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Eco-epidemiologia e dinâmica espaço-temporal da hantavirose com contribuições para geração e uso de dados abertos

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Que esta tese ajude pessoas a ajudar pessoas.

"Diz o mestre:

Escreva. Seja uma carta, ou um diário, ou algumas anotações enquanto fala ao telefone – mas escreva. Escrever nos aproxima de Deus e do próximo. Se você quiser entender melhor o seu papel no mundo, escreva. Procure colocar a sua alma por escrito, mesmo que ninguém leia – ou, o que é pior, mesmo que alguém termine lendo algo que você não queria. O simples fato de escrever nos ajuda a organizar o pensamento e ver com clareza o que nos cerca. Um papel e uma caneta operam milagres – curam dores, consolidam sonhos, levam e trazem a esperança perdida. A palavra tem poder. "

Paulo Coelho (texto enviado por MM)

Resumo

Os hantavírus provocam doenças de alta letalidade e já foram alvo de diversas propostas de investigação. Com o avanço da tecnologia, da Ciência e dos movimentos Open, trabalhar com um volume massivo de dados é muito mais possível hoje do que 20 anos atrás. Há uma demanda por estudos que possam sumarizar, disponibilizar e avaliar o papel da biodiversidade em processos de difusão de doenças zoonóticas. Nesta tese, que se iniciou como um entendimento da extensão e distribuição da biodiversidade da Mata Atlântica, busquei compreender a patogeografia da hantavirose. A dinâmica da infecção por hantavirose pode depender de diversos fatores interagindo, como clima e paisagem, bem como a distribuição de populações de roedores hospedeiros. No primeiro capítulo eu apresento a iniciativa ATLANTIC que permite livre acesso a dados de biodiversidade. No segundo capítulo eu busco compreender a extensão espacial da Mata Atlântica e levantar a discussão sobre áreas para delimitação de estudos ecológicos, um aspecto essencial para se investigar patogeografia. No terceiro capítulo busco entender os fatores que melhor explicam a variação na proporção de roedores de espécies potencialmente reservatório de tipos letais de hantavírus encontrados na Mata Atlântica. Neste capítulo também exploro a ideia de *hotspots* de vulnerabilidade à doença em humanos. No quarto capítulo, investiguei as consequências da alteração da paisagem na incidência de hantavirose no Brasil, gerando mapas de risco a partir de dados abertos ou públicos. Os resultados aqui encontrados mostram que: a) iniciativas de open data levaram a mobilização de grandes grupos que sumarizaram mais de 100 anos de dados sobre a biodiversidade da Mata Atlântica em menos de quatro anos, beneficiando a ciência e a aplicação do conhecimento científico para medidas de conservação da biodiversidade; b) é preciso discutir amplamente a delimitação de uma área de investigação, pois dependendo do limite adotado a Mata Atlântica pode ter meio milhão de km^2 a mais ou a menos. c) espécies de roedores relevantes para a hantavirose tendem a ser capturados até em amostragens de baixo esforço, em áreas de alta heterogeneidade da paisagem, tipicamente agrícolas e com níveis amenos de pluviosidade. As comunidades de hospedeiros de hantavírus patogênicos na Mata Atlântica é influenciada por distúrbios antrópicos que aumentam a diversidade de cultivos agrícolas (heterogeneidade espacial) em detrimento da redução de áreas florestais (<20% de floresta na paisagem); d) Áreas de risco foram mais relevantes em municípios do Cerrado e Mata Atlântica, e o mecanismo para isso é a maior presença de roedores reservatório, associada a uma grande população de trabalhadores rurais e monoculturas em contato com uma quantidade substancial de áreas de vegetação nativa. Ressalta-se a importância de averiguar as hipóteses de amplificação e diluição para a hantavirose nesses locais, que são alvos da expansão e intensificação agrícola, bem como medidas de controle e prevenção da doença.

Palavras-chave: ecologia de doenças, ecologia da paisagem, biodiversidade, open data, Mammalia, INLA

Abstract

Hantaviruses cause diseases with high lethality and have been the target of several research proposals. With the advancement of technology, science, and Open movements, working with massive data is much more possible today than it was 20 years ago. There is a demand for studies that can summarize, make available and evaluate the role of biodiversity in processes of diffusion of zoonotic diseases. In this thesis, which began as an understanding of the extent and distribution of Atlantic Forest biodiversity, I aimed to understand the dynamics and eco-epidemiology of hantavirus. The dynamics of hantavirus infection may depend on several interacting factors such as climate and landscape, as well as the distribution of host rodent populations. In the first chapter I introduce the ATLANTIC initiative that allows free access to biodiversity data, which I have participated in intensely. In the second chapter I seek to understand the spatial extent of the Atlantic Forest and to raise the discussion about delimiting areas of ecological studies, an essential aspect to investigate pathogeography. In the third chapter I seek to understand the drivers that best explain the variation in the proportion of rodents of potentially reservoir species of lethal types of hantavirus found in the Atlantic Forest. In this chapter I also explore the idea of disease vulnerability hotspots in humans. In the fourth and final chapter, I investigated the consequences of landscape change on the incidence of hantavirus in Brazil, generating risk maps from open or public data. The results found here show that: a) individual open data initiatives led to the mobilization of large groups that summarized more than 100 years of data on Atlantic Forest biodiversity in less than four years, benefiting science and the application of scientific knowledge to biodiversity conservation measures; b) It is necessary to discuss the delimitation of an area of investigation, because depending on the limit adopted the Atlantic Forest may be half a million km^2. c) rodent species relevant to hantavirus tend to be captured even in low effort samples, in areas of high landscape heterogeneity, typically agricultural and with mild rainfall levels. Pathogenic hantavirus host communities in the Atlantic

Forest are influenced by anthropogenic disturbances that increase crop diversity (landscape heterogeneity) to the detriment of reduced forest areas (less than 20% forest in the landscape); d) Hazardous areas were most relevant in Cerrado and Atlantic Forest municipalities, and the mechanism for this is the greater presence of reservoir rodents, associated with a large population of rural workers and monocultures in contact with a substantial amount of native vegetation areas. The importance of investigating the hypotheses of amplification and dilution for hantavirus in these places, which are targets of agricultural expansion and intensification, as well as control and prevention measures of the disease, is emphasized.

Keyword: disease ecology, landscape ecology, biodiversity, open data, Mammalia, INLA

Sumário

Apresentação

Esta tese une temáticas com as quais eu comecei a trabalhar em 2013. A enorme curva de aprendizagem do mestrado (2012-2014) me permitiu ousar sair do mundo dos morcegos para desbravar o mundo da Ecologia e Biodiversidade durante o doutorado. Essa ampliação de temas de pesquisa se iniciou a partir de empolgantes colaborações com virologistas (SABINO-SANTOS et al., 2015; SABINO-SANTOS JR et al., 2018), que me permitiram aprender muito e também constatar que continuo sabendo muito pouco. As ferramentas de SIG (Sistemas de Informação Geográfica), a capacidade de processamento computacional e novas abordagens de análise cresceram absurdamente desde que entrei na pós-graduação, bem como meu interesse por *open data*, mamíferos, ecologia espacial e a interface entre seres humanos e outros animais por meio de interações patogênicas. Como filha de médico, hoje não me surpreendo por ter tentado unir a Ecologia com a Epidemiologia numa tese consolidada que, a meu ver, pode ajudar pessoas a ajudar outras pessoas através da Ciência e do Ensino. Esta tese é introduzida e concluída por meio de uma linguagem mais simples do que se esperaria para literatura científica, o que talvez motive uma variedade de pessoas a lê-la. Também optei por usar infográficos para ilustrar as ideias principais e atingir um público que talvez procure por uma informação sumarizada, ao invés de um texto aprofundado em forma de artigo científico. Mais importante, essa tese não representa fim nenhum. Ela é apenas o começo de uma discussão! Boa leitura.

Introdução Geral

Doenças emergentes são motivo de preocupação em todo o planeta, e conhecer quais são os fatores que levam uma doença a emergir em uma localidade é importantíssimo, principalmente frente ao rápido crescimento populacional global (JONES et al., 2008). Dentre as origens das doenças emergentes se destacam as que são associadas aos vírus e bactérias (JONES et al., 2008).

Os mecanismos para a dispersão de um vírus patogênico em uma população ao longo do tempo, podem ser entendidos de uma forma clássica, descrita na epidemiologia como modelo SIR (susceptível, infectado e recuperado/removido). O patógeno (no caso desta tese, um vírus) pode infectar um organismo susceptível. Este organismo passa a estar infectado e depois é removido do sistema, ou por morte ou por recuperação. De forma simplificada podemos descrever o processo de adoecimento com sendo resultado de uma interação que envolve o contato e o contágio. Sendo a Ecologia a ciência que estuda interações que determinam a abundância e a distribuição de organismos, e a Epidemiologia a ciência que estuda as doenças, penso que devemos intensificar o diálogo entre estas duas áreas do saber. De fato, estamos vivendo na era da Eco-Epidemiologia, que busca entender interações entre patógenos e hospedeiros sob a perspectiva de diferentes níveis de organização e escalas (SUSSER; SUSSER, 1996).

