog-conflict, diurnally activities and/or use of open areas. The species with low sightings was *Puma concolor* (leão-baio) (72.3%; N = 26) – related by many informants such as a predator of young cattle and sheep – due is an elusive species and that occupies large-areas. More than 1/3 of informants (N = 13) perceived a decrease in species richness and 2/3 (N = 23) in species abundance, linked mainly to the hunting, predation (e.g. armadillos by leões-baios), and changes in landscape (reflex of the past selective logging together with the subsistence hunting and currently to native grassland changing to “*massegas*”: dense herbaceous-shrub vegetation, characterized by the presence of *Pteridium* spp., *Bacharis* spp., *Drimys* spp. and *Myrcia* spp.). The species with largest population decrease are *Dasypus* spp. (tatu-mulita and tatu-galinha) and the species most cited as extinct locally are *Ozotoceros bezoarticus* (veado-campeiro), *Allouatta guariba* (bugio) and *Sapajus nigritus* (macaco-prego).

By unanimity among the informants, the *Cyonocorax caeruleus* (gralha-azul) are the main *Pinhão* dispersers, yet four informants also cited the Cricetidae (native small rodents), *Pyrrhura frontalis* (tiriva) and the *Penelope obscura* (jacú) such as *Pinhão* disperser, and only one informant related that the *Dasyprocta azarae* are *Pinhão* disperser. The network of interaction among vertebrates and *Pinhão* and Feijoa (including seed predation and seed dispersal) showed that the average degree of tree resource is 27 and the animals' degree is 1.8 (Figure 2), among them 20 native mammals (62.5%) have a relationship with the resources, 18 (56.2%) them with Araucaria and 17 (53.1%) with Feijoa. The network connectance was high (C = 0.9).

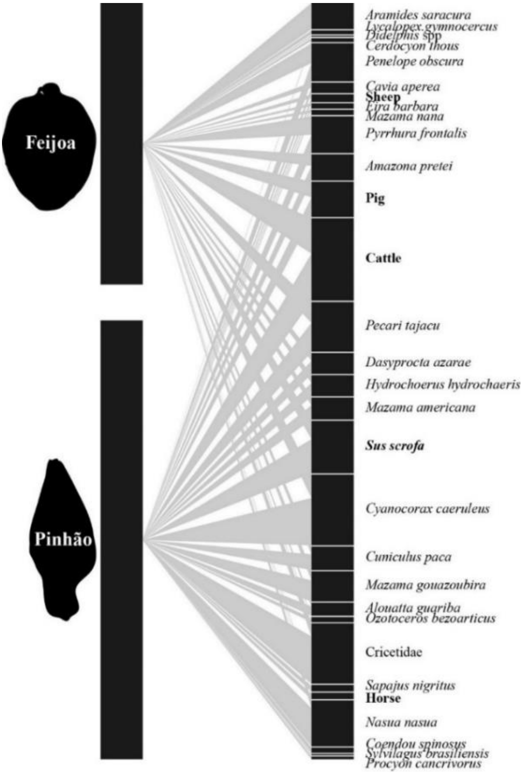

Figure 2. Bipartite network among resources of Mixed Ombrophilous Forest (FOM) and animals (native mammals, well-known birds, exotic

species and domestic species) based on information produced by local people resident within the National Park of São Joaquim (NPSJ) and surroundings, Santa Catarina highlands. Allochtonus elements (i.e. non-native species) are highlighted in bold

Timeline and future perspectives

According to the informants, the past decades (≤ the 1980s) were characterized by the reduction of forest, resources (*Pinhão* and Feijoa fruits) and mammals (mainly herbivores). Recent decades (> the 1980s) are determined by an increase in forest cover, resources amount and abundance of carnivores. Yet, herbivores and omnivores mammals abundance continue decreasing (Figure 3). Circa 60% (N = 22) of informants perceived changes in local climate, mainly (N = 11; 30.6%) the extremes (colder winter and warmer summer) and increase in annual temperature (N = 8; 22.2%). However, when the informants were questioned about the distribution of Araucaria, Feijoa and mammals against a temperature increase scenario, on average 71.3% of then manifested that there were no changes in the actual distribution of Araucaria (mainly in slopes areas), Feijoa (colder areas in association with Araucaria) and mammals (within the landscape as a whole).

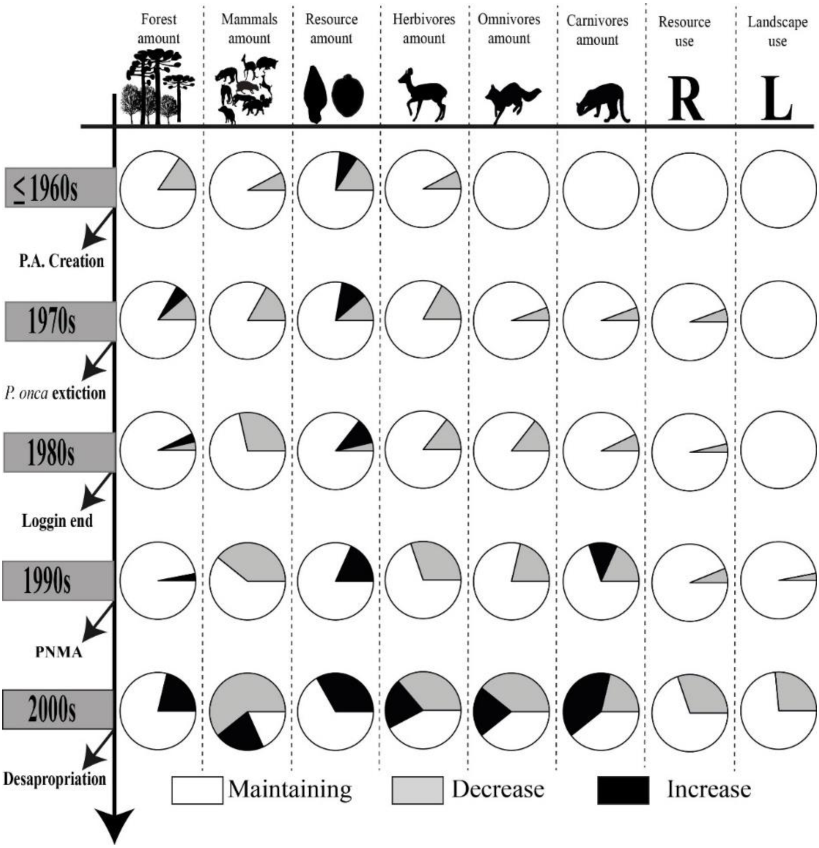

Figure 3. Timeline based on information provided by 36 interviews with local resident within the National Park of São Joaquim (NPSJ) and surroundings, Santa Catarina highlands. Where: P. A.: Protected Area; PNMA: Brazilian Program of Environment implementation.

Discussion

Several ecosystems are profoundly influenced by human management. Local people depend on the physical world of the landscapes, creating new niche spaces or rearranging them (Laird 1999; Zeder 2016). The historical ecology is part of convergent trends toward transdisciplinary science, eroding the scientific boundaries between the natural and cultural science (Baleé 2006; Albuquerque et al. 2017; Armstrong et al. 2017). Accordingly, the main result of our research showed that the fire and the cattle management along the time are the main maintaining of landscape mosaics, resulting in a typical human-induced niche construction. Cattle is an allochthonous element that has been managed for a long time (> 100 years) by local small-scale landowners in subtropical highlands and their impact can change the forest composition (Mello and Peroni, 2015). The combined regimen of fire and cattle grazing contribute to the maintenance of the forest-grassland vegetation mosaic (Oliveira and Pillar 2004). Yet, the contribution to the mosaic maintenance is associated with other factors, from a long-term historical perspective. The reconfiguration of the proportion of animal and vegetal elements within the landscapes can be associated both by Pre-Colonial practices (e.g. Araucarias expansion by indigenous people favoring the associated fauna) and by contemporaneous activities (e.g. Araucaria logging and mammalian defaunation [i.e. an inverse process]). The selective logging of Araucarias made that remained into the forest patches only individuals with DHP > 30 cm, promoting a densification of small unproductive individuals.

In Santa Catarina state, circa 67% of forest coverage had constituted by Araucaria Forest (Mattos 1972). Yet, due to logging currently remain only from 3% to 13% of FOM (Koch and Corrêa 2002; Bauermann and Behling 2009). In the NPSJ region, the average age of remnant Araucarias according to the informants are 79.4 years, representing trees ranging from 56.2 to 71.5 of DHP (according Ricken 2014 and Mattos et al. 2007 incremental rates), i.e. the majority of these individuals are the remnant (DHP > 30 cm) of the past logging. The logging in the 1940s are responsible for 38% of exportation of Santa Catarina state, 70% from 80% constituted by Araucarias (Eduardo 1974) and this exploitation is continuous until the 1980s/1990s, being the logging prohibited nationally only in 2006 (Brazilian Law 11428/2006; Brasil 2006). Moreover, according to the interviewers, together with the selective logging have defaunation events, directly (i.e. hunt by lumbermen) or indirectly (e.g. reduction of key resources [e.g. *Pinhão*]).

The mammal richness according to the informants is lower variable. These metrics, proportionally compared with the alpha diversity, demonstrate a current reduction in species richness and a non-random changes in composition, respectively (Bogoni et al. 2016; Bogoni et al. 2017), such as implications for functional diversity (Ricotta and Burrascano 2008). In Santa Catarina plateaus, the defaunation are lower than in the coast and west areas, but it is high in all regions [from 0.27 to 0.79, average 0.50] (Bogoni et al. 2016). Some species are cited as extinct locally (e.g. veado-campeiro, bugio and macaco-prego) or in a constant decrease (*Dasypus* spp. [tatus]), thus there was a perception of defaunation by the informants (1/3 of them on mammal richness and 2/3 of them on mammal abundance).

The hunt and fragmentation are the main responsible for defaunation (Dirzo et al. 2014; Galetti et al. 2016). Another factor that can influence the species richness is the "*massegas*" increase, that can difficult the species visualization, because the species cited such as "most commons" generally have occurrence in open areas (e.g. graxaim-do-campo, veado-catingueiro and lebre). The "*massegas*" is a clear change in the mosaics of the local landscape, due to the abandonment of the management activities (i.e. niche construction) after the indemnification process of the proprieties. Other factors can ensure the maintaining of mosaics grasslands/forest patches, according to the informants, the establishment of Araucarias and Feijoas generally is together, in slopes areas with fertile soil, with Feijoas occupying riparian areas within fitted valleys. Araucaria have a good ecophysiological performance under stressful conditions promoting a local dominance and healthy regeneration (Franco et al. 2005), and are a pioneer in grasslands, near the forests borders modifying local environmental conditions and creating habitats suitable for the establishment of the others species (Oliveira and Pillar 2004; Silva et al. 2009; Sühs et al. unpublished data). However, according to our informant the forest patches did not advance on the grasslands, even without management (except by the "*massegas*"). The Araucaria is resisting to the frost and dry, tolerating hot climates, yet is best established on slopes with well-distributed rainfall and humidity, leading to the establishment of other species such as Feijoa (Mattos 2011; Silva et al. 2009).

These climatic conditions also influenced the species growth and productivity (Mattos 2011). The productivity of these resources (*Pinhão* and Feijoa) are cyclic (Mattos 2011; Bogoni et al. unpublished data). Our result showed that as a whole the productivity is maintained across the time, showing a productivity similar (107.3 kg/ha^{-1}) to the inventories (e.g. 106.6 kg/ha^{-1}; 117 kg/ha^{-1}; 160 kg/ha^{-1}) in Araucarias *in situ* (Mantovani et al. 2004; Bogoni et al. unpublished data). Despite the *Pinhão* are explored in local proprieties and commercially, remain into the forest patches circa 2/3 of productivity, shared among native mammals and birds, exotic species and domesticated animals (e.g. cattle, sheep, horse and pig). For the local-people viewpoint, this dynamic is lasting since the creation/acquisition of proprieties, on average to over a century and can promote an average income of 6,500 Brazilian Reais (US$ 2,100) per crop to the local residents, considering an average price of 5.00 Brazilian Reais per kilo. Still, circa 2/3 of native mammal species have a direct relationship with Araucaria and Feijoa. For the local fauna, both resources are crucial for diversity maintaining due to the high connectivity of network and low nestedness, even including main birds, exotic and domesticated mammals. Among 30 species of mammals, birds, exotic and domesticated species, the resources share 27 (resources degrees) of the interactor, when the interactors shared both resources (with species degree of 1.88). Yet, from the Araucaria (*Pinhão*) viewpoint, only some species are described as dispersers, mainly the gralha-azul, from the Feijoa viewpoint the dispersion can be much larger, but currently is being intensively made by cattle and medium-bodied omnivorous mammals (Bogoni et al. in review).

The Feijoa is little used and according to the local people their productivity is 4.5 times (i.e. 13.4 kg/ind) larger than observed *in situ* (3.03 kg/ind) (Bogoni et al. unpublished data). The high variation in productivity probably is associated with two factors: (1) the Feijoa fruits not is explored commercially; and (2) the use of Feijoa fruits is selective to some plants (generally managed) more productive and accessible (nearby to the informant's houses) (Santos et al. 2009). How the Feijoa fruits are poorly used, remain into the forest patches all production that, such as *Pinhão* is shared among the animal groups (natives, exotics and domesticated) (Bogoni et al. unpublished data). The interaction among the resources (*Pinhão* and Feijoa) and fauna is high and has alternation (Iob and Vieira 2008; Bogoni et al. unpublished data).

The elevated age of informants and their proprieties, well spatially distributed together with the high territorial coverage obtained in our research, is an important factor to ensure the patterns obtained. Thus, summarizing the past decades we can reconstruct the recent history of the exploitation of these highland areas, show that the forest amount was decreased from the 1960s to 1980s recovering in recent decades. Differently, mammals continue to decrease steadily in abundance and richness, when the resources available in general may be increasing, due the decrease of resource and landscape uses by local peoples. This functional diversity loss can create a seed dispersal gap and can lead to microevolutionary changes. Futures perspective at local people viewpoint on potential changes in the local climate showed that apparently there would be no change in the distribution sites of the species. The consequences of recent human-induced alterations in the atmosphere and climate over the species are still unknown (Silva et al. 2009). Under climate changes, the tendencies have showing a large reduction in Araucaria distribution (Wrege et al. 2016), even in less dramatic scenarios of climate changes (Bogoni et al. unpublished data).

We showed that the resources changed over space and time, causing a non-random change in the interactors and interactions among species. The local people are important for the maintenance of the landscape thought management and suitable use of resources, creating new niche spaces by the introduction of practices (e.g. fire, Araucaria expansion, mammalian species favoring or extirpation) and allochthones elements within the landscape (e.g. cattle) that from short to long-term are able to change or maintain the highlands forest-grassland mosaic. Environmental assessment and co-management are public policy-making tools that are open and responsive to both public opinion and stakeholder rights and interests (Usher 2000). Brazilian protection laws are established vertically and most of the time disregard the socio-environmental situation of the places and others public politics and proposals are extremely harmful to the maintenance of biodiversity. According to our main results, we conclude that the Araucaria and Feijoa are essential to local people, shared among them and their domesticated animals and the native fauna, maintain the health of a reduced ecosystem into Atlantic Forest highlands. Still, the human footprint on landscape and resources management is “at least” able to the construction of niche spaces that influencing the local diversity patterns and process.

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Supporting Information

Supporting Information S1. Questionnaire applied to local people within the National Park of São Joaquim (NPSJ) and surroundings, Santa Catarina highlands.

Universidade Federal de Santa Catarina
Programa de Pós-Graduação em Ecologia
Laboratório de Ecologia Humana e Etnobotânica

ECOHE

Roteiro de Entrevista (Doutorando: Juliano A. Bogoni; Orientação: Prof. Dr. Nivaldo Peroni)

N:

DADOS DE IDENTIFICAÇÃO

Pesquisador_________________________ Área____________Município e localidade___________________________________
Georreferenciamento ______________S_________________N____________A Data ______________

Entrevistado ____
Idade ________________ Sexo: ( ) M ( ) F
Profissão/Ocupação _______________________ Área da propriedade (ha): __________
Principal atividade na propriedade ______________________ Tempo de residência _____ E dos antepassados___________

PARTE A (HISTÓRICO DA FLORESTA COM ARAUCÁRIA) [10]

A1. Qual a idade (anos) das matas de araucárias da propriedade? ________
A2. Qual o percentual de área ocupado pelas matas no passado (≥20 anos) na propriedade? _______ Ano? _______
A3. Nessa época, qual era a produtividade de araucárias e de goiabas-serranas?
1) ( ) alta 2) ( ) média 3) ( ) baixa
A4. Qual o percentual de área ocupado pelas matas atualmente? _________
1) ( ) reduziu 2) ( ) aumentou 3) ( ) se manteve igual
A5. Atualmente, na mesma área, como é a produtividade?
1) ( ) alta kg_____ 2) ( ) média kg_____ 3 ( ) baixa kg ______
A6. Se houve diminuição do número de fêmeas (produtividade), qual o principal motivo?
1) ( ) ausência de araucárias machos (polinização) 2) ( ) exploração madeireira
3) ( ) queimadas (lavouras/pastagens) 4) ( ) ausência de dispersores
5) ( ) mudança no clima regional. Qual? _______________ 6) ( ) aumento de predadores de sementes
7) ( ) outro ____
A7. Se houve aumento, qual o principal motivo?
1) ( ) áreas protegidas (governo) 2) ( ) participação comunitária na proteção
3) ( ) aumento animais de dispersores 4) ( ) plantio
5) ( ) mudança no clima regional. Qual? ____
6) ( ) outro ____
A8. Conhece ou ouvir falar de pessoas expandindo as áreas (plantio ao acaso) de araucárias no passado?_____ Há quanto tempo? _______
A9. Quais grupos de pessoas?
1) ( ) indigenas 2) ( ) antigos agricultores
3) ( ) atuais proprietários 4) ( ) antigos tropeiros
5) ( ) outros ___________________________

A10. Com o mapa em mãos (Rafael)

Identifique no mapa quais eram as áreas que você, seus pais ou avós moravam (o ano de moradia) e desenhe no mapa as divisas aproximadas da sua propriedade.

PARTE B (ESPÉCIES VEGETAIS, USO DOS RECURSOS E USO DAS PAISAGENS) [14]

B1. Me fale das principais condições para que nasçam e cresçam araucárias nas áreas da região?
1) ( ) água (proximidade de rios) 2) ( ) solo profundo e fértil
3) ( ) ausência de sobra (e.g campos) 4) ( ) áreas de difícil acesso e sombreadas (e.g. vales; canhadas)
5) ( ) frio regularmente e intenso 6) ( ) não há uma condição específica (nasce e qualquer lugar)
7) ( ) outra ____
B2. Quais as principais condições para que nasçam e cresçam goiabas-serranas?
1) ( ) água (rios) 2) ( ) solo profundo e fértil
3) ( ) presença de araucárias (sombra) 4) ( ) áreas de difícil acesso (e.g. vales; canhadas)
5) ( ) frio regularmente e intenso 6) ( ) não há uma condição específica (nasce e qualquer lugar)
7) ( ) outra ____
B3. Faz algum tipo de manipulação nas mudas de araucárias?
1) ( ) não meche 2) ( ) replanta em outro lugar
3) ( ) elimina o inço 4) ( ) corta a muda
5) ( ) outro ____

B4. E nas mudas de goiabeira-serrana?
1) ( ) não meche 2) ( ) replanta em outro lugar
3) ( ) elimina o inço 4) ( ) corta a muda
5) ( ) outro ____

B5. Você e sua família usam recursos (listados abaixo) das florestas de araucária? E para qual finalidade?
1) ( ) jerivá ________________ 2) ( ) araçá __________________ 3) ( ) jabuticaba __________
4) ( ) guabiroba ______________ 5) ( ) pitanga _________________ 8) ( ) outra
6) ( ) butiá __________________ 7) ( ) sete-capotas ______________

B6. Quais recursos são utilizados mais frequentemente?
1) ( ) pinhão 2) ( ) goiaba-serrana
3) ( ) outras frutas citadas acima ____
4) ( ) outros ____

B7. Em média, qual o consumo na propriedade de pinhão e de goiaba-serrana (em kg) anualmente? _____ e _____

B8. Havendo venda de pinhão, qual a quantidade anual (incluindo outros extratores)? ______________

B9. Vocês têm quais dessas "áreas" (unidades de paisagem) na propriedade?
1) ( ) roça/lavoura 2) ( ) pinus/eucalipto
3) ( ) invernada (mantida com manejo) 4) ( ) pomar
5) ( ) campos de altitude (nativos)

B10. Usa/Usou as matas de araucária, matinhas nebulares (capões) e campos para alguma atividade? ______

B11. Quais e ao longo de quanto tempo (anos)?
1) ( ) invernada _______ 2) ( ) lavoura _______ 3) ( ) turismo _______
4) ( ) extração de pinhões _____ 5) ( ) extração de goiaba-serrana _______ 6) ( ) gado _________
7) ( ) outra_____

B12. Usa técnicas de manejo dos recursos (pinhão e goiaba-serrana) e das unidades de paisagens (e.g potreiro; roça)? _____ e ______

B13. Quais?
1) ( ) não remove todas as sementes/frutas | deixa aproximadamente (%) _______
2) ( ) planta algumas sementes/frutas | aproximadamente quanto (%) _____ e a distância (m) média de _______ do local coletado
3) ( ) seleciona frutos das melhores goiabeiras para plantio
4) ( ) queimada | freqüência ao ano ______
5) ( ) roçada | freqüência ao ano ______
6) ( ) outros ____

B.14. Em que época (meses) frutifica a goiaba-serrana e qual a quantidade média (kg) produzido por árvore anualmente? __________________________ e _________

PARTE C (MASTOFAUNA* E INTERAÇÕES) [13] *** Duas perguntas inclui aves**

C1. Quais as espécies (tipo) de mamíferos (bichos de pêlo) nativos há na região atualmente? _________________________
____
____
____
____

C2. Qual a espécie mais avistada? ______________ Por quê? ____________________________________

C3. Qual a espécie menos avistada? ______________ Por quê? ___________________________________

C4. Houve diminuição no número de espécies ao longo dos anos?
1) ( ) sim 2) ( ) não

C5. E no número de avistamentos/vestígios (abundância)
1) ( ) sim 2) ( ) não

C6. Por qual motivo?
1) ( ) diminuição natural 2) ( ) diminuição e recortes (fragmentação) de áreas de floresta
3) ( ) queimadas 4) ( ) doenças
5) ( ) outro ____

C7. Quais espécies de mamíferos, que você conhece, estão associadas (consomem pinhões) à araucária (incluindo ratos)?
____
____

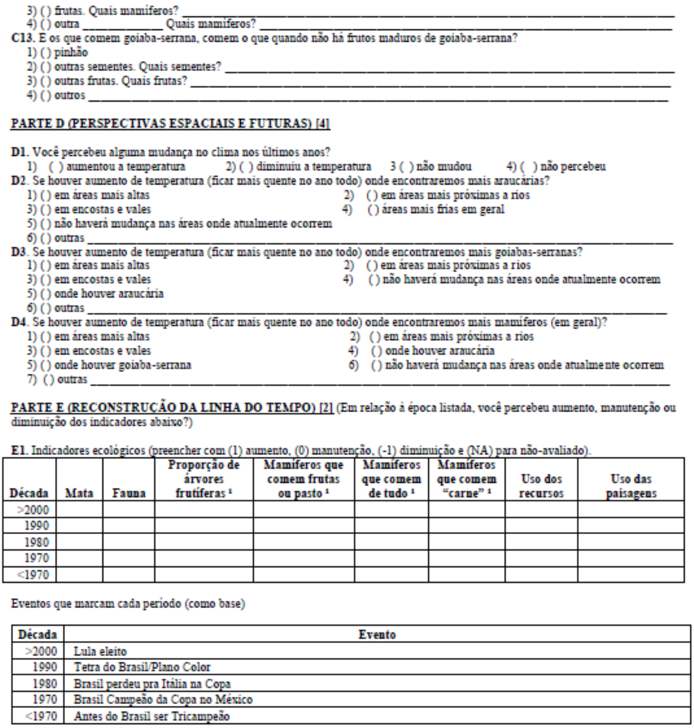
C8. Quais espécies de aves, que você conhece, estão associadas (consomem pinhões) à araucária? ______________________
____
____

C9. Quais espécies de mamíferos e aves, que você conhece, que dispersam (pegam e levam embora) o pinhão?
____

C10. E quais mamíferos consomem frutos à goiaba-serrana?______________________________________
____
____

C11. E quais aves comem goiaba-serrana? ____
____

C12. O que comem os mamíferos (associados à araucária) quando não há pinhão?
1) ( ) goiaba-serrana ____
2) ( ) outras sementes. Quais mamíferos? ____



3) ( ) frutas. Quais mamíferos? ____
4) ( ) outra ____________ Quais mamíferos? ____________________________________

C13. E os que comem goiaba-serrana, comem o que quando não há frutos maduros de goiaba-serrana?
1) ( ) pinhão
2) ( ) outras sementes. Quais sementes? ____
3) ( ) outras frutas. Quais frutas? ____
4) ( ) outros ____

PARTE D (PERSPECTIVAS ESPACIAIS E FUTURAS) [4]

D1. Você percebeu alguma mudança no clima nos últimos anos?
1) ( ) aumentou a temperatura   2) ( ) diminuiu a temperatura   3 ( ) não mudou   4) ( ) não percebeu

D2. Se houver aumento de temperatura (ficar mais quente no ano todo) onde encontraremos mais araucárias?
1) ( ) em áreas mais altas   2) ( ) em áreas mais próximas a rios
3) ( ) em encostas e vales   4) ( ) áreas mais frias em geral
5) ( ) não haverá mudança nas áreas onde atualmente ocorrem
6) ( ) outras ____

D3. Se houver aumento de temperatura (ficar mais quente no ano todo) onde encontraremos mais goiabas-serranas?
1) ( ) em áreas mais altas   2) ( ) em áreas mais próximas a rios
3) ( ) em encostas e vales   4) ( ) não haverá mudança nas áreas onde atualmente ocorrem
5) ( ) onde houver araucária
6) ( ) outras ____

D4. Se houver aumento de temperatura (ficar mais quente no ano todo) onde encontraremos mais mamíferos (em geral)?
1) ( ) em áreas mais altas   2) ( ) em áreas mais próximas a rios
3) ( ) em encostas e vales   4) ( ) onde houver araucária
5) ( ) onde houver goiaba-serrana   6) ( ) não haverá mudança nas áreas onde atualmente ocorrem
7) ( ) outras ____

PARTE E (RECONSTRUÇÃO DA LINHA DO TEMPO) [2] (Em relação à época listada, você percebeu aumento, manutenção ou diminuição dos indicadores abaixo?)