Diversos fatores ambientais podem influenciar na dinâmica populacional dos hospedeiros de diferentes patógenos, como clima (ASTORGA et al., 2018), diversidade local de competidores (LUIS; KUENZI; MILLS, 2018) e presença de predadores (OSTFELD; HOLT, 2004). Os efeitos dos fatores mencionados podem alterar a dinâmica da dispersão de patógenos e sua transmissão entre espécies diferentes (*spillover*), incluindo o ser humano (KARESH et al., 2012).

Há diversos processos que podem modificar a possibilidade de contato entre patógenos e organismos hospedeiros. Mudanças no uso da terra e novas práticas agrícolas são apontados como causadores da emergência de diversas doenças em humanos (*spillover* para humanos), e isto está tanto associado a mudança na demografia e comportamentos humanos, como também à ecologia dos hospedeiros e do patógeno (ALLEN et al., 2017). Outros aspectos também podem facilitar a dispersão de patógenos, como viagens internacionais, comércio, subnutrição, contaminação de alimentos e água e as mudanças climáticas globais (ALLEN et al., 2017; FAUST et al., 2018). Os componentes nesta lista de fatores são conhecidos como *drivers* da emergência de doenças, e em decorrência de sua complexidade, a modelagem de risco de transmissão de doenças é bastante desafiadora e quase que necessariamente multidisciplinar.

Modelos estatísticos e matemáticos podem ser desenvolvidos para investigar doenças quando observações de campo ou experimentos grandes são impraticáveis. Tais modelos, aliados à quantidade massiva de dados hoje disponíveis, permitem que cientistas compreendam a dinâmica espaço-temporal de diferentes fenômenos. O uso massivo de dados só é possível por conta do que hoje chamamos de *Open Data movement* ou *Open Science*. "*Open Data*" (Dados abertos) é um movimento que defende que dados devem estar livremente disponíveis para todos, sem restrições de direitos autorais, patentes, ou outros mecanismos de controle (Wikipedia; https://opendatahandbook.org/guide/pt_BR/what-is-open-data/). Dados abertos ou *open data* permitem que novos estudos importantes possam ser realizados, e iniciativas de *open data* surgem quase que diariamente (https://opendataimpactmap.org/map).

A Ecologia se alinhou com o movimento de *Open data* e *Big data*, estando a par de uma era de "*Big Science*" (POWERS; HAMPTON, 2019). A era de *Big Science* inclui o desenvolvimento de ferramentas que facilitam a manutenção, processamento, análise, comunicação de dados, e de métodos para colaboração e disseminação de informação. Dentre os tipos de dados e *softwares* que são abertos, pode haver um certo controle como aqueles impostos por licenças *Creative Commons*, ou GNU (*General Public License*, Softwares livres, *copyleft*), como os softwares utilizados nesta tese – R, GRASS (NETELER et al., 2012; R CORE TEAM, 2016) e dados de repositórios *online* como é o caso do GitHub (github.com).

Nesta tese, eu utilizei a abordagem de modelos estocásticos para calcular a probabilidade de transmissão de hantavirose (risco) nos municípios brasileiros com base na presença dessa zoonose em humanos e em fatores ambientais. Neste processo, alinhado a filosofia do *Open Science* foram utilizados tanto dados como *softwares* livres. A tese foi organizada em quatro capítulos. No primeiro capítulo eu compilei, analisei e promovi a facilitação do acesso de dados sobre a ocorrência e abundância de morcegos na Mata Atlântica (ATLANTIC BATS; MUYLAERT et al., 2017). Morcegos foram a ponte para que eu iniciasse as pesquisas com hantavírus, pois detectamos anticorpos para hantavírus bem como material RNA viral em morcegos em estudos recentes (SABINO-SANTOS et al., 2015; SABINO-SANTOS JR et al., 2018). O capítulo 1 integra a iniciativa do projeto ATLANTIC SERIES publicado na *Ecology*, no qual eu também tive a oportunidade de colaborar em diversas frentes, como no ATLANTIC CAMTRAPS (LIMA et al., 2017), ATLANTIC MAMMAL TRAITS (GONÇALVES et al., 2018), ATLANTIC BIRDS (RODRIGUES et al., 2019) e ATLANTIC BIRD TRAITS (RODRIGUES et al., 2019). No segundo capítulo organizei bases e disponibilizei limites territoriais do bioma da Mata Atlântica, realizando uma análise de suas diferenças e discutindo aspectos relacionados aos usos de cada alternativa, o que incluiu um limite consensual e um limite integrador (MUYLAERT et al., 2018). Os limites da Mata Atlântica até então nunca tinham sido avaliados e disponibilizados de uma maneira operacional e livre, de forma a comparar os limites existentes, e sintetizar suas principais diferenças e usos em potencial. Desta forma, entendo os dois primeiros capítulos e projetos ATLANTIC que eu colaborei em paralelo, como contribuintes dos movimentos *open data, open science* e *open access*. Já os dois últimos capítulos (3 e 4) foram elaborados utilizando o método hipotético-dedutivo para investigar a ecologia da hantavirose e de seus hospedeiros no Brasil.

Hantavirose

Cerca de 58% dos organismos causadores de doenças podem levar a zoonoses, doenças causadas por patógenos que podem ser transmitidos por animais (WOLFE; DUNAVAN; DIAMOND, 2007). Dessas zoonoses, a hantavirose é ao mesmo tempo uma doença intrigante e emergente. Intrigante porque, embora rara, ela é fatal em muitos casos (FONSECA; OLIVEIRA; DUARTE, 2018). Emergente, pois após sua primeira detecção oficial em 1993 em Juquitiba (hoje sabe-se que já havia pessoas na década de 80 infectadas no Brasil, BADRA et al., 2012), o número de casos é cada vez maior, e novos casos têm sido confirmados a cada ano em cada vez mais municípios (foco do Capítulo 4). A hantavirose é causada por algumas espécies de vírus da Família *Hantaviridae*, gênero *Orthohantavirus* (LAENEN et al., 2019), comumente chamados de hantavírus. Vírus sãos microrganismos que dependem dos seus reservatórios naturais para sobreviver. Quando os vírus infectam hospedeiros acidentais, como seres humanos, eles podem levar ao desenvolvimento de doenças. Não há indícios de que os hantavírus matem ou prejudiquem seus hospedeiros naturais no Brasil, embora haja alguma evidência de redução da taxa de sobrevivência de roedores infectados por hantavírus na Europa durante o inverno (KALLIO et al., 2007). Sendo assim, entender a ecologia dos potenciais reservatórios (foco do Capítulo 3) pode nos trazer uma melhor compreensão sobre a circulação do vírus no ambiente.

Aspectos clínicos

O tipo de hantavirose tipicamente diagnosticado no Brasil é a síndrome cardio-pulmonar por hantavírus (SAGGIORO et al., 2007). Na Europa e Ásia, há uma versão diferente causada por vírus do mesmo gênero chamada de síndrome renal por hantavírus (LEE; LEE; JOHNSON, 1978). Na América do Sul a hantavirose é clinicamente caracterizada por levar a edema pulmonar e miocardite (inflamação no tecido muscular do coração), comumente seguido de choque circulatório e morte. Em inglês, nos referimos à hantavirose (síndrome cardiopulmonar) pelas siglas HCPS (*hantavirus cardiopulmonary syndrome*, sigla utilizada nesta tese) e HPS (*hantavirus pulmonary syndrome*). A HCPS é frequentemente confundida com outras doenças cardiorrespiratórias como leptospirose e dengue (DE OLIVEIRA et al., 2017). Considerando o Brasil, em geral há casos durante todo o ano, e a maior parte dos casos evolui rapidamente para quadros perigosos, sendo que mais de 90% dos pacientes infectados necessitam de hospitalização (DA ROSA ELKHOURY et al., 2012), o que leva a ser mais um fator preocupante quando há surtos.

Como e onde se pega hantavirose?

O ser humano se infecta com hantavírus quando uma série de condições são satisfeitas (Capítulo 4). A principal delas é que haja contato entre o ser humano e as excretas de roedores infectados. Isso ocorre quando, por exemplo, se varre um local com excretas infectadas e elas sobem em forma de poeira (aerossol) contento partículas virais. Outra situação de risco é quando, por exemplo, um trabalhador rural se abaixa para cortar e colher algum produto agrícola, o que acaba levantando essa poeira com material infectado e aumentando a chance de aspirar o material contido nela. Estima-se que um cortador de cana tenha que abaixar-se mais de 1000 vezes por dia, chegando a realizar mais de 3000 flexões de coluna e mais de 3000 golpes de podão (LEITE et al., 2018; VILELA et al., 2015); com isto esses trabalhadores correm um grande risco de contrair hantavirose e outras injúrias. Ainda que alguns tipos de prevenção sejam aplicados, como tecido ou máscara cobrindo o rosto, o constante movimento e a exposição a ambientes de risco por si só já incrementam a chance de entrar em contato com o vírus. Mas é importante salientar que outras pessoas, que não trabalhadores da cana, contraem a doença em diferentes situações e em paisagens não necessariamente dominadas por cana-de-açúcar (TERÇAS-TRETTEL et al., 2019).