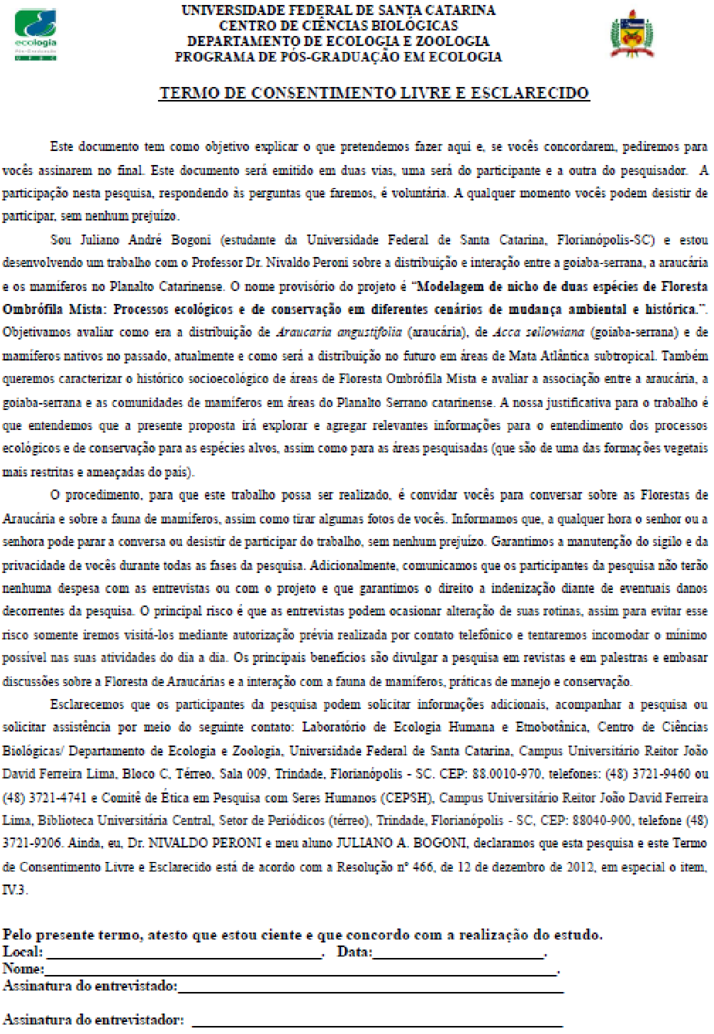
E1. Indicadores ecológicos (preencher com (1) aumento, (0) manutenção, (-1) diminuição e (NA) para não-avaliado).

Década	**Mata**	**Fauna**	**Proporção de árvores frutíferas** ^{1}	**Mamíferos que comem frutas ou pasto** ^{1}	**Mamíferos que comem de tudo** ^{1}	**Mamíferos que comem "carne"** ^{1}	**Uso dos recursos**	**Uso das paisagens**
>2000								
1990								
1980								
1970								
<1970								

Eventos que marcam cada período (como base)

Década	**Evento**
>2000	Lula eleito
1990	Tetra do Brasil/Plano Color
1980	Brasil perdeu pra Itália na Copa
1970	Brasil Campeão da Copa no México
<1970	Antes do Brasil ser Tricampeão

Supporting Information S2. Consent term distributed *a priori* to local people interviewed within the National Park of São Joaquim (NPSJ) and surroundings, Santa Catarina highlands.



UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

TERMO DE CONSENTIMENTO LIVRE E ESCLARECIDO

Este documento tem como objetivo explicar o que pretendemos fazer aqui e, se vocês concordarem, pediremos para vocês assinarem no final. Este documento será emitido em duas vias, uma será do participante e a outra do pesquisador. A participação nesta pesquisa, respondendo às perguntas que faremos, é voluntária. A qualquer momento vocês podem desistir de participar, sem nenhum prejuízo.

Sou Juliano André Bogoni (estudante da Universidade Federal de Santa Catarina, Florianópolis-SC) e estou desenvolvendo um trabalho com o Professor Dr. Nivaldo Peroni sobre a distribuição e interação entre a goiaba-serrana, a araucária e os mamíferos no Planalto Catarinense. O nome provisório do projeto é "**Modelagem de nicho de duas espécies de Floresta Ombrófila Mista: Processos ecológicos e de conservação em diferentes cenários de mudança ambiental e histórica.**". Objetivamos avaliar como era a distribuição de *Araucaria angustifolia* (araucária), de *Acca sellowiana* (goiaba-serrana) e de mamíferos nativos no passado, atualmente e como será a distribuição no futuro em áreas de Mata Atlântica subtropical. Também queremos caracterizar o histórico socioecológico de áreas de Floresta Ombrófila Mista e avaliar a associação entre a araucária, a goiaba-serrana e as comunidades de mamíferos em áreas do Planalto Serrano catarinense. A nossa justificativa para o trabalho é que entendemos que a presente proposta irá explorar e agregar relevantes informações para o entendimento dos processos ecológicos e de conservação para as espécies alvos, assim como para as áreas pesquisadas (que são de uma das formações vegetais mais restritas e ameaçadas do país).

O procedimento, para que este trabalho possa ser realizado, é convidar vocês para conversar sobre as Florestas de Araucária e sobre a fauna de mamíferos, assim como tirar algumas fotos de vocês. Informamos que, a qualquer hora o senhor ou a senhora pode parar a conversa ou desistir de participar do trabalho, sem nenhum prejuízo. Garantimos a manutenção do sigilo e da privacidade de vocês durante todas as fases da pesquisa. Adicionalmente, comunicamos que os participantes da pesquisa não terão nenhuma despesa com as entrevistas ou com o projeto e que garantimos o direito a indenização diante de eventuais danos decorrentes da pesquisa. O principal risco é que as entrevistas podem ocasionar alteração de suas rotinas, assim para evitar esse risco somente iremos visitá-los mediante autorização prévia realizada por contato telefônico e tentaremos incomodar o mínimo possível nas suas atividades do dia a dia. Os principais benefícios são divulgar a pesquisa em revistas e em palestras e embasar discussões sobre a Floresta de Araucárias e a interação com a fauna de mamíferos, práticas de manejo e conservação.

Esclarecemos que os participantes da pesquisa podem solicitar informações adicionais, acompanhar a pesquisa ou solicitar assistência por meio do seguinte contato: Laboratório de Ecologia Humana e Etnobotânica, Centro de Ciências Biológicas/ Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Campus Universitário Reitor João David Ferreira Lima, Bloco C, Térreo, Sala 009, Trindade, Florianópolis - SC. CEP: 88.0010-970, telefones: (48) 3721-9460 ou (48) 3721-4741 e Comitê de Ética em Pesquisa com Seres Humanos (CEPSH), Campus Universitário Reitor João David Ferreira Lima, Biblioteca Universitária Central, Setor de Periódicos (térreo), Trindade, Florianópolis - SC, CEP: 88040-900, telefone (48) 3721-9206. Ainda, eu, Dr. NIVALDO PERONI e meu aluno JULIANO A. BOGONI, declaramos que esta pesquisa e este Termo de Consentimento Livre e Esclarecido está de acordo com a Resolução nº 466, de 12 de dezembro de 2012, em especial o item, IV.3.

Pelo presente termo, atesto que estou ciente e que concordo com a realização do estudo.
Local: ____________________________. **Data:**____________________.
Nome:____.
Assinatura do entrevistado:____

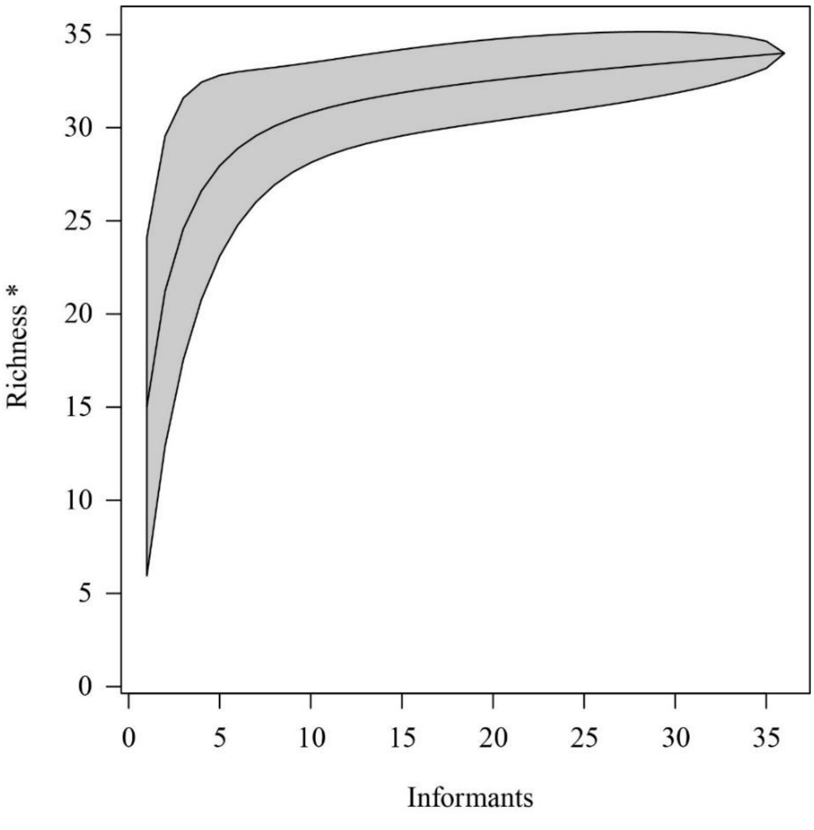
Assinatura do entrevistador: ____

Supporting Information S3. Medium- to large-bodied mammals (and some small mammals) cited by 36 local people interviewed within the National Park of São Joaquim (NPSJ) and surroundings, Santa Catarina highlands.

Species	**English name**	**Local name**	**Number of citations**
Alouatta guariba clamitans	Southern Brown Howling Monkey	Bugio	14
Cabassous tatouay	Greater Naked-tailed Armadillo	Tatu-do-rabo-mole	8
Cavia aperea	Brazilian Guinea Pig	Preá	7
Cerdocyon thous	Crab-eating Fox	Graxaim-do-mato	12
Coendou spinosus	Porcupine	Ouriço/Porco espinho	12
Conepatus chinga	Molina's Hog-nosed Skunk	Zorilho/Jurilho	18
Cricetidae	Native small rodents	Ratos	36
Chrysocyon brachyurus	Maned wolf	Lobo-guará	1
Cuniculus paca	Spotted paca	Paca	16
Dasyprocta azarae	Azara's Agouti	Cutia	14
Dasypus novemcinctus	Nine-banded Armadillo	Tatu-capoeira/Tatu-galinha	26
Dasypus septemcinctus	Brazilian Lesser Long-nosed Armadillo	Tatu-mulita/Mulitinha	28
Didelphis spp.	Opossums	Gambás	14
Eira barbara	Tayra	Irara	16
Galictis cuja	Lesser Grison	Furão	8
Hydrochoerus hydrochaeris	Capybara	Capivara	16
Leopardus pardalis	Ocelot	Jaguatirica	14
Leopardus spp.	Southern tigrinas/Margays	Gatos-do-mato	17
Lepus europaeus	European hare	Lebre/Lebra	23

Lontra longicaudis	Neotropical otter	Lontra	3
Lycalopex gymnocercus	Pampas fox	Graxaim-do-campo	24
Mazama americana	Red brocket	Veado-mateiro/veado-vermelho	17
Mazama gouazoubira	Gray brocket	Veado-catingueiro/veado-baio	31
Mazama nana	Brazilian Dwarf Brocket	Veado-anão/veado-poca	5
Nasua nasua	South American Coati	Quati	34
Ozotoceros bezoarticus	Pampas deer	Veado-campeiro/Veado-branco	11
Pecari tajacu	Collared Peccary	Tateto	27
Procyon cancrivorus	Crab-eating Raccoon	Mão-pelada	17
Puma concolor	Puma	Puma/Leão-baio/Leão	33
Puma yagouaroundi	Jaguarundi	Jaguarundi	1
Sapajus nigritus	Black-horned Capuchin	Macaco-prego/macaco	4
Sus scrofa	Wild Boar	Javali	25
Sylvilagus brasiliensis	Tapeti	Coelho	1
Tamandua tetradactyla	Southern Tamandua	Tamanduá-de-colete/Tamanduá-mirim	12

Supporting Information S4. Accumulation curve of species to medium- to large-bodied mammals (including *Cavia* aff. *aperea*, Cricetidae, *Sus scrofa* and *Lepus europaeus*) cited by 36 local people interviewed within the National Park of São Joaquim (NPSJ) and surroundings, Santa Catarina highlands.