Na China, a incidência de síndrome renal por hantavírus atinge valores máximos em valores baixos de urbanização (TIAN; STENSETH, 2019), o que nos leva a pensar se a doença tem um caráter rural e ocupacional na sua paisagem patogênica ótima também no Brasil. Já havia indício de que o risco de hantavirose é grande em áreas rurais (DE OLIVEIRA et al., 2015), pois os roedores hospedeiros de hantavírus são nativos e podem usar matrizes agrícolas. Entretanto, esse risco nunca foi quantificado no Brasil. Portanto, qual seria a paisagem patogênica ótima da hantavirose no Brasil? Estas questões são focos do estudo conduzido no Capítulo 4 desta tese.

No Brasil, o portal da saúde do Sistema Único de Saúde (DATASUS, Ministério da Saúde) disponibiliza livremente informações sobre casos de hantavirose, propiciando o desenvolvimento de pesquisas científicas. É notável que, para essa doença, o número de casos confirmados é somente 8% do número de casos suspeitos (FONSECA; OLIVEIRA; DUARTE, 2018). Por conta disso, na presente tese foram utilizados casos confirmados para a análise espaço temporal da doença (Capítulo 4). A falta de comunicação sobre a doença pelos órgãos competentes e a população em risco já foi relatada na América do Central (veja *preprint* sobre hantavirose em Barbados, Caribe (DOUGLAS; SAMUELS; HILAIRE, 2019) e, embora somente 8% dos casos notificados sejam confirmados, é muito provável que a hantavirose seja subnotificada também no Brasil.

Após compreender o que pode influenciar na dispersão de uma zoonose, é essencial que os conhecimentos sejam comunicados amplamente, tanto para os tomadores de decisões e agendes de controles, como para a sociedade como um todo. Desta forma, coloquei como um objetivo adicional da presente tese promover esta divulgação científica (links na Seção de Comunicação Científica) das descobertas realizadas ao longo do doutorado.

Análises de risco

A análise de risco é um procedimento para estimar a chance ou probabilidade e as consequências de efeitos adversos ocorrendo em uma população específica, levando em conta a exposição aos *drivers* de risco potenciais e à natureza de seus efeitos. Análises de risco contribuem para o manejo dessa probabilidade, normalmente buscando diminuir o risco. Essas análises são muito utilizadas na área de finanças (e.g. controlar a chances de tomar prejuízo em um investimento), ciências ambientais (e.g. estimar perdas associadas a contaminantes no ambiente) e engenharia (e.g. estudar a segurança de reatores nucleares)(THRUSFIELD; CHRISTLEY, 2018). Cabe ao pesquisador ou grupo responsável definir o quanto de risco é aceitável ou inaceitável, exigindo medidas de controle quando necessário.

Não existe uma definição única de risco e nesta tese o risco foi considerado de duas maneiras distintas. Avaliei o risco de hantavirose na Mata Atlântica (Capítulo 3) e no Brasil (Capítulo 4), respectivamente. No capítulo 3, o valor de risco é baseado em pontos quentes (*hotspots*) a partir de um índice de vulnerabilidade humana (DE OLIVEIRA et al., 2015) e a partir da estimativa da proporção local de roedores hospedeiros. No Capítulo 4, calculei o risco como a probabilidade de haver pelo menos um caso de hantavirose em um dado município e em um dado ano, embora também tenha estimado a quantidade de casos.

Em análises de risco, comumente se avalia a probabilidade e a severidade das consequências de haver um evento, considerando a probabilidade local (risco) do evento acontecer, como um surto de doença. Neste estudo, me limitei a calcular o risco e especular sobre a severidade, pois não pudemos contemplar este aspecto importante da avaliação de risco de transmissão de doença. Embora não tenha calculado ou previsto a severidade operacionalmente, o modelo desenvolvido para número de casos foi validado utilizando casos atuais da doença no Capítulo 4.

Estrutura da tese

Esta tese foi desenvolvida sob uma abordagem de *Open Data*. Iniciei minhas pesquisas compreendendo e operacionalizando a extensão da Mata Atlântica e promovendo o livre acesso a dados de biodiversidade de morocegos para o bioma. Busquei também compreender a distribuição de roedores hospedeiros de diferentes hantavírus e a distribuição do *spillover* (transmissão entre diferentes espécies de hospedeiros) de hantavírus patogênicos no Brasil ao longo do espaço e do tempo. Os seguintes capítulos foram gerados, com o conteúdo relacionado:

Capítulo 1. Este capítulo marca o processo de transição entre minhas pesquisas focadas em morcegos para pesquisas multidisciplinares em ecologia espacial. A partir dele eu disponibilizei todo o material organizado junto aos colaboradores do ATLANTIC SERIES, no meu caso focando em comunidades de morcegos (MUYLAERT et al., 2017).

Capítulo 2. Operacionalizei espacialmente os limites territoriais da Mata Atlântica, quantificando e comparando os principais limites utilizados e propondo o uso dos limites de forma integrada ou consensual, dependendo do objetivo de cada trabalho em potencial (MUYLAERT et al., 2018a).

Capítulo 3. Investiguei como o ambiente (paisagem, clima) e a comunidade biológica do ponto de vista da diversidade local de pequenos mamíferos e da defaunação (perda local de médios e grandes mamíferos) – podem influenciar diferentes roedores hospedeiros de hantavírus. Também avaliei como o espaço pode modular o efeito desses *drivers* na proporção de roedores em uma dada comunidade.

Capítulo 4. No último capítulo, investiguei quais fatores podem influenciar na emergência da hantavirose a partir de um modelo espaço-temporal para todos os municípios do Brasil. Dentre os fatores investigados, estavam clima, alteração na paisagem, população de risco e diversidade de hospedeiros potenciais.

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Capítulo 1

ATLANTIC BATS: a dataset of bat communities from the Atlantic Forests of South America

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MORCEGOS DA MATA ATLÂNTICA

ATLANTIC BATS

DADOS SOBRE MAIS DE 205 COMUNIDADES

A MAIOR COMPILAÇÃO SOBRE COMUNIDADES DE MORCEGO NA MATA ATLÂNTICA

O conjunto de dados compreende 135 estudos quantitativos que abrangem a maioria dos tipos de vegetação da Mata Atlântica tropical e subtropical: floresta Ombrófila Densa, Floresta Ombrófila Mista, Floresta Estacional Semidecidual, Floresta Estacional Decidual, Savana, Estepe e Floresta Ombrófila Aberta.

CAPTURAS
> 90 mil

RIQUEZA MÉDIA
12 espécies

ESPÉCIES
98

RIQUEZA MÁXIMA
SOORETAMA (ES)

ALTA BIODIVERSIDADE

A Mata Atlântica abriga 8% da diversidade global de morcegos

LEEC unesp FAPESP

Abstract:

Bats are the second most diverse mammal order and they provide vital ecosystem functions (e.g., pollination, seed dispersal, and nutrient flux in caves) and services (e.g., crop pest suppression). Bats are also important vectors of infectious diseases, harboring more than 100 different virus types. In the present study, we compiled information on bat communities from the Atlantic Forests of South America, a species-rich biome that are highly threatened by habitat loss and fragmentation. ATLANTIC BATS dataset comprises 135 quantitative studies carried out in 205 sites, which cover most vegetation types of the tropical and subtropical Atlantic Forest: dense ombrophilous forest, mixed ombrophilous forest, semideciduous forest, deciduous forest, savanna, steppe, and open ombrophilous forest. The dataset includes information on more than 90,000 captures of 98 bat species of 8 families. Species richness averaged 12.1 per site, with a median value of 10 species (ranging from 1 to 53 species). Six species occurred in more than 50% of the communities: *Artibeus lituratus*, *Carollia perspicillata*, *Sturnira lilium*, *Artibeus fimbriatus*, *Glossophaga soricina*, and *Platyrrhinus lineatus*. The number of captures divided by sampling effort, a proxy for abundance, varied from 0.000001 to 0.77 individuals/hour*m^2 (0.04±0.007 individuals/hour*m^2). Our dataset reveals a hyper-dominance of eight species that together that comprise 80% of all captures: *Platyrrhinus lineatus* (2.3%), *Molossus molossus* (2.8%), *Artibeus obscurus* (3.4%), *Artibeus planirostris* (5.2%), *Artibeus fimbriatus* (7%), *Sturnira lilium* (14.5%), *Carollia perspicillata* (15.6%), and *Artibeus lituratus* (29.2%).

D. Key words: forest fragmentation, mist nets, Chiroptera, Phyllostomidae, biodiversity hotspot, mammal communities, hyper-dominance, emerging diseases, seed dispersal, pollination, crop pest suppression, nutrient flux.

Introduction

Bats are one the most successful mammalian orders, as they represent 25% of all extant species with ~1,300 described species (Fenton and Simmons 2014). Because of their widespread distribution, diverse morphology, and complex behavior, bats successfully occupy a great variety of niches, which makes these flying mammals excellent models for understanding several ecological and evolutionary processes (Kunz and Fenton 2005, Gunnell and Simmons 2012). Bats draw a lot of attention from the public, as they transmit lethal diseases to humans, domestic animals, and wildlife (Leroy et al. 2005, Field 2009). For instance, bats can host more than 100 virus types (Luis et al. 2015). However, bats are also known to play vital roles as seed dispersers and pollinators of many tropical plants (Fleming and Kress 2013). Recently, several studies have shown the importance of bats in controlling invertebrate pests in agriculture providing an enormous ecosystem service (Boyles et al. 2011, Karp and Daily 2014, Cassano et al. 2016). Furthermore, bats are very important in cave ecosystems due to the large input of nutrients they provide (Kunz et al. 2011).

Studies on Neotropical bats date back to over 50 years ago, but ecological studies have been traditionally focusing on Central America (Heithaus et al. 1975, Fleming 1988). Although highly diverse, ubiquitous, and substantially studied in tropical ecosystems, bats are one of the least known mammalian orders in tropical forests. There are still many questions to be investigated about the biology of Neotropical bats (Mello 2010), and they are poorly represented in macroecological studies (Weber et al. 2014, Stevens and Willig 2002).

Community studies on Neotropical bats usually focus on the family Phyllostomidae due to the sampling bias introduced by mist-netting, the most common method used to capture bats in the wild (Meyer et al. 2015). In the last twenty years, a large number of studies on bats have been carried out in South

America. One of the regions with highest bat diversity is the tropical and subtropical Atlantic Forest of South America (Galindo-Leal and Câmara 2003). The Atlantic Forest comprises several types of habitat with different rainfall regimes, altitudes, and land uses (Ribeiro et al. 2011). In Brazil, this region hosts at least 117 bat species (Varzinczak et al. 2016), and in Misiones, a biodiverse province in Argentina, it harbors 38 bat species (Alurralde et al. 2016). The Atlantic Forest was one of the largest rainforest in South America, originally covering around 150 million ha along the Brazilian coast, and the inland Argentina and Paraguay. Nowadays, the Atlantic Forest are highly fragmented with about 12% of original area remaining, where 80% of the fragments are <50 ha in size and the mean distance between them being 1.4 km (Ribeiro et al. 2009).

In the present study, we compiled a dataset of bat communities comprising 135 studies carried out in 205 sites of the Atlantic Forest in Brazil, Argentina, and Paraguay (Figure 1). Bat inventories became popular in the region in the 90s (Marinho-Filho 1996) and have been carried out in most ecoregions within the Atlantic Forest domain. ATLANTIC BATS represent the largest dataset of bat species inventories for the Neotropical region. This dataset comprises the species composition, richness, and relative abundance (captures/net nights) for all the sites. This data-paper is part of the large effort of the ATLANTIC Research Team to compile information on the biodiversity of the Atlantic Forest, and some articles of this series have already been published or are under review: ATLANTIC FRUGIVORY (Bello et al. 2017), ATLANTIC SMALL MAMMALS (Bovendorp et al. 2017), ATLANTIC CAMTRAPS (Lima et al. 2017), and ATLANTIC BIRDS (Hasui et al. unpublished manuscript).

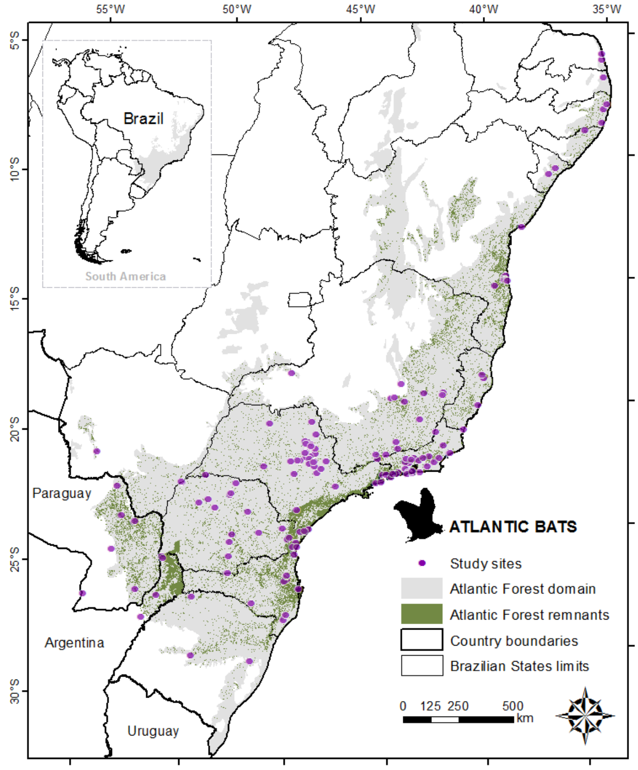

Fig. 1. Distribution of sampling locations included in ATLANTIC BATS. We only included studies where capture numbers were available, composing useful information for community studies.

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity:

Title: ATLANTIC BATS: a dataset of bat communities from the Atlantic Forests of South America

B. Data set identification code:

Suggested Data Set Identity Codes:

ATLANTIC_BATS_Study_site.csv

ATLANTIC_BATS_Reference.csv,

ATLANTIC_BATS_Capture.csv,

C. Data set description:

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E. Description:

The dataset covers the main vegetation types found in the Atlantic Forest of tropical and subtropical Brazil (195 sites), Paraguay (7), and Argentina (3) (Ribeiro et al. 2009) (Figure 1). About 75% of data were obtained from published articles in peer reviewed journals, whereas 25% origin from unpublished data from the authors, as well as theses and dissertations. The duration of the studies varied from 1 night to over 4 years of continuous sampling in the same site.

The data set comprises 205 sites sampled in 135 quantitative studies and three data files. In total, the dataset contains 98 confirmed bat species (Table 1, Table 2), one not confirmed species (*Peropteryx* cf. *kappleri*), and five cases where the actual specific name could not be specified (*Artibeus* sp., *Carollia* sp., *Lonchophylla* sp., *Micronycteris* sp., and *Molossus* sp.), which might represent a larger number of species. Among the species, one is classified as endangered and two as near threatened according to the IUCN global assessment (IUCN 2013, Figure. 2).

We included 91,906 capture records in the dataset, which varies between 1 and 7,725 captures per site (448.32 ± 58.71 SE). The most frequently captured bat species was *Carollia perspicillata* (87.3% of the sites), followed by *Artibeus lituratus* (84.8%) and *Sturnira lilium* (75.6%). The average frequency of occurrence was 12.3%, and there were 12 species as singletons (0.48%), 11 as doubletons (0.97%), and 5 species appeared in only three locations (1.46%). The most frequent non-phyllostomid bats were from the genus *Myotis* (41% sites, Figure 2).