* Include small mammals (Cricetidae as a unique species and *Cavia* aff. *aperea*) and exotic species (*Lepus europaeus* and *Sus scrofa*).

CAPÍTULO 5

Run to the hills: Past, present and future biogeographic distribution of Araucaria Forest elements

(*Run to the hills*: Passado, presente e futura distribuição biogeográfica de elementos das Florestas de Araucárias)

Revista alvo: Diversity and Distribution
(ISSN: 1472-4642)

Exploração comercial da Araucária (*Araucaria angustifolia*) durante a década de 1950. Balseiros do Rio Uruguai se largavam do porto de Goio-ên (Chapecó), no Alto Uruguai Catarinense – durante as cheias do Rio Uruguai – com destino ao município de Uruguaiana ou até a Argentina. Informações obtidas no vídeo "Balseiros do Uruguai", feito pelo extinto Instituto Nacional do Pinho, durante a década de 1950. Fotografia de Silvério Osmaro Weimer (obtida em: http://passarazzi.blogspot.com.br/2010/05/um-roteiro-pelo-rio-uruguai-catarinense.html; acesso: 2015-10-15).

Run to the hills: Past, present and future biogeographic distribution of Araucaria Forest elements

RH: **Araucaria Forest SDMs**

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Abstract

Understanding species distribution and abundance is one the fundamental aims in ecology and conservation. Species distribution models (SDMs) estimate the relationship between species presence and environmental variables to predict suitable areas of occurrence. We create SDMs for the main element of Araucaria Forest for past climate conditions (Mid-Holocene), current and future climate conditions (2060s and 2080s). We used the species *Araucaria angustifolia*, *Dasyprocta azarae*, *Acca sellowiana*, *Eira barbara*, *Mazama gouazoubira* and *Puma concolor* to compose the base of the trophic-web and their co-occurrence. We developed the SDMs based on presence and pseudo-absence points performed on combined predictors methods of Profile and Learning Machine, basing the main model on average weighed by best-adjusted model evaluated by test Area Under the Receiver Operator (AUC), personal observations and distribution maps. We showed that elements of the threatened Araucaria Forest may decrease their distribution ranges depending on future climate changes and that the species distributions at Mid-Holocene was smaller than the current distributions. There are several pieces of evidence of past and current interaction between the species with human populations which molded their distribution areas together with climatic processes along time. We conclude that the Araucaria Forest and their elements are threathed by climate changes. The species with larger reduction are highly associated with the *Araucaria angustifolia* and with altitudinal grasslands and their co-occurrence are related intimately with restrict highlands, making it current and future refugia. Thus, the rare highland mosaic existence, the historic and cultural importance of this formation and the ecosystems process and species interactions are extremely dependent on public policies of climate changes mitigation from local to regional scales.

Key-words: highlands, climate change, Mid-Holocene, trees, mammals, Atlantic Forest, niche modeling, species distribution, co-occurrence

Introduction

Understanding the process that influence the species distributions is a critical point in ecology and conservation (Hutchinson 1957; Franklin 2009). Thus, for designing a plan of conservation species under threat is necessary to known where and in which conditions they live (Phillips et al. 2004). Species distribution models (SDMs) are widely used in biogeography, ecology and conservation biology to estimate the relationship between species records and the environment (Elith and Leathwick 2009; Franklin 2009; Elith et al. 2011). The SDMs approach enable exploring questions on the conservation, ecology, and evolution, such as: (1) defining priority areas for conservation and contributions to the conservation of species (Chen and Peterson 2002; Garcia 2006; Lópes-Arévalo et al 2011; Faleiro et al. 2013); (2) understanding invasive process of species (Ficetola et al. 2007; Giovanelli et al. 2008); (3) generating ecocultural niche modeling that reflects ecological influences on past human culture distributions (Banks et al. 2008); (4) proposing past distributions of species (Hugall et al. 2002; Carnaval and Moritz 2008); and (5) predicting future distributions of species under changing environmental characteristics (Siqueira and Peterson 2003).

The increasing availability of detailed datasets, together with algorithms to explore the association of occurrence of species with explanatory environmental variables (Elith et al. 2006), foment an increasing of SDMs use (Phillips et al. 2006). The modeling is based on the niche concept, which considers the sum of environmental factors that exercise influences under an organism (Franklin 20009). However, in nature the realized ecological niche is observed – i.e. parts of the fundamental niche available where the species is not excluded from biotic interactions and/or resource limitations (Guisan and Thuiller 2005). The theoretical duality of niche concept provides a way to evaluate and analyzing biogeographic distributions in relation to spatial environmental patterns (Brown 1995; Colweel and Rangel 2009). The spatial extension of Hutchison's biotope is known as "map", each point within the "map" characterize – besides the coordinates – the local values of *n* attributes at determined time and is defined the correspondent niche space, allowing reciprocal projections, real or potential, of geographic distribution of a species (Colwell and Rangel 2009). This projection can be executed for current, past or in the future conditions, through stochastic models that include since speciation to evolutionary adaptation on changing the environment (Colwell and Rangel 2009; Peterson et al. 2011).

The climate of the Earth regions (mainly the precipitation anomalies) are interlinked and largely associated with the El Niño-Southern Oscillation (ENSO) (Seager et al. 2005). The ENSO magnitude results from the relationship between changes in seasonality, which involves wave propagation along the thermocline (Luan et al. 2012). Thus, the effects of ENSO is generally seasonal (Seager et al. 2005), varying in intensities between historical periods (e.g. larger in the Early Holocene when compared to the Mid-Holocene (~6,000 years before present [y.b.p.])) (Luan et al. 2012). At Mid-Holocene, an amplifying influence of orbital forcing on precipitation changes in Africa established the so-called "Green Sahara" (Hély et al. 2014) and an increase in winter-season precipitation in Mediterranean (Roberts et al. 2011). The America's climate of Mid-Holocene could have influenced the species distribution and composition of vegetation, due to an increase in the monsoonal precipitation in some parts of the continent, consequently causing an aridity in others– and all these conditions were largely driven by increases in land-surface temperature (Harrison et al. 2003). Furthermore, many studies suggest that current and future global warming is driving species ranges of distributions (Colwell et al. 2008) and others ecological dynamics (e.g. hydrological cycle; Seager et al. 2010). In the tropics, the evidence for warming range shifts is scarce (Colwell et al. 2008).

Among many terrestrial ecosystems that can be threatened by climate changes, there are the highlands of subtropical Atlantic Forest (Lima et al. 2015; Lacerda 2016; Souza et al. 2016). This region is composed by Araucaria Forest, a vegetation mosaic characterized by the remarkable presence of the threatened conifer *Araucaria angustifolia*

Bertol. Kuntze 1898 (Araucaria) (Mattos 1972) – utilized as a proxy to conservation strategies (Lacerda 2016) – and by patches of cloud forests, swamps, and native grassland (Mattos 1972; Lacerda 2016). Currently, this vegetal formation is extremely reduced (remnants of 3 to 13%) by anthropogenic influences, such as logging and habitat fragmentation (Koch and Correa 2002; Bauermann and Behling 2009; Ribeiro et al. 2009). Araucaria Forest had several processes of expansion and reduction since Late Quaternary (Behling et al. 2004). However, it is marked by prehistoric anthropogenic influence during the Late Holocene, that results in an increase of distribution area (Bitencourt and Krauspenhar 2006; Reis et al. 2014). The Araucaria provides an important resource for fauna—including humans—structuring the fauna of vertebrates from primary to top-predators (Iob and Vieira 2008; Bogoni et al. unpublished data). Araucarias dominate the upper stratum, while Myrtaceae and Lauraceae are the main families forming the middle and lower strata (Rambo 1951; Souza 2007) and all groups are ecologically associated with fauna (Ribeiro and Vieira 2014; Bogoni et al. unpublished data). Among the Myrtaceae, the *Acca sellowiana* [Berg] Burret (Feijoa) is a native tree of southern Brazil and northern Uruguay, with occurrence restricted to areas higher than 800 meters above sea level (m.a.s.l.). Feijoa is naturally associated with FOM (Santos et al. 2009; Amarante and Santos 2011) and with great relationship with local fauna (Bogoni et al. unpublished data). Moreover, Feijoa has been received an incipient domestication by local people aiming the increase of productivity and fruit-size (Santos et al. 2009).

Among the mammals, the main disperser of Araucaria seed is *Dasyproca azarae* (Iob and Vieira 2008; Ribeiro and Vieira 2014) while the species *Eira barbara* is the main consumer of Feijoa fruit (Bogoni et al. unpublished data). Other species also have a direct and indirect relationship with Araucaria and Feijoa. For example, the most abundant large grazer in highlands (*Mazama gouazoubira*) also feeds on Feijoa fruits and Araucaria seeds (Bogoni et al. unpublished data), and the apex predator (*Puma concolor*) regulates the population of several vertebrate species in highlands (Bogoni et al. 2016). Thus, generating a scenario of the past, current and future conditions of distribution and co-occurrence of elements of Araucaria Forest can provide a theoretical framework to understand the historical and ecological process and support conservation efforts and forest resource management. We aimed to generate SDMs for the main element of Araucaria Forest for past climate conditions (Mid-

Holocene), current (1950s from 2000s) and future climate conditions (2060s and 2080s). For this objective, we selected the species *Araucaria angustifolia*, *Acca sellowiana*, *Dasyprocta azarae*, *Eira barbara*, *Mazama gouazoubira* and *Puma concolor* to compose the base of the trophic-web. Additionally, we considered only the "fundamental climate niche" of species, and within the time-scale adopted (~6,100 years), the niche remained static at evolutionary view's point (Franklin 2009). We hypothesize that the past distribution of species and the species co-occurrence in space are more restricted than in current climate conditions, and in future climate conditions the current area of species occurrence and species co-occurrence will be reduced.

Material and methods

Species definition criteria and definition of projection area

We use the conifer Araucaria because it is the key species that represents the Mixed Ombrophilous Forest (FOM: Araucaria Forest), and provides an important resource for the native fauna, human populations and domestic animals (Mattos 1972; Bogoni et al. unpublished data). Representing the Myrtaceae, we use the Feijoa because it is spatially associated with Araucarias (Santos et al. 2009) and it serves as resource to fauna when there are no Araucaria seeds (*Pinhão*) (Bogoni et al. unpublished data). We selected four mammal species to represent the basic trophic-web in the FOM, using the following criteria: (1) *Dasyprocta azarae* (Azara's Agouti) because they predate and disperse Araucaria seeds (Ribeiro and Vieira 2014); (2) *Eira barbara* (Tayra) because they remove Feijoa fruit (Bogoni et al. unpublished data); (3) *Mazama gouazoubira* (Grey Brocket) because it is the most abundant large grazer in the area (Bogoni et al. 2016); and (4) *Puma concolor* (Puma) because it is the apex-predator in the area (Mazzoli et al. 2002; Bogoni et al. 2016). We defined an area of ~2,346,675 km² (excluding the Atlantic Ocean portion) to perform the SDMs, from -10°S to -40°S and from -60°W to -35°W. This area covers the current distribution of tree species (Araucaria and Feijoa) such as the main portion of Atlantic Forest and Pampa ecoregions, localities of occurrence of the mammals selected (Rambo 1951; Reitz and Klein 1966; Santos et al. 2009; Lima et al. 2017).

Data of species occurrence

We use the scientific name of species for obtained secondary data of occurrence in search engines (Web of Knowledge [https://webofknowledge.com], Scopus [http://www.scopus.com/], Scielo [http://www.scielo.br/]), and Global Biodiversity Information Facility (GBIF) (http://data.gbif.org). Whereby, we made a data validation to avoid erroneous or redundant data, and crosschecked the species presence evaluating whether the distribution data is in accordande with species distribution ranges (Hijmans et al. 1999). For records without georeferencing and only textual descriptions of locations, we use the *Biogeomancer* tool (Guralnick et al. 2006) that gives the coordinates as the description of the location. We complemented the occurrence points with georeferenced data where the presence is secured, based on personal observations in fieldwork, demographic plots, data from camera traps distributed at different areas in subtropical Atlantic Forest and information from Floristic Forest Inventory of Santa Catarina State (IFFSC: http://www.iff.sc.gov.br/; Gasper et al. 2013).