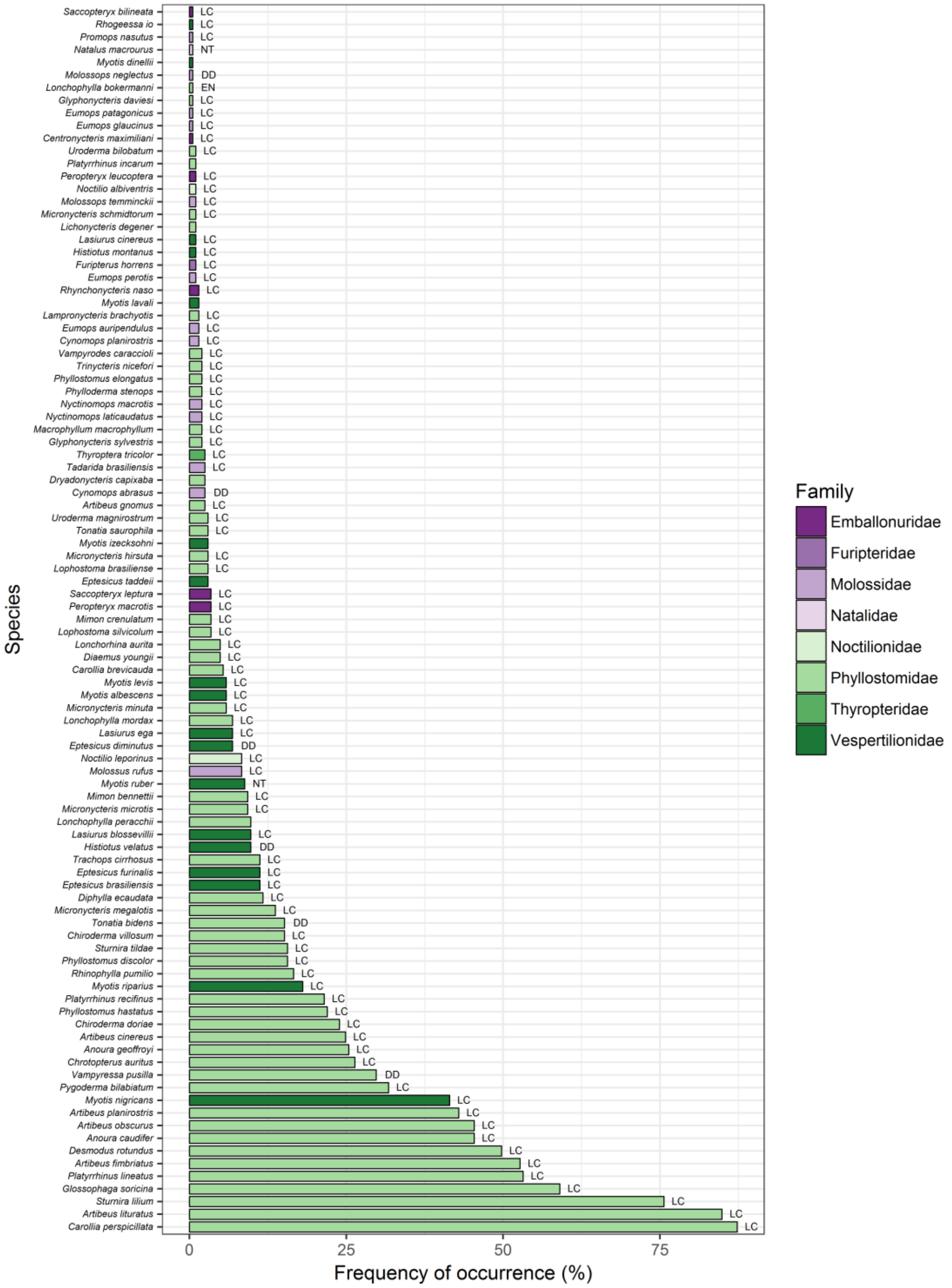

Fig. 2. Distribution of frequencies of occurrence of bat species in communities in the Atlantic forests colored by family and IUCN status. The symbols from the global assessment were: LC = least concern, NT = near threatened, VU =

vulnerable, EN = endangered, CR = critically endangered, DD = data deficient. Not available data were left in blank.

The most abundant bat species was *Artibeus lituratus*, followed by *Carollia perspicillata* and *Sturnira lilium*, clearly showing their hyper-dominance in mist net studies. Eight species were responsible for 80% of captures: *Platyrrhinus lineatus* (2.3%; 2,175), *Molossus molossus* (2.8%; 2,628), *Artibeus obscurus* (3.4%; 3167), *Artibeus planirostris* (5.2%; 4,789), *Artibeus fimbriatus* (7%; 6,454), *Sturnira lilium* (14.5%; 13,392), *Carollia perspicillata* (15.6%; 14,423), and *Artibeus lituratus* (29.2%; 26,928). On the contrary, 90 species were responsible for only 10% of captures (Figure 3). The rarest species were *Glyphonycteris daviesi*, *Promops nasutus*, *Eumops glaucinus*, *Myotis dinellii*, *Rhogeessa io*, and *Micronycteris schmidtorum*. Together, they represent less than a thousandth (0.001) of all captures.

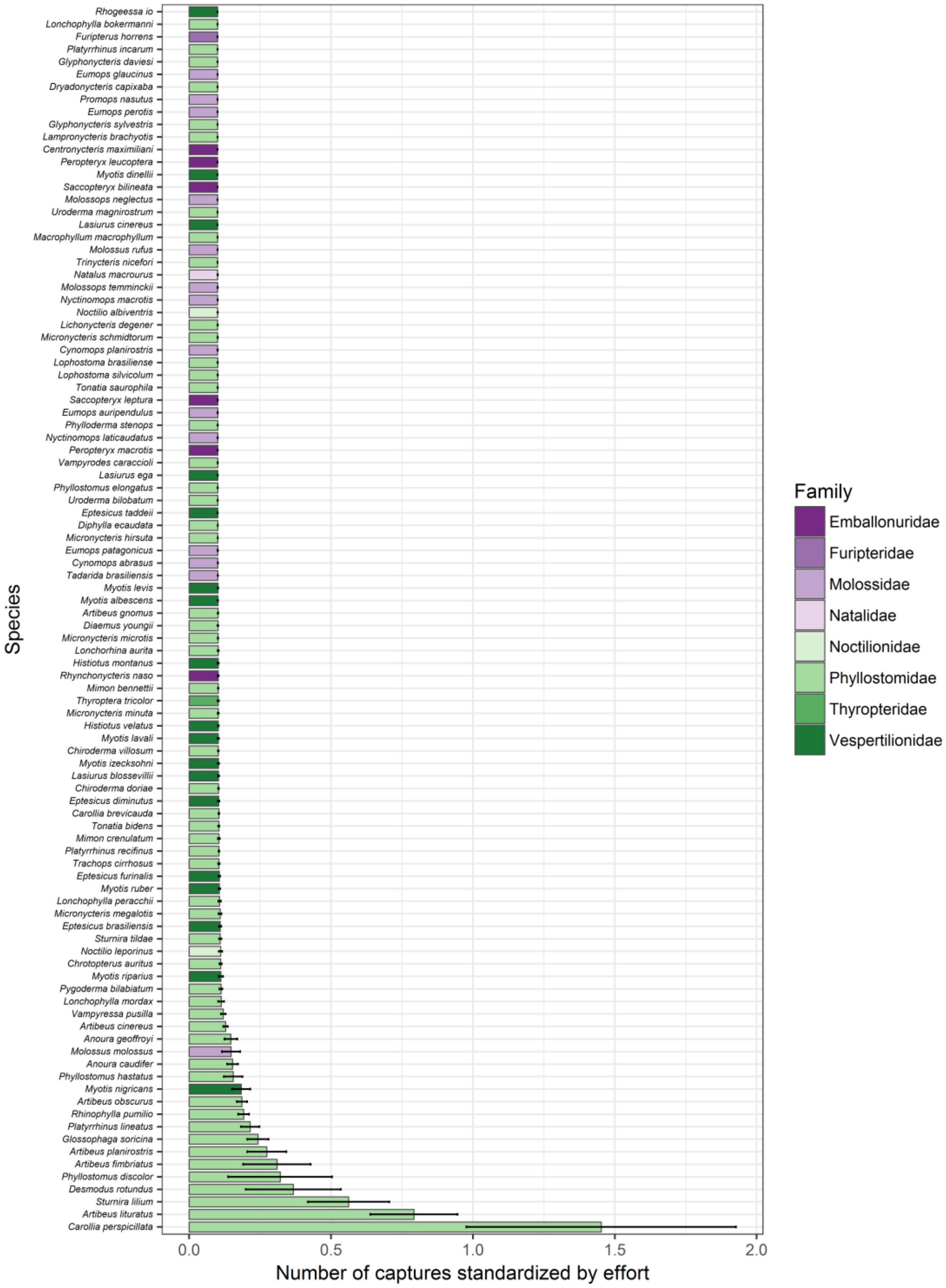

Fig. 3. Standardized bat capture numbers per survey. Capture success was standardized following Straube and Bianconi (2002), and given in number of captures/hours net area (100*hours*m^2). For better visualization of low values, 0.001 was added to values.

The sampling effort standardized using the Straube and Bianconi unit (Straube and Bianconi 2002) averaged 28,875 h.m^2 (total number of hours of capture multiplied by the average area of the mist nets used), with a median of 7,513.33 and a maximum of 534,240. The number of mist nets used in a single night in each site reached up to 30 (regardless of size, see metadata). Canopy nets were used on only nine sites. The total number of captures, which can be used as a proxy for local abundance, increased with sampling effort (adjusted $R^2 = 0.31$, slope = 5.75 ± 0.66, df = 155, $p<0.001$, Figure 4).

Voucher specimens of the studies were deposited in 37 collections (Table 3) most of them located in Brazil. Surveys per State/Province/Department varied with a mean of 10 surveys per state. São Paulo/Brazil (49) and Rio de Janeiro/Brazil (49) were the states with the largest numbers of sampling sites. The states with the largest total number of captures were Canindeyu/Paraguay (12,225 captures) and Rio de Janeiro/Brazil (33,769 captures), reaching a maximum of 7,725 captures and 3,509, respectively (Table 4). Most studies were conducted in the following Brazilian Atlantic Forest subregions (BSRs *sensu* Ribeiro et al. (2009): Serra do Mar (62 sites), Pernambuco (7), Araucária Forest (11), Interior Forest (78), and Bahia (37). Among the studied sites with information on the type of protected area (Table 2), 84% were located in protected areas, including biological reserves, ecological stations, indigenous lands, national parks, national reserves, natural monuments, parks, private reserves, protected forests, wildlife refuges, and world heritage sites. The area of the study sites ranged from 1 to for more than 60,000 ha, e.g. Iguaçu National Park (Brazil and Argentina), and Mbaracayu Forest Nature Reserve (Paraguay).

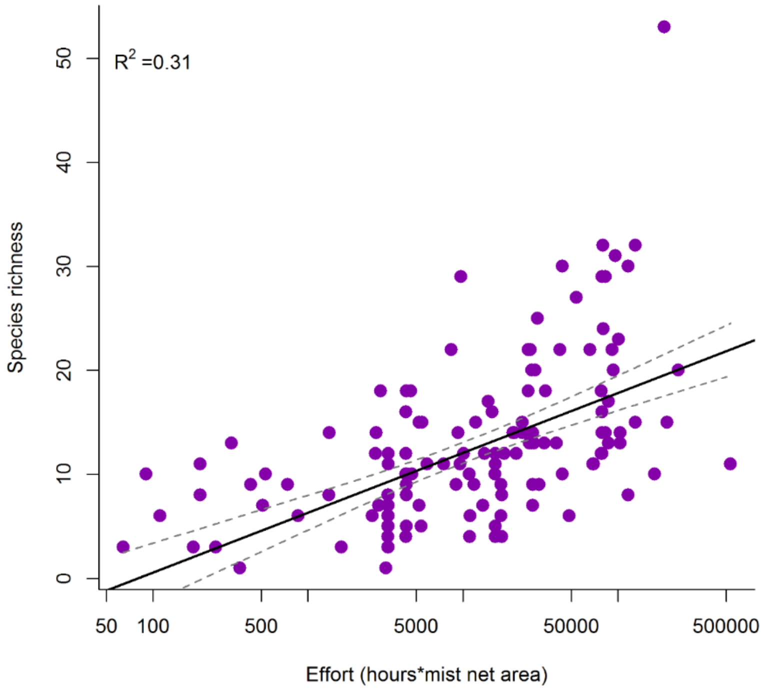

Fig. 4. Taxonomic richness and sampling effort applied on capturing bat species in communities in the Atlantic forests. Non-confirmed records (see the text) were removed for species counting. Linear regression shows a positive effect of sampling effort on observed taxonomic richness from the ATLANTIC BATS dataset (adjusted R^2= 0.31, slope= 5.75 ± 0.66, df=155, $p<0.001$). Grey dashed lines represent 95% confidence intervals of predicted values.

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description:

Identity: Compilation of bat communities captured with mist nets in the Atlantic Forests of South America.

Period of study: Data collection reported on studies range from 1991 to 2016.

Objectives: We aimed to 1) make available a large amount of data collected and available only in the literature in Portuguese, Spanish or English; 2) describe main patterns of data regarding species captured; and 3) inform the status of knowledge on assemblages to facilitate use of the ATLANTIC database. This work is part of the ATLANTIC biodiversity series, providing information on Atlantic Forest diversity and community composition (e.g. Bovendorp et al. 2017, Bello et al. 2017, Lima et al. submitted).

Abstract: Same as above.

Sources of funding: The data construction is supported by São Paulo Research Foundation (FAPESP 2014/01986-0, 2015/17739-4, 2013/50421-297/07075-1). The studies that produced the information compiled in our dataset were funded by grants, scholarships, and fellowships given by the Brazilian Council for Scientific and Technological Development (CNPq 153423/2016-1, 303757/2012-4, 312045/2013-1, 312045/2013-1, 312292/2016-3), US National Science Foundation, Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES: Science Without Borders and PNPD programs), São Paulo Research Foundation (FAPESP 2011/06810-9, 2016/02568-2, 2011/22663-6, 2013/50421-2, 2014/24219-4, and 2015/17739-4), Rio de Janeiro Research Foundation (PAPDRJ FAPERJ/CAPES), Research Council of Norway through its Centres of Excellence Funding Scheme (223257), the Norwegian University of Science and Technology (NTNU), Project for the Conservation and Sustainable Use of Brazilian Biological Diversity (PROBIO-PRONABIO/MMA-CNPq), Research Program of the Biodiversity of the Atlantic Forest (PPBio-MA/CNPq), Bat Conservation International (BCI), Lincoln Park Zoo, Idea Wild, Ecotone, Minas Gerais Research Foundation (FAPEMIG), German Academic Exchange Service (DAAD), and Alexander von Humboldt Foundation (AvH).

Site description:

The Atlantic Forest of South America is a biome originally distributed in the tropical and subtropical coast of Brazil and in the countryside of Argentina and Paraguay (Olson et al. 2001). It harbors 8% of the world's total species richness, and at least 15,519 plant species (3,343 trees) (Zappi et al. 2015), 891 birds (Moreira-Lima 2014), 543 amphibians (Haddad et al. 2013), 200 reptiles (Bérnils and Costa 2015), 350 fishes (MMA 2010), and 298 mammals (Paglia et al. 2012), out of which 117 species are bats (Varzinczak et al. 2016). The Atlantic Forest comprises tropical and subtropical evergreen and semideciduous forests with highly heterogeneous environmental conditions (Morellato and Haddad 2000).

Seventy-two percent of the Brazilian population live in areas originally covered by the Atlantic Forests domain (~145 million people) (IBGE 2013). Therefore, many anthropogenic activities such as logging, forest fragmentation, agricultural fields, industrialization, and unplanned urban expansion have contributed to the ecosystem deterioration. The conservation of Atlantic Forest is critical, the natural remnants accounting for only 12% of the original biome, and more than 80% of these remnants are less 50 ha in size (Ribeiro et al. 2009).

Data compilation:

We conducted a wide literature search for published and unpublished documents found on the internet. Additionally, we invited several researchers to contribute with unpublished data on bat communities. Then, we checked for taxonomy and compiled information on mammal collections. We searched the literature on Google Scholar and included also studies to which the PIs already had access. The following keywords in English were used on Google Scholar: "bats, survey, inventory, abundance, Atlantic forest, mist nets" with (439 results). In Portuguese, we used the following keywords: "morcegos, inventário, abundância, Mata Atlântica, redes-de-neblina" (223 results). We also looked for following keywords in Spanish: "murciélagos, inventario, abundancia, Bosque Atlantico, redes-de-neblina" (21 results). Studies with no information on capture number were excluded from our compilation, such as from Willig et al. (2000). We also searched for theses and dissertations on the online libraries of South American universities.

Research Methods:

In this database, we included studies that reported sampling of bat species, survey design and methods, strata sampled, sampling effort, and number of captures. Lacking information was labelled with NA. However, some studies that did not provide substantially detailed information on captures were excluded. We also included information from the geographical location (latitude, longitude, locality, municipality, state and country). Species information (occurrence and abundance) were compiled from 108 articles and from personal database on bat diversity mentioned as follows: Bat Diversity Laboratory LADIM, UFRRJ; Database on bat diversity from the Ecological Synthesis Lab, UFMG; Database on bat diversity from the Stevens Lab, Texas Tech University; and Database on bat diversity from the Evolutionary Ecology Lab, UNESP.

Bat capture data were compiled from (Campanha and Fowler 1993, Peracchi and Albuquerque 1993, Aguiar 1994, Sipinski and Reis 1995, Reis et al. 1996, 2003, 2006, Graipel et al. 1997, Pedro and Taddei 1998, Geraldes 1999, Portfors et al. 2000, Pedro et al. 2001, Sekiama et al. 2001, Dias et al. 2002, Bergallo et al. 2003, Esbérard 2003, Falcão et al. 2003, Félix 2003, Passos et al. 2003, Sa Neto 2003, Aguiar and Marinho-Filho 2004, 2007, Bianconi et al. 2004, Gorresen and Willig 2004, Rosa 2004, Mello and Schittini 2005, Ortêncio-Filho et al. 2005, 2014, Bertola et al. 2005, Esbérard et al. 2006, Faria 2006, Carvalho and Zocche 2007, Althoff 2007, Mikalauskas 2007, Arnone and Passos 2007, Zanon and Reis 2007, Bosco-Breviglieri 2008, Carvalho 2008, Alves 2008, Camargo et al. 2009, da Silva 2009, Evangelista 2009, Luz et al. 2009, Nobre et al. 2009, Oprea et al. 2009, Ortêncio-Filho and Reis 2009, Reus 2009, Bernardi et al. 2009, Tahara 2009, Mello 2009, Brito et al. 2010, Gallo et al. 2010, Lourenço et al. 2010, Oliveira 2010a, 2010b, Silveira et al. 2010, Brito 2011, Cirignoli et al. 2011, Munster 2011, Muylaert and Mello 2011, Weber et al. 2011, Brito and Bocchiglieri 2012, Gruener et al. 2012, Sánchez et al. 2012, Carvalho et al. 2013, Godoy 2013, Morais 2013, Nascimento et al. 2013, Nunes 2013, Pimenta 2013, Pires and Fabián 2013, Muylaert et al. 2014, 2016, Rubio et al. 2014, Bortolotti 2015, Cherem and Althoff 2015, Gomes et al. 2015, Jacomassa 2015, Martins et al. 2015, Miranda and Zago 2015, Souza et al. 2015, Milano 2016, Pedrozo et al. 2016, Pereira 2016, Angelo et al. 2017, Barros et al. 2017).