Data of fundamental climate niche

We obtained the past climate data – Mid-Holocene (~6,000 years before the present [y.b.p.]) – in the platform of *Paleoclimate Modelling Intercomparison Project Phase III* (PMIP3) (http://pmip3.lsce.ipsl.fr/) based on simulations at CNRM-CM5 and MIROC-ESM scenarios, calibrated with a study on pollen-based (Bartlein et al. 2011). In *WordClim: Global Climate Data* (WC) database (http://www.worldclim.org/download), we obtained the current climatic conditions, generated by interpolated climatic data since 1950s to 2000s (Hijmans et al. 2005). The WC interpolated climate layers were made using the major climate databases compiled by the *Global Historical Climatology Network* (GHCN), the FAO, the WMO, the *International Center for Tropical Agriculture* (CIAT), R-HYdronet, and a number of additional minor databases. The ANUSPLIN software is the program used for interpolating noisy multi-variate data using smoothing splines and use latitude, longitude, and elevation as independent variables (Hijmans et al. 2005). Future climatic conditions (simulations for 2060s and 2080s) was obtained at *Intergovernmental Panel on Climate Change Fifth Assessment Report* (IPCC5) (http://www.ccafs-climate.org/data/). These future projections are generated – using the "downscaling delta" in the original data – for three general models of atmosphere-ocean circulation (AOGCMs: CCCMA_CGCM2, CSIRO-MK2.0 and UKMO_HADCM3) of B2a emission scenario from *Special Report on Emissions Scenarios* (SRES) (Hijmans et al. 2005). The B2a scenario describes a world, in which the emphasis is on local solutions to economic, social, and environmental sustainability, are more conservative, simulates a slow human population growth rate, limited land use changes, and reflects a more technologically innovative world (Solomon et al. 2007). Thus, the B2a scenario is comparable to the RCP4.5 at *Coupled Model Intercomparison Project Phase 5* (CMIP5) projections (Maloney et al. 2013; Harris et al. 2014). In all search engines, we obtained the data consisting in: (a) maximal, minimal and average temperature (average except for ~ 6000 y.b.p.); and (b) average precipitation; both at 5 arc-minutes (10 km grids) resolution. We do not include altitude because was no variation along the time-scale adopted, and is multicollinear with climate data according to *a priori* validation via correlation tests.

Niche modelling and model validation

To develop the SDMs we assumed two premises: (1) the niche evaluated is the fundamental climatic niche of species; and (2) the niche of species is static at the evolutionary viewpoint, to the time-scale adopted (~6,100 years) (Franklin 2009). We based the modeling combined predictors methods of Profile (Bioclim) and Learning Machine (Random Forest and Support Vector Machine) to decrease model uncertainty, basing the main model on average weighed by the best fit model (Hijmans and Elith 2013). Therefore, initially we modeled each species current conditions, extracting the niche values at each presence points and randomizing 1,000 absence points within the projection area. For past and future conditions, we kept only the current presence points who were within a confidence interval of 95% of current niche values (Yu et al. 2011). The evaluation process was performed by prevision, adjust and model evaluation through the test Area Under the Receiver Operator (AUC). AUC is a measure of rank-correlation that ranges from 0 to 1, a score of AUC = 0.5 means that the model is as good as random, thus a good model has AUC next to 0 or next to 1 (Phillips et al. 2006). Additionally, we evaluate the models visually by comparison on data *in situ* (personal observations and distribution maps available at the

International Union for Conservation of Nature [IUCN: http://www.iucnredlist.org/search]) (López-Arévalo et al. 2011).

Results

Climatic niche values to projection area

The climate in projection area has a current minimum temperature of 16.1°C (±3.1; ranging from 12.3 to 19.2). This niche dimension at 6,000 y.b.p. was 0.3°C lower, while for 2060s and 2080s will be 2.3°C and 3.8°C higher, respectively. In the period evaluated, the average of maximum temperature ranged from 28.1°C (±3.6) to 30.8°C (±4.0) and the average ranged from 22.1°C (±3.2) to 24.8°C (±3.6). The precipitation in projection area was 107.7 mm (±48.7) at 6,000 y.b.p., 114.6 mm (±51.3) currently, 116.9 mm (±52.3) for 2060s and 115.3 mm (±51.3) for 2080s (Figure 1; Supporting Information 1; Supporting Information S1 and S2). Yet, along the year, the climate pattern observed in 6,000 y.b.p., 2060s and 2080s have a temporal displacement. This result showed drier and colder months from June/August to September/October (Figure 1; Supporting Information S1and S2).

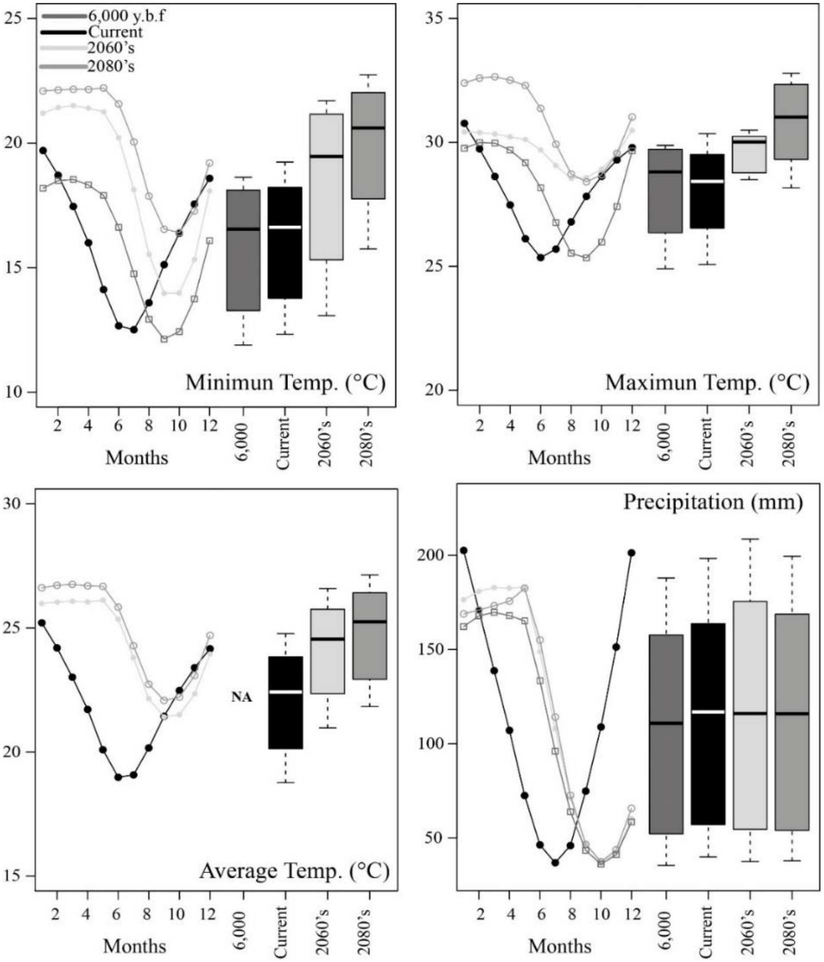

Figure 1. Climate niche summary of projection area (10°S – 40°S; 60°W – 35°W) used to perform past, current and future SDMs for *Araucaria angustifolia* (Araucaria), *Dasyprocta azarae* (Azara's Agouti), *Acca sellowiana* (Feijoa), *Eira barbara* (Tayra), *Mazama gouazoubira* (Gray brocket) and *Puma concolor* (Puma).

Species Distribution Models (SDMs)

We obtained 1,754 presence points (Figure 2) in the area selected for SMDs, ranging from 190 to 613 among species in current conditions and ranging from 73 to 488 in restriction to 95% of confidence intervals to past and future climate conditions (Table 1). The SDMs showed a current suitable distribution (probability of presence ≥ 0.50) from 25,590 km² (Grey Brocket) to 86,668 km² (Araucaria). These current distributions was reduced on average of 65.3% in 6,000 y.b.p., 31.4% in 2060s and in 19.2% in 2080s (Figure 3; Table 2). Moreover, the current species co-occurrence is 28,048 km², 94.8% bigger than 6,000 y.b.p. and 46.4% and 32.5% major than 2060s and 2080s, respectively (Figure 3; Table 2). Considering all algorithms utilized, the evaluation showed that SDMs are a good adjust, due the value of AUC ranged from 0.83 to 1.00 (Supporting Information S3), and current SDMs are in accordance with species distribution (Figure 3; Table 2; Supporting Information S4).

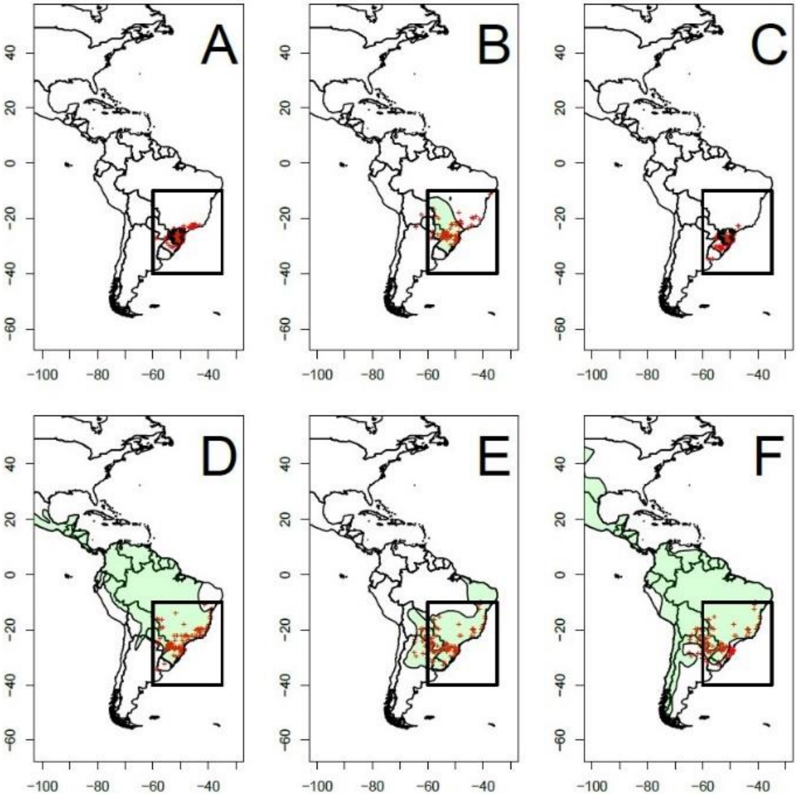

Figure 2. Current presence points (red) within projection area (10°S – 40°S; 60°W – 35°W: delimited by the black rectangle) utilized to perform past, current and future SDMs for (A) *Araucaria angustifolia* (Araucaria), (B) *Acca sellowiana* (Feijoa), (C) *Dasyprocta azarae* (Azara's agouti), (D) *Eira barbara* (Tayra), (E) *Mazama gouazoubira* (Gray Brocket) and (F) *Puma concolor* (Puma). In light green is the current species distribution according to IUCN (2016).

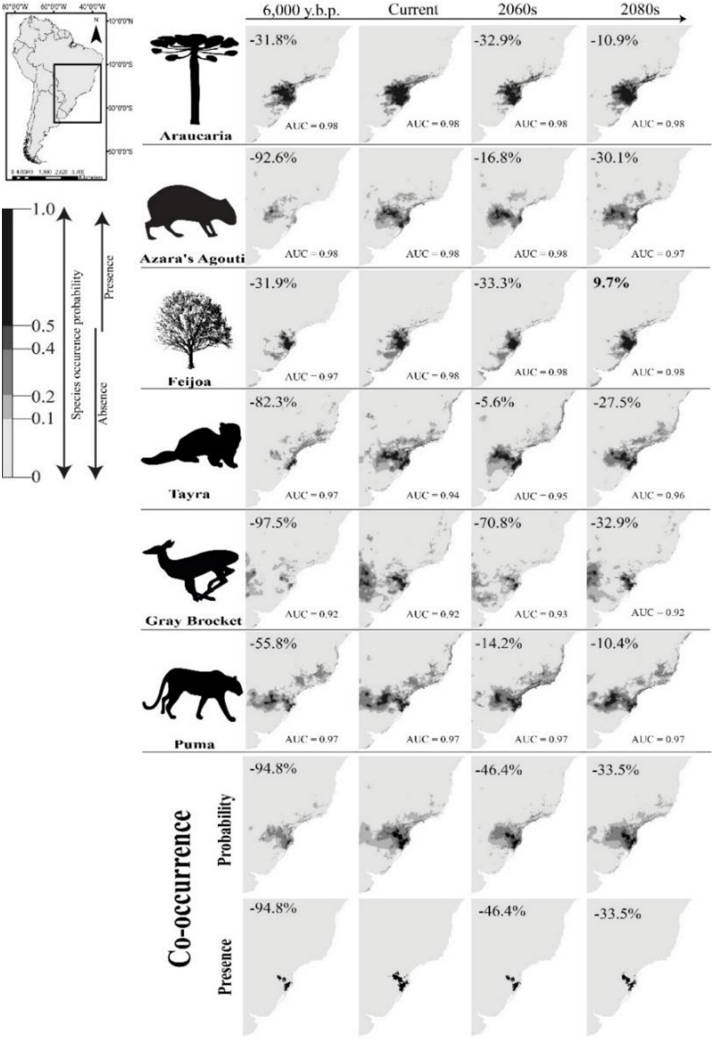

Figure 3. SDMs for past, current and future climate conditions for the species *Araucaria angustifolia* (Araucaria), *Dasyprocta azarae* (Azara's agouti), *Acca sellowiana* (Feijoa), *Eira barbara* (Tayra), *Mazama gouazoubira* (Gray Brocket) and *Puma concolor* (Puma) and for species co-occurrence (based on species average) within projection area (10°S – 40°S; 60°W – 35°W).