We extracted spatial and geographical information through available databases (IBGE in Brazil) and Google maps. We used the spatial join function in ArcGIS 10.5 to extract values to the points representing localities where bats were sampled. Then, we checked locations with missing information of protected area types filling with information from reserve websites. Here we only provide studies that reported capture number and our own data stored in personal databases. Studies where information on number of captures (used to calculate standardized abundance) were not informed were removed from dataset.

To define Atlantic Forest boundaries, we followed the same procedure as Lima et al. (submitted). We merged available geographic information from the main used limits informing Atlantic forest extents: the Brazilian government limit (IBGE 2016), the limit provided by the Atlantic Forest Law initiative (MMA 2006), the one used as mask to calculate the remaining Atlantic Forest (Ribeiro et al. 2009), and the one reported in (Olson et al. 2001) also adopted by WWF and available online (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world). From the terrestrial ecosystem shapefile (Olson et al. 2001) we made a subset from Atlantic Forests and Atlantic dry forests categories inside and outside Brazil.

Taxonomy and systematics:

We used the *taxize* package in R to update taxonomy and conservation status via the IUCN Red List of threatened species (R Core team 2015, Chamberlain et al. 2016). Taxonomy was then checked by a bat taxonomist (G. Garbino). Then, Taxize outputs were double checked in IUCN website to verify the category for each species from the Red List. When reported, the location where specimens were kept or where vouchers were deposited was noted. We used collection names in their original language, since they are indexed in the databases by these names.

We followed the taxonomic arrangement of Gardner (2008), with the following exceptions: 1) we use the name *Platyrrhinus incarum* instead of *P. helleri*, following Velazco et al. (2010), who recognized both taxa as distinct species with the latter restricted to northern South America and Central America; 2) we use *Natalus macrourus* for the Atlantic Forest populations of *Natalus*, following the taxonomic revision of Tejedor (2011) and nomenclatural correction of Garbino and Tejedor (2013); 3) for *Myotis,* we include *M. izecksohni* and *M. lavali*, considered distinct from *M. nigricans* Moratelli et al. (2011) and consider *M.*

dinellii separate from *M. levis* following (Miranda et al. 2013); 4) we include the recently described *Lonchophylla peracchii*, following Dias et al. (2013) who recognized it as distinct from *L. bokermanni*. Considering the restrict distribution of the latter (Teixeira et al. 2015), we assigned only the records from the Serra do Cipó to this species. All previous records of *L. bokermanni* from Rio de Janeiro (i.e. Pão de Açúcar and Poço das Antas), and the one from Rio Doce State Park, from the Database on bat diversity from the Ecological Synthesis Lab, and from Baptista and Mello (2001) and Mello (2009) were assigned to *L. peracchii*; 5) we include *Dryadonycteris capixaba*, a recently described species which has been previously mistaken by *Choeroniscus minor* in southeastern Brazil (Nogueira et al. 2014, Rocha et al. 2014). We agree with Rocha et al. (2014) that the records of *"Choeroniscus minor"* in the Atlantic Forest probably refer to *D. capixaba*, and, also taking into consideration that it has been recently recorded for the geographically close Rio Doce State Park (Gregorin et al. 2014), assign the record from Caratinga (Aguiar 1994) to this species.

We decided not to use the generic name *Dermanura*, keeping instead *Artibeus* for *A. cinereus* and *A. gnomus*, following (Gardner 2008) and the more recent classification of (Baker et al. 2016). We consider all records of *Uroderma bilobatum* from São Paulo, Paraná and Rio de Janeiro states to be erroneous and thus have removed the record of this species from "Mata dos Godoy", which is located in Paraná (see discussion in Garbino and Nogueira 2017). The specimens identified as *U. bilobatum* by the authors were released and their identity cannot be ascertained, as it could be a misidentified *Chiroderma* or *Platyrrhinus* species.

The *Thyroptera* sp. captured in Guapimirim (from the Database on bat diversity from the Ecological Synthesis Lab) is identified as *Thyroptera tricolor* due to this being the only species of *Thyroptera* occurring in southeastern Brazil (Esbérard et al. 2007). In addition, we considered the records of *Lichonycteris obscura* as erroneous, since it only occurs in South America along the Pacific coast of Colombia and Ecuador (Griffiths and Gardner 2008). Records of *Lichonycteris obscura* reported at Una (Faria 2006) and at Usina Serra Grande (Sa Neto 2003) probably refer to *L. degener*, and we assigned them to this species.

Finally, we could not accurately determine the identity of *Peropteryx* cf. *kappleri*, *Artibeus* sp., *Carollia* sp., *Lonchophylla* sp., *Molossus* sp., and *Micronycteris* sp., and thus we have maintained on the main table the identification as they were originally reported, and this information was not considered in further analyses.

C. Data limitations and potential enhancements:

We recognize that documenting all bat species present in megadiverse ecosystems is a challenging task because many species are hard to capture in mist nets. New techniques, such as bioacoustics, thermal images, and cave roost counting, can also provide important complementary information on the bat community, but are still hardly used. Most surveys in our database are heterogeneous, with sampling efforts unstandardized (e.g. sampling design, number of nets, sampling days), precluding more comprehensive diagnosis of diversity. In addition, the length of studies is highly variable, and most of them have been conducted recently, with usually up to one year of captures, limiting the ability to obtain reliable population estimates.

There are mist nets of several kinds of mesh, material, heights, and lengths that could affect the capture of bats, but this information is rarely reported in the studies. Moreover, despite some tests that have been made (Lazo 2011), mist net position or configuration does not seem to be a consensus among bat ecologists, and there are few studies testing efficiency of net trap position (see Lazo 2011, Kunz and Brock 1975). Usually, studies set the nets transversally or perpendicularly to some possible route for bats, such as trails in the forest, or roost entrances, but this is not an information clearly exposed in the publications. Additionally, most studies do not provide information on the mist net length, mesh size, model, or material. Standard mist net models vary from 2.5 m to 3 m height (Peracchi and Nogueira 2010).

Bats are prone to exhibit population fluctuations in response to seasonal changes associated to rainfall, fruit production, and temperature. In addition, population sizes of bats may also respond to more drastic events, climatic (as El Niño and La Niña) and this data set comprises a "snapshot" of the communities in a given year and location. Recently, a paper gave a simple solution for standardizing effort on mist net inventories (Straube and Bianconi 2002). This was welcomed among scientists and became commonly used. We retrieved Straube and Bianconi effort values from 84% of surveys (174/205) by readily obtaining the value reported on paper, or when possible, by checking the availability of information to calculate the effort ourselves.

We obtained the two main measures of effort used by researchers to quantify bat abundance, one is the product of the number of hours times the total area of mist nets (Straube and Bianconi 2002), and the other is the total number of captures (Peracchi and Nogueira 2010). We found that our dataset is spatially biased and there is a clear gap in the northeast portion of the Atlantic forests, especially in transition areas between Atlantic forest and the Caatinga. Some regions are poorly inventoried in Brazil (Alagoas, Mato Grosso do Sul, Paraíba) and Paraguay. Future initiatives should aim to fill these gaps. On the other hand, the species accumulation curve comprising the 205 points of study does increase but nearly stabilizes, suggesting that ATLANTIC BATS dataset covers an adequate representation of the bat communities within Atlantic Forest (Figure 5). It worth mentioning that sites such as Sooretama (Espírito Santo, Brazil) have more than 53 recorded species during one survey (Pimenta 2013), and other sites in Espírito Santo may inhabit over 50 bat species (Peracchi et al. 2011). Mist nets usually present a significant bias because of potential vertical stratification of certain species. Detectability and rarity are not well studied among bat taxa, and gap analysis should enlighten this issue improving the palling of long term or even rapid assessments (Bernard et al. 2011). Little is known about insectivorous bats that occur in the high canopy (Kalko 1998).

We found only four studies that used canopy mist nets, making a huge effort to distinguish between understory, midstory, and canopy strata. Therefore, most studies presented here sample bats that forage up to 3 m in the forest strata. Moreover, our dataset best represents phyllostomid species, but we also include information of other species that forage above the canopy wherever they were captured.