Table 1. Current values of climate niche for presence points of *Araucaria angustifolia* (Araucaria), *Dasyprocta azarae* (Azara's agouti), *Acca sellowiana* (Feijoa), *Eira barbara* (Tayra), *Mazama gouazoubira* (Gray Brocket) and *Puma concolor* (Puma) within SDMs projection area (10°S – 40°S; 60°W – 35°W). C.I.: confidence intervals of 95%.

	Minimum			**Maximum**		**Average**		**Precipitation**		**Occurrence remaining**		
Species	**N**	**Average**	**C.I.**	**Average**	**C.I.**	**Average**	**C.I.**	**Average**	**C.I.**	**N 6,000**	**N 2060**	**N 2080**
Araucaria	235	11.27	11.14 - 11.41	22.32	22.19 - 22.46	16.77	16.64 - 16.90	138.63	137.10 - 140.17	96	138	161
Azara's Agouti	307	13.8	13.68 - 13.92	26.33	26.22 - 26.45	20.04	19.91 - 20.16	141.26	139.92 - 142.59	135	178	157
Feijoa	195	11.07	10.93 - 11.21	21.29	21.14 - 21.44	16.16	16.02 - 16.31	136.94	135.79 - 138.10	73	102	113
Tayra	214	13.04	12.87 - 13.20	24.2	24.23 - 24.38	18.59	18.43 - 18.76	136.05	134.13 - 137.98	97	145	154
Grey Brocket	190	13.37	13.58 - 13.96	25.45	25.22 - 25.67	19.58	19.38 - 19.79	111.15	109.06 - 113.24	72	103	130
Puma	613	13.65	13.56 - 13.74	26.02	25.93 - 26.12	19.81	19.72 - 19.90	137.73	136.76 - 138.70	270	488	487
Total/Average	**1754**	**12.7 (1.2)**	**-**	**24.3 (2.1)**	**-**	**18.5 (1.7)**	**-**	**133.7 (11.2)**	**-**	**743**	**1154**	**1202**

Table 2. Results of past, current and future SDMs for *Araucaria angustifolia* (Araucaria), *Dasyprocta azarae* (Azara's agouti), *Acca sellowiana* (Feijoa), *Eira barbara* (Tayra), *Mazama gouazoubira* (Gray Brocket) and *Puma concolor* (Puma) within projection area (10°S – 40°S; 60°W – 35°W). * In relation to the current results.

Specie	**Km² of occurrence**				**% of territorial occupation**			
	6,000 y.b.p.	**Current**	**2060s**	**2080s**	**6,000 y.b.p.**	**Current**	**2060s**	**2080s**
Araucaria	59,113.9	86,668.0	58,081.2	77,195.1	2.52	3.69	2.48	3.29
Azara's Agouti	1,601.7	21,678.8	18,041.8	15,158.1	0.07	0.92	0.77	0.65
Feijoa	23,355.0	34,306.2	22,885.0	37,636.3	1.00	1.46	0.98	1.60
Tayra	7,375.3	41,606.9	39,300.0	30,168.2	0.31	1.77	1.67	1.29
Grey Brocket	633.3	25,590.0	7,468.1	17,154.5	0.03	1.09	0.32	0.73
Puma	17,171.7	38,888.0	33,347.8	34,826.5	0.73	1.66	1.42	1.48
Co-occurrence	**1,462.7**	**28,048.4**	**15,047.1**	**18,929.1**	**0.06**	**1.20**	**0.64**	**0.81**

Specie	**Increase/Decrease (km²)***				**Increase/Decrease (%)***			
	6,000 y.b.p.	**Current**	**2060s**	**2080s**	**6,000 y.b.p.**	**Current**	**2060s**	**2080s**
Araucaria	-27,554.1	-	-28,586.8	-9,472.9	-31.8	-	-33.0	-10.9
Azara's Agouti	-20,077.1	-	-3,637.0	-6,520.7	-92.6	-	-16.8	-30.1
Feijoa	-10,951.2	-	-11,421.2	**3,330.1**	-31.9	-	-33.3	**9.7**
Tayra	-34,231.6	-	-2,306.9	-11,438.7	-82.3	-	-5.5	-27.5
Grey Brocket	-24,956.7	-	-18,121.9	-8,435.5	-97.5	-	-70.8	-33.0
Puma	-21,716.3	-	-5,540.2	-4,061.5	-55.8	-	-14.2	-10.4
Co-occurrence	**-26,585.7**	**-**	**-13,001.3**	**-9,119.3**	**-94.8**	**-**	**-46.4**	**-32.5**

Discussion

One of the goals in ecology is to know the patterns of distribution and abundance of species to understand their evolution along spatiotemporal variations on the niche (Hutchinson 1957; Colwell and Rangel 2009). Our main results – that disregarded intra- and interspecific interactions – showed that the distribution ranges elements of the threatened Araucaria Forest may have been smaller in the Mid-Holocene than currently and may decrease astoundingly in the future following climate changes. In the Mid-Holocene, the SDMs suggest that the species co-occurrence was circa 1,400 km², mainly based in Azara's Agouti and Grey Brocket small-simulated distributions. Although the averages of climate variables in Mid-Holocene and currently are lower (e.g., minimal temperature of 15.8 (±3) and 16.1 (±3.1), precipitation of 107.7 (±48.7) and 114.6 (±51.3), respectively), there are different among the months of years. Current projection is 20 times larger than Mid-Holocene; our SDMs predict that this distribution will reduce in circa 40% in 2080s due to climate changes. These lower variations on climate averages are sufficient for the algorithm sensibility in SMDs (Franklin 2009). The SDMs results agree with several studies that show reduction in diversity, species distribution ranges and communities composition both for Mid-Holocene and on climate future projections (Lyons et al. 2015; Rodrigues et al. 2016; Wrege et al. 2016).

The *Araucaria* genera (i.e. *Araucaria araucana* and *Araucaria angustifolia*) in South America has undergo a great expansion from Pleistocene to Holocene due human activities (Bitencourt and Krauspenhar 2006; Reis et al. 2014). *Araucaria angustifolia* since 4,000 y.b.p. at last 100 y.b.p maintaining a *quasi*-constant expansion, performed by Xokleng, Kaingang ethnics groups and Creole farmers (Reis et al. 2014). The higher Araucaria seed production becomes an attractive for local people consume and for protein obtention via hunting (Reis et al. 2014). The Azara's Agouti – an important consumer of Araucaria seeds and a game species – SDMs also showed an expansion (~93%) in the territory from Mid-Holocene to current SDM, probably in a co-expansion with Araucaria Forest. Archeological records of game species (such as Caviomorphs) is present at several sites in South America, including sites within Araucaria Forest domain (Kipnis 2002; Hadler et al. 2008; Hadler et al. 2013), showing co-occurrence and suggesting co-expansion.

There are no studies on the pre-Colombian expansion of Feijoa, but this species also have a degree of domestication and genotypic selection in recent centuries (Santos et al. 2009; Borsuk et al. 2015). Our SDMs also showed an expansion in the Feijoa distribution (~32%) from Mid-Holocene to the present, probably in a co-expansion with Araucaria, because it is a species associated with Araucaria Forest (Santos et al. 2009). The Tayra – the main species associated with Feijoa –also expanded (~82%) from Mid-Holocene to current distribution based on our SDMs and other carnivores also have a presumed pre-Columbian interaction with humans (Martin 2012). The main grazer within the Araucaria Forest mosaics – Gray Brocket – was the mammal with greatest territory expansion from Mid-Holocene to current (~98%). From Pleistocene to Holocene, and from Mid-Holocene to current conditions the geographical configuration of major vegetation types in South America was changed from mosaics of open areas and savannas mainly to forested areas (Cione et al. 2009). This condition associated with the human occupation of South America mainland caused the extinction of large mammals and particular floristic elements beyond the general inferences about grazing and/or browsing habits (Vivo and Carmignotto 2004; Cione et al. 2009). This issue potentially made it easier the expansion of medium-bodied grazer's species (e.g. *Mazama* genera) along the South America territory due to the decrease of competition. For Puma – the current apex-predator with major abundance in South America – there is evidence supporting that the species suffered a severe demographic decline in the Late Pleistocene throughout their distribution, followed by population expansion and re-colonization of the range, initiating from South America (Matte et al. 2013). Thus, our SDMs showing an increase (~56%) from Mid-Holocene to the present agrees with this expansion.

However, future distributions of species are extremely affected by climate changes scenarios. According to our simulations, Araucaria will decrease in 33% (2060s) and 11% (2080s) in relation to the present. These results are less dramatic than other study showing a decrease of 75% until 2100s at RCP 4.5 (least pessimistic scenario; Chou et al. 2014a) (Wrege et al. 2016). In future conditions, it is expected that other vegetal formations (e.g. Dense Ombrophilous Forest [FOD]) will expand under the surroundings of the Araucaria Forest (Wrege et al. 2009; Wrege et al. 2016). Thus, Araucarias trees will be restricted to greatest altitude, where today are grasslands (Chou et al. 2014b). Azara's Agouti also accompanied the Araucaria pattern of reduction for future conditions of climate, but with values inverted (i.e. 17% in 2060s and 30% in 2080s), probably due to a co-retraction of distributions.

Feijoa showed a decrease in 2060s (33%) and an increase in 2080s (9.7%), which is surprising due to the co-occurrence with Araucaria Forest. Yet, our SDMs for Feijoa still maintain the Araucaria-Feijoa overlapping distributions. The Feijoa main interactor (Bogoni et al. unpublished data) – Tayra – will decrease at minor rates. Tayra is an opportunistic species, less susceptible to environmental changes, with a wide geographical distribution in America and featured by the occupation of more densely wooded areas (e.g. FOD) (Emmons and Feer 1997). Grey Brocket is the species with the greatest decrease in distribution (ranging from 33% to 71%), and it is expected due the Araucaria Forest advance on grasslands and the FOD advance on Araucaria Forest (e.g. Wrege et al. 2009; Chou et al. 2014b; Wrege et al. 2016). According to the climate niche, Puma is the species with minor distribution decrease. Despite being a large carnivore, Puma had a reasonable plasticity in environmental occupation and a large distribution area (Currier 1983; Astete et al. 2017). Yet, within an intensely modified habitat in Atlantic Forest and under a complete set of predictors (e.g. forest cover), the Puma distribution was positively influenced by the percentage of native vegetation, elevation and slope, and negatively by road density, watercourse density and edge density of native vegetation (Angelieri et al. 2016).

Although SDMs validation via AUC has been criticised (e.g. Lobo et al. 2007), our SDMs results and their evaluation can demonstrate how much the main elements of Atlantic Forest highlands was endangered by climate changes, corroborating some research to this vegetation mosaic (e.g. Souza et al. 2011; Ferraz et al. 2012; Wrege et al. 2016). Moreover, the presence data also influences the SDMs. For example, in our simulation the Puma distribution is larger than observed in IUCN distribution map, a phenomenom also observed in other SDMs studies with this species (Bluckin et al. 2015). We found a minor distribution to northwest than the species potential, and this issue is observed in other studies due to the background data (Angelieri et al. 2016).

Another important issue that emerges before the climate changes are the non-random alteration on plant productivity and their peaks (Haferkamp 1987). Even in not defaunated forest patches, the several native fruit is often so abundant that there is little competition for it (Morton 1973). However, the Araucaria and Feijoa provide resources (i.e.

Pinhão and fruits) able to structure the mammal communities (Iob and Vieira 2008; Paludo et al. 2009; Bogoni et al. submitted). Recently, the Araucaria forest was suffered by logging explorers in the early twentieth century (Eduardo 1974; Lacerda 2016). The human fostering on Araucaria and Feijoa lead to ensure the mammals abundance, such as occurs actually (Iob and Vieira 2008; Bogoni et al. unpublished data). However, the mammal species in South America have been hunted by several people groups (Redford and Robinson 1987; Redford 1992), resulting in a reduction of their distribution and abundance (Bogoni et al. 2016). We can conclude that the Araucaria Forest and their elements are endangered same under a mild climate change scenario. The species with major reduction are highly associated with the Araucaria and with altitudinal grasslands (Azara's Agouti and Gray Brocket). The species co-occurrence is related with the Santa Catarina state highlands, making it current and future refugia from these six species. Thus, the rare highland mosaic existence, the historic and cultural importance of this formation and the ecosystems process and species interactions are extremely dependent on public policies of climate changes mitigation from local to regional scales.

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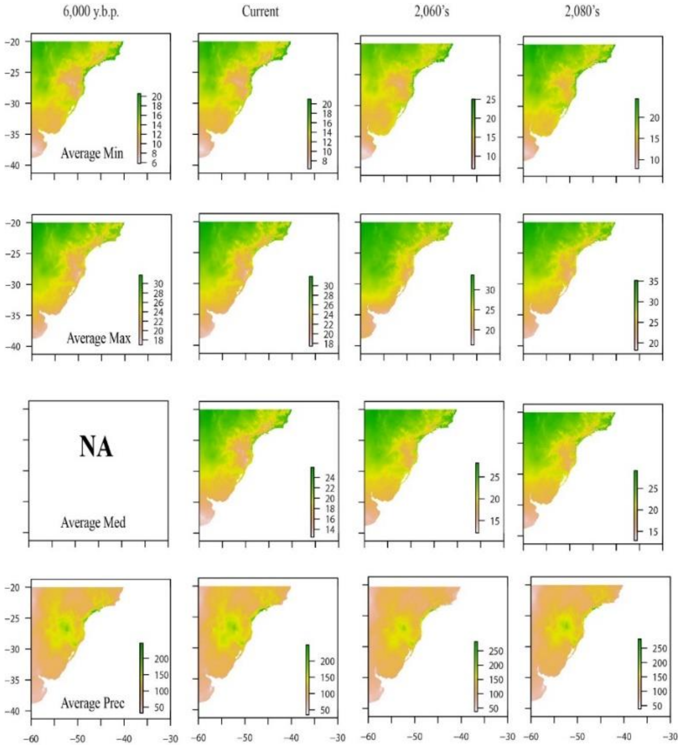
Supporting Information

Supporting Information S1. Climate conditions (top to bottom: average minimal temperature, average maximal temperature, average medium temperature, and average precipitation) for Mid-Holocene (~6,000 y.b.p.), current (average from 1950s to 2000s), and future (2060s and 2080s). Projection area: 10°S – 40°S; 60°W – 35°W; Data from: Paleoclimate Modelling Intercomparison Project Phase III (PMIP3) (http://pmip3.lsce.ipsl.fr/), WordClim (http://www.worldclim.org/download) and Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC5) (http://www.ccafs-climate.org/data/).



Supporting Information S2. Detailed climate conditions (mean and standard deviation) for Mid-Holocene (~6,000 y.b.p.), current (average from 1950s to 2000s), and future (2060s and 2080s). Projection area: 10°S – 40°S; 60°W – 35°W; Data from: Paleoclimate Modelling Intercomparison Project Phase III (PMIP3) (http://pmip3.lsce.ipsl.fr/), WordClim (http://www.worldclim.org/download) and Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC5) (http://www.ccafs-climate.org/data/).

Month	**Minimum Temperature (°C)**				**Maximum Temperature (°C)**			
	6000 y.b.p.	**Current**	**2060s**	**2080s**	**6000 y.b.p.**	**Current**	**2060s**	**2080s**
1	18.6 (2)	19.2 (2.1)	21.7 (2)	22.7 (2.3)	29.9 (2)	30.4 (2)	30.5 (2.4)	32.8 (2.1)
2	17.8 (3.5)	19.1 (2.1)	20.8 (4.5)	21 (4)	29.9 (3.9)	30.1 (2)	30.5 (4.5)	32.2 (4.5)
3	18.4 (2.8)	18.3 (2.4)	21.1 (3.5)	22.3 (3.5)	29.8 (2.6)	29.3 (2.3)	29.9 (3.4)	32.2 (3.4)
4	18.2 (2.3)	16.3 (3.1)	21.2 (2.5)	21.8 (2.7)	29.6 (2.4)	27.7 (3.3)	30.2 (3)	32.5 (3)
5	18.1 (2.1)	14 (3.5)	21.3 (2.1)	22.3 (2.4)	29.3 (2)	26.1 (4.2)	30.2 (2.3)	32.8 (2.2)
6	16.9 (2.4)	12.5 (3.5)	20.6 (2.3)	21.8 (2.8)	28.3 (2.3)	25.1 (5.1)	29.9 (2.5)	31.2 (2.5)
7	14.6 (3)	12.3 (3.7)	18.3 (3.2)	20.2 (3.6)	26.8 (3.2)	25.5 (5.3)	28.9 (3.7)	30 (3.6)
8	12.8 (3.4)	13.5 (3.8)	15.3 (3.7)	18 (3.8)	25.5 (3.9)	27 (5.3)	28.5 (4.9)	28.6 (4.7)
9	11.9 (3.5)	15.4 (3.8)	13.7 (3.3)	15.9 (3.8)	24.9 (4.9)	28 (4.8)	28.7 (5.5)	28.2 (5.4)
10	12.2 (3.6)	17 (3.4)	13.1 (4)	15.8 (4)	25.9 (5.2)	28.8 (3.8)	28.6 (6)	28.7 (5.6)
11	13.7 (3.9)	17.9 (2.8)	15.4 (4.5)	17.6 (4.3)	27.8 (5.5)	29.3 (2.6)	30.1 (5.9)	29.9 (5.7)
12	16.2 (4)	18.2 (2.4)	18.3 (4.7)	19.3 (4.3)	29.5 (5.1)	29.7 (2.4)	30.2 (5.5)	30.8 (5.5)
Average	**15.8 (3)**	**16.1 (3.1)**	**18.4 (3.4)**	**19.9 (3.5)**	**28.1 (3.6)**	**28.1 (3.6)**	**29.7 (4.1)**	**30.8 (4)**

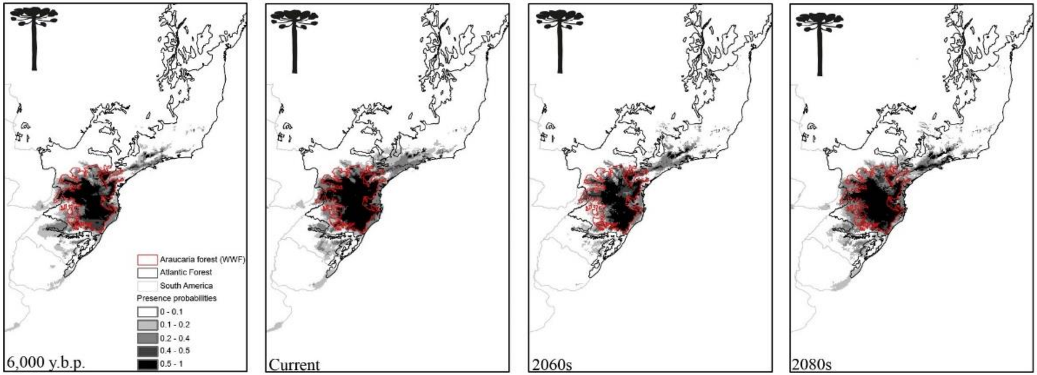
Month	Average Temperature (°C)				Precipitation (mm)			
	6000 y.b.p.	Current	2060s	2080s	6000 y.b.p.	Current	2060s	2080s
1	-	24.8 (1.9)	26.6 (2)	27.1 (2)	184.5 (71)	198.4 (79.2)	208.7 (80.7)	199.5 (80.1)
2	-	24.6 (1.9)	25.2 (3.9)	26.1 (4)	130.5 (42.1)	168.6 (67.8)	123.4 (41.5)	120.1 (39.4)
3	-	23.8 (2.2)	25.7 (3)	26.3 (3.2)	161.9 (51.8)	158.8 (57.1)	180.3 (53.9)	163 (47.3)
4	-	22 (3.1)	25.8 (2.6)	26.5 (2.7)	187.9 (73.4)	107.8 (37.8)	206.1 (72)	198.4 (76.9)
5	-	20 (3.8)	26.6 (2)	27.1 (2.1)	153.5 (59.8)	65.9 (41.3)	170.7 (68.8)	162.4 (67.9)
6	-	18.8 (4.1)	25.4 (2.4)	25.8 (2.4)	144.8 (55.7)	48.1 (46.5)	156.1 (59.6)	174.5 (56.2)
7	-	18.9 (4.4)	23.9 (3.5)	24.3 (3.5)	91.2 (30)	39.9 (41.2)	108.6 (41)	111.8 (42)
8	-	20.2 (4.4)	22.1 (4.2)	22.6 (4.2)	58.3 (34.9)	41 (38.4)	64.4 (47.4)	62.3 (40.3)
9	-	21.7 (4.2)	21 (4.6)	21.8 (4.5)	46.1 (44.1)	68.8 (39.5)	46.1 (44.7)	45.6 (46.9)
10	-	22.9 (3.5)	21.4 (4.6)	22.1 (4.6)	35.4 (38.6)	125.9 (39.3)	37.6 (41.8)	37.8 (40.4)
11	-	23.6 (2.6)	22.6 (4.6)	23.3 (4.9)	37.1 (39)	158.7 (50.1)	37.4 (36.8)	40.6 (38.2)
12	-	23.9 (2.3)	23.9 (4.7)	24.6 (4.9)	60.7 (44)	192.9 (77.7)	63 (38.8)	67.4 (40.1)
Average	-	**22.1 (3.2)**	**24.2 (3.5)**	**24.8 (3.6)**	**107.7 (48.7)**	**114.6 (51.3)**	**116.9 (52.3)**	**115.3 (51.3)**

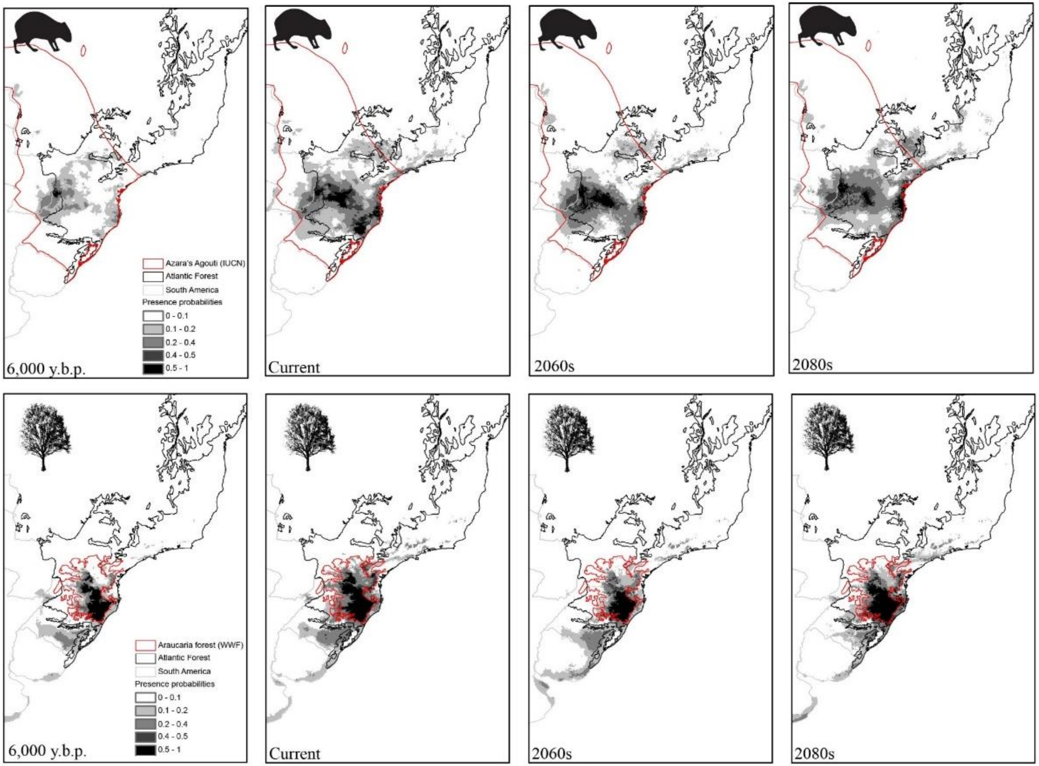
Supporting Information S3. Area Under the Receiver Operator (AUC) values for each model (algorithm) and each species SDMs within the projection area (10°S – 40°S; 60°W – 35°W). AUC range from 0 to 1, a score of AUC = 0.5 means that the model is as good as a random, thus a good model have AUC next to 0 or next to 1 (Phillips et al. 2006).

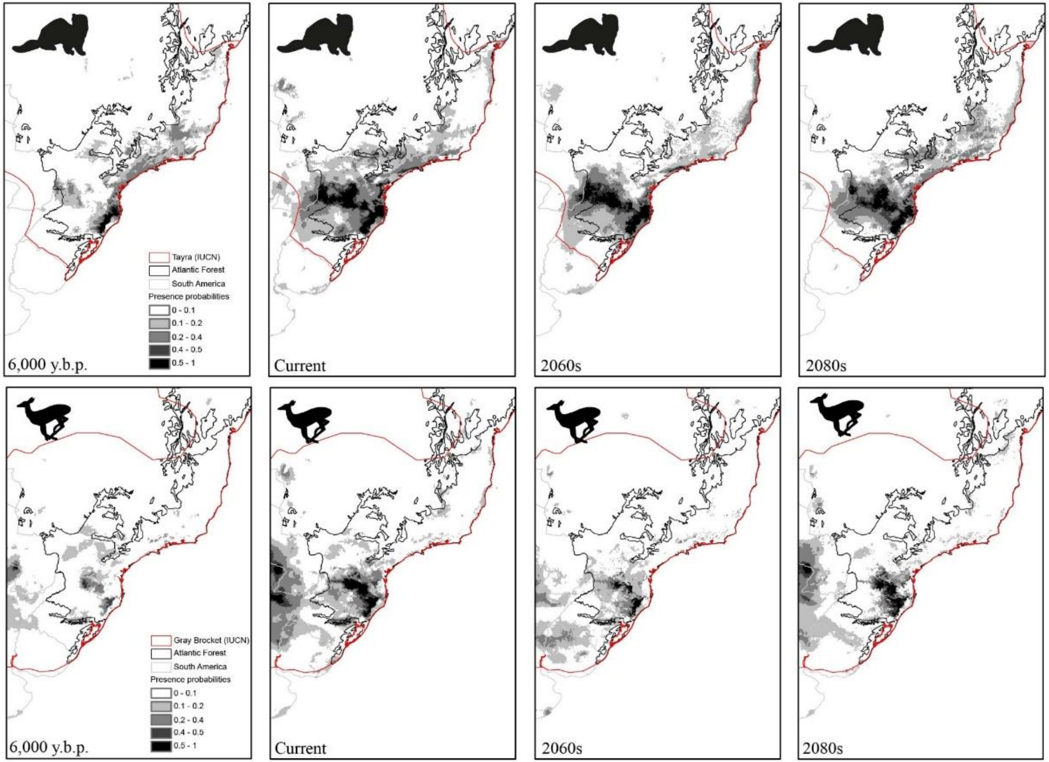
Species	Condition	Algor.	AUC	Species	Condition	Algor.	AUC
Araucaria	6,000 y.b.p.	Bioclim	0.977	Tayra	6,000 y.b.p.	Bioclim	0.949
		RF	1			RF	1
		VSM	0.961			VSM	0.955
	Current	Bioclim	0.972		Current	Bioclim	0.881
		RF	1			RF	1
		VSM	0.978			VSM	0.947
	2060s	Bioclim	0.976		2060s	Bioclim	0.893
		RF	1			RF	1
		VSM	0.96			VSM	0.95
	2080s	Bioclim	0.969		2080s	Bioclim	0.916
		RF	1			RF	1
		VSM	0.971			VSM	0.954
Azara's Agouti	6,000 y.b.p.	Bioclim	0.971	Grey Brocket	6,000 y.b.p.	Bioclim	0.86
		RF	1			RF	1
		VSM	0.967			VSM	0.909
	Current	Bioclim	0.966		Current	Bioclim	0.836
		RF	1			RF	1

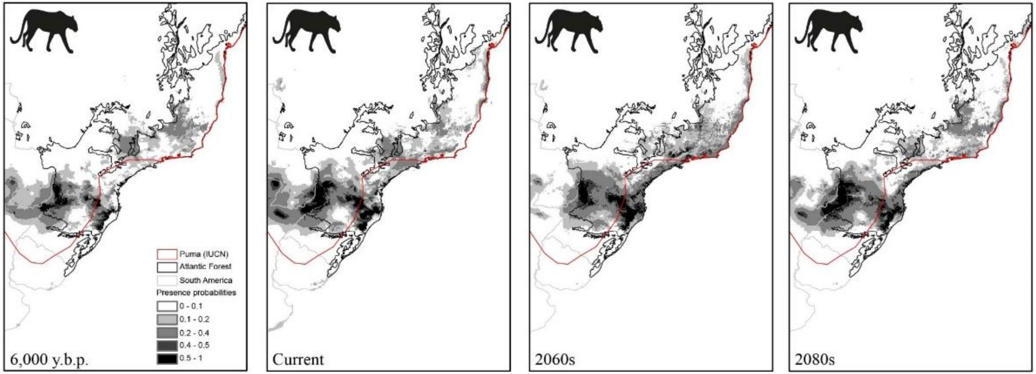
		VSM	0.976			VSM	0.916
	2060s	Bioclim	0.96		2060s	Bioclim	0.846
		RF	1			RF	1
		VSM	0.973			VSM	0.934
	2080s	Bioclim	0.94		2080s	Bioclim	0.845
		RF	1			RF	1
		VSM	0.968			VSM	0.918
Feijoa	6,000 y.b.p.	Bioclim	0.982	Puma	6,000 y.b.p.	Bioclim	0.934
		RF	1			RF	1
		VSM	0.937			VSM	0.967
	Current	Bioclim	0.972		Current	Bioclim	0.942
		RF	1			RF	1
		VSM	0.96			VSM	0.982
	2060s	Bioclim	0.978		2060s	Bioclim	0.942
		RF	1			RF	1
		VSM	0.971			VSM	0.973
	2080s	Bioclim	0.975		2080s	Bioclim	0.933
		RF	1			RF	1
		VSM	0.967			VSM	0.975

Supporting Information S4. Detailed SDMs for past, current and future climate conditions for the species *Araucaria angustifolia* (Araucaria), *Dasyprocta azarae* (Azara’s agouti), *Acca sellowiana* (Feijoa), *Eira barbara* (Tayra), *Mazama gouazoubira* (Gray Brocket) and *Puma concolor* (Puma) (in this order) within projection area (10°S – 40°S; 60°W – 35°W).




Azara's Agouti (IUCN)
Atlantic Forest
South America
Presence probabilities
0 - 0.1
0.1 - 0.2
0.2 - 0.4
0.4 - 0.5
0.5 - 1
6,000 y.b.p.
Current
2060s
2080s
Araucaria forest (WWF)
Atlantic Forest
South America
Presence probabilities
0 - 0.1
0.1 - 0.2
0.2 - 0.4
0.4 - 0.5
0.5 - 1
6,000 y.b.p.
Current
2060s
2080s


Tayra (IUCN)
Atlantic Forest
South America
Presence probabilities
0 - 0.1
0.1 - 0.2
0.2 - 0.4
0.4 - 0.5
0.5 - 1
6,000 y.b.p.
Current
2060s
2080s
Gray Brocket (IUCN)
Atlantic Forest
South America
Presence probabilities
0 - 0.1
0.1 - 0.2
0.2 - 0.4
0.4 - 0.5
0.5 - 1
6,000 y.b.p.
Current
2060s
2080s


Puma (IUCN)
Atlantic Forest
South America
Presence probabilities
0 - 0.1
0.1 - 0.2
0.2 - 0.4
0.4 - 0.5
0.5 - 1
6,000 y.b.p.
Current
2060s
2080s

CONCLUSÃO GERAL

Em primeiro plano florescência de Asteraceae, ao fundo os campos de altitude entremeados por manchas de Florestas de Araucária no Parque Nacional de São Joaquim, Urubici, Santa Catarina, Brasil. Foto: Bogoni, 2016.

4. CONCLUSÃO GERAL

Ao todo, trabalhei com 1.735 registros de presença de 62 espécies de mamíferos ao longo de 118 áreas na Mata Atlântica, obtidos em literatura e outros 1.754 registros de presença de Araucária, Feijoa, cutia, irara, veado-catingueiro e puma, obtidos em plataformas de busca, literatura e dados empíricos. Ainda, estabeleci 32 parcelas (51.200 m²) com 1.017 indivíduos de Araucária e Feijoa amostrados, quantifiquei a produtividade por dois anos em 245 Araucárias e 28 Feijoas, tive um esforço de 11.956 armadilhas/dia e fiz 2.224 registros fotográficos de mamíferos e 2.099 vídeo-registros de mamíferos e aves, entrevistei 36 moradores do Planalto Catarinense, perfazendo uma área de 10.898 ha.

Os principais resultados do capítulo 1 mostraram uma grande diversidade beta (entre comunidades) para mamíferos em comparação com a diversidade alpha média (dentro das comunidades) e a diversidade beta em escalas espaciais menores (e.g. áreas tropicais e subtropicais). A alta diversidade beta evidencia que entre as 118 comunidades de mamíferos avaliadas ao longo de toda a Mata Atlântica, a rotatividade espacial de espécies é de 4 espécies diferentes de uma comunidade para outra, representando 41% da média alpha (local), 11% da diversidade gamma (biogeográfica) e 27% da riqueza média observada. A diversidade de mamíferos de médio a grande porte ao longo da Mata Atlântica é composta por um resumo aninhado de diversidades locais a regionais e tanto o paradigma neutro como outros paradigmas de meta-comunidades têm forças complementares na diversidade de espécies nas várias escalas espaciais. Os resultados do segundo capítulo mostram que a Feijoa atua como atrator e estruturador da comunidade de mamíferos e aves, pois a fauna teve um aumento diversidade em congruência com a oferta espaço-temporais de seus frutos. Portanto, a domesticação incipiente da Feijoa pode ter favorecido a fauna associada, com um aumento ou manutenção da diversidade local, suprimindo a ausência sazonal do Pinhão. Os principais resultados do capítulo 3 mostraram que – com exceção das condições climáticas – a paisagem, o meio ambiente, a demografia das Araucárias e Feijoas e suas produtividades são altamente variáveis ao longo dos planaltos subtropicais dentro da Mata Atlântica. A diversidade de mamíferos no espaço e no tempo está relacionada parcialmente e positivamente com a produtividade dos recursos. A demografia e a produtividade das Araucárias e Feijoa e sua coocorrência estão relacionadas principalmente com características climáticas e ambientais e os mamíferos promovem feedbacks para a demografia e para a composição florestal. Os resultados do capítulo 4 mostram que a longa gestão histórica de fogo e gado é a principal manutenção de mosaicos de paisagem nas terras altas, e esse manejo junto com outras ações de menor escala reconfigura a proporção de elementos animais e vegetais dentro das paisagens. Os principais resultados do capítulo 5 mostram que os elementos da ameaçada Floresta de Araucária podem diminuir suas distribuições diante de futuros cenários de mudanças climáticas e, ainda, mostram que as distribuições das espécies foram menores no Holoceno Médio do que são atualmente. No Holoceno Médio a coocorrência de todas as espécies-chave era cerca de 1.400 km², baseado principalmente em distribuições simuladas da cutia e do veado-catingueiro. No entanto, a projeção atual mostrou um aumento de 20 vezes na área, mas que tende a ser reduzida em cerca de 40% até 2080 devido às mudanças climáticas.

Ainda, os resultados me permitiram avaliar a magnitude das interações entre vertebrados e árvores com processos de domesticação (i.e. Feijoa e Araucária), em uma paisagem cultural e ambiente altamente ameaçado, sob uma abordagem basal de teia alimentar com implicações complementares das forças de cascata ascendente e descendente. Esses resultados contribuem para a compreensão das relações vertebrados-plantas e mostram que as ações humanas (passadas e contemporâneas) podem mudar não apenas padrões de distribuição e abundância, mas também a diversidade e direção das interações interespecíficas entre espécies. Concluo, ainda, que a Araucária e a Feijoa são essenciais para as pessoas locais. Os recursos (i.e. frutos de Feijoa e o Pinhão) são compartilhadas entre elas e seus animais domesticados e a fauna nativa e isso ajuda a manter a característica e saúde de um dos ecossistemas mais reduzidos das terras altas da Mata Atlântica. A “pegada humana” na paisagem e no gerenciamento de recursos são "pelo menos" capazes de construir espaços de nicho que influenciam os padrões e processos de diversidade local. Por fim posso concluir que as Florestas de Araucárias e seus elementos estão em perigo mesmo sob um cenário de mudança climática menos dramático. As espécies com grande redução de distribuição no futuro estão altamente associadas à Araucária e aos campos altitudinais. A co-ocorrência das espécies está intimamente relacionada com os planaltos sul brasileiros, tornando-os um refúgio atual e futuro dessas espécies. Assim, a existência de raro mosaico nas terras altas, a importância histórica e cultural desta formação, os processos ecossistêmicos e as interações entre as espécies estão inevitavelmente dependentes de políticas públicas de mitigação das mudanças climáticas.

Meu trabalho mostrou como inúmeras questões afetam os padrões de diversidade de mamíferos. Questões como escala, influências humanas (positivas e negativas, Pré e Pós-Colombiana), fatores indiretos e diretos, como clima, ambiente, paisagem, produtividade das florestas, implicações ecológicas dos atributos das espécies e o tempo evolutivo moldaram a composição e a diversidade dos mamíferos. Mostrando, portanto, como o acaso e o determinismo influencia os elementos de maior porte da sobrevivente megafauna – os médios e grandes mamíferos, remanescentes de uma outrora mais majestosa biota – na floresta tropical com o maior gradiente latitudinal do mundo.

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6. MATERIAL SUPLEMENTAR

Adicionalmente, outros artigos no mesmo escopo da tese (com e sem dados oriundos da tese) foram publicados ao longo do período de doutoramento, e podem ser acessados através dos links abaixo:

1) http://jinsectscience.oxfordjournals.org/content/14/1/299
2) http://jmammal.oxfordjournals.org/content/early/2016/01/18/jmammal.gyv215
3) http://www.oecologiaaustralis.org/ojs/index.php/oa/article/viewArticle/954
4) http://link.springer.com/article/10.1007/s10531-016-1147-1?wt_mc=Internal.Event.1.SEM.ArticleAuthorOnlineFirst
5) https://www.degruyter.com/view/j/mamm.ahead-of-print/mammalia-2015-0165/www.degruyter.com/view/j/mamm.ahead-of-print/mammalia-2015-0165/mammalia-2015-0165.xml
6) https://periodicos.ufsc.br/index.php/biotemas/article/view/2175-7925.2017v30n1p113/33716
7) http://onlinelibrary.wiley.com/doi/10.1002/ecy.1998/full
8) https://academic.oup.com/jmammal/article/doi/10.1093/jmammal/gyx103/4372291