In addition, many species of bats, like small rodents and marsupials, are difficult to identify to the species level in the field. Many studies did not collect voucher specimens or did not report the collection where vouchers or genetic samples were placed. Nevertheless, we recognize the massive research effort by field ecologists and biologists who carried out these studies. This impressive collection of data represents the best information of communities of bats in tropical and subtropical forests. We expect that the community of scientists will be able to characterize macro-ecological patterns as well as determine: i) the priority areas to sample bat communities; ii) the minimum sampling effort to obtain consistent information on bat assemblages; iii) lists of voucher specimens and reference material, and the institutions where they are housed; and iv) the minimal sampling protocol that will standardize the study of bats for species-rich ecosystems.

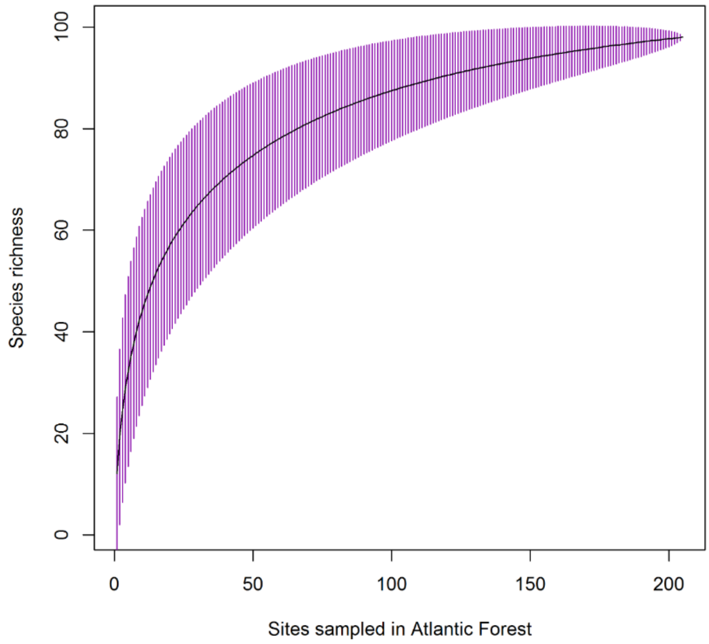

Fig. 5. Species accumulation curve of the number of confirmed species with expected number of species along 205 site surveys in ATLANTIC BATS dataset. Note that asymptote is almost reached, and it accumulates in 98 species from 117 found in the entire biome.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: May 2017

Latest archive date: May 2017

Metadata status: Last updated May 2017, version submitted

Data verification: Assemblage abundance information were compiled as is, except for taxonomic checking. Geographic coordinates were double-checked since many studies give wrong coordinates that represent city centroids or base stations of conservation units. Most corrected geographic coordinates represent an approximation of the survey locality reported in decimal degrees (Datum WGS 84) using maps, coordinates provided by from papers, personal information of authors, and Google Maps. In most cases, they are inaccurate but provide accessibility or reproducibility approximation.

B. Accessibility

Contact persons: Renata Muylaert (renatamuy@gmail.com), Mauro Galetti (mgaletti@rc.unesp.br), or Richard D. Stevens (richard.stevens@ttu.edu).

Copyright restrictions: None

Proprietary restrictions: Please cite this *Ecology* Data Paper (DOI: 10.1002/ecy.2007) if the data are used in publications and teaching events.

Costs: None

CLASS IV. Data structural descriptors

A. Data set file

Identity:

(1) ATLANTIC_BATS_Study_Site.csv
(2) ATLANTIC_BATS_Reference.csv
(3) ATLANTIC_BATS_Capture.csv

Size:

(1) ATLANTIC_BATS_Study_Site.csv, 205 locations, 46.8 KB
(2) ATLANTIC_BATS_Reference.csv, 135 studies, 60.7 KB
(3) ATLANTIC_BATS_Capture.csv, 20,604 records, 4.12 MB

Format and storage mode: data tables formatted as comma-separated values (*.csv)

Alphanumeric attributes: Mixed

Data anomalies: If no information is available for any cell, this is indicated as 'NA'. In this dataset, we have NA values.

B. Variable information

1) Table 2. Site Information

2) Table 3. Reference Information

3) Table 4. Capture Information

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

1. Data request history: None

2. Data set updates history: None

3. Data entry/verification procedures

G. History of data set usage:

Stevens (2013) used a small part of this dataset to investigate gradients of bat diversity in Atlantic Forest.

ACKNOWLEDGMENTS:

This paper is part of the ATLANTIC research group. We thank Carolina Bello, Fernando Lima, Felipe Martello, Andreia Magro, and Annia Streher. To the many students, technicians and colleagues who helped us in the field. To the brave bat workers and to the property owners and guards, who helped us with kindness and security measures during the long nights. This paper is dedicated to important bat specialists: Ivan Sazima, Adriano Peracchi and Valdir A. Taddei (in memoriam) for their long contribution and formation of Brazilian researchers.

TABLES

Table 1. Species information: Description of species present in ATLANTIC BATS. Species without confirmed identification (cf. and sp.) were not used for species counting: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, DD = data deficient, NA= not available at the time.

Superfamily	**Family**	**Species**	**Status**
Emballonuroidea	Emballonuridae	*Centronycteris maximiliani*	LC
Emballonuroidea	Emballonuridae	*Peropteryx leucoptera*	LC
Emballonuroidea	Emballonuridae	*Peropteryx macrotis*	LC
Emballonuroidea	Emballonuridae	*Rhynchonycteris naso*	LC
Emballonuroidea	Emballonuridae	*Saccopteryx bilineata*	LC
Emballonuroidea	Emballonuridae	*Saccopteryx leptura*	LC
Noctilionoidea	Furipteridae	*Furipterus horrens*	LC
Noctilionoidea	Noctilionidae	*Noctilio albiventris*	LC
Noctilionoidea	Noctilionidae	*Noctilio leporinus*	LC
Noctilionoidea	Phyllostomidae	*Anoura caudifer*	LC

Noctilionoidea	Phyllostomidae	*Anoura geoffroyi*	LC
Noctilionoidea	Phyllostomidae	*Artibeus cinereus*	LC
Noctilionoidea	Phyllostomidae	*Artibeus fimbriatus*	LC
Noctilionoidea	Phyllostomidae	*Artibeus gnomus*	LC
Noctilionoidea	Phyllostomidae	*Artibeus lituratus*	LC
Noctilionoidea	Phyllostomidae	*Artibeus obscurus*	LC
Noctilionoidea	Phyllostomidae	*Artibeus planirostris*	LC
Noctilionoidea	Phyllostomidae	*Carollia brevicauda*	LC
Noctilionoidea	Phyllostomidae	*Carollia perspicillata*	LC
Noctilionoidea	Phyllostomidae	*Chiroderma doriae*	LC
Noctilionoidea	Phyllostomidae	*Chiroderma villosum*	LC
Noctilionoidea	Phyllostomidae	*Chrotopterus auritus*	LC
Noctilionoidea	Phyllostomidae	*Desmodus rotundus*	LC
Noctilionoidea	Phyllostomidae	*Diaemus youngii*	LC
Noctilionoidea	Phyllostomidae	*Diphylla ecaudata*	LC
Noctilionoidea	Phyllostomidae	*Dryadonycteris capixaba*	NA
Noctilionoidea	Phyllostomidae	*Glossophaga soricina*	LC
Noctilionoidea	Phyllostomidae	*Glyphonycteris daviesi*	LC
Noctilionoidea	Phyllostomidae	*Glyphonycteris sylvestris*	LC
Noctilionoidea	Phyllostomidae	*Lampronycteris brachyotis*	LC
Noctilionoidea	Phyllostomidae	*Lichonycteris degener*	NA
Noctilionoidea	Phyllostomidae	*Lonchophylla bokermanni*	EN
Noctilionoidea	Phyllostomidae	*Lonchophylla mordax*	LC
Noctilionoidea	Phyllostomidae	*Lonchophylla peracchii*	NA
Noctilionoidea	Phyllostomidae	*Lonchorhina aurita*	LC

Noctilionoidea	Phyllostomidae	*Lophostoma brasiliense*	LC
Noctilionoidea	Phyllostomidae	*Lophostoma silvicolum*	LC
Noctilionoidea	Phyllostomidae	*Macrophyllum macrophyllum*	LC
Noctilionoidea	Phyllostomidae	*Micronycteris hirsuta*	LC
Noctilionoidea	Phyllostomidae	*Micronycteris megalotis*	LC
Noctilionoidea	Phyllostomidae	*Micronycteris microtis*	LC
Noctilionoidea	Phyllostomidae	*Micronycteris minuta*	LC
Noctilionoidea	Phyllostomidae	*Micronycteris schmidtorum*	LC
Noctilionoidea	Phyllostomidae	*Mimon bennettii*	LC
Noctilionoidea	Phyllostomidae	*Mimon crenulatum*	LC
Noctilionoidea	Phyllostomidae	*Phylloderma stenops*	LC
Noctilionoidea	Phyllostomidae	*Phyllostomus discolor*	LC
Noctilionoidea	Phyllostomidae	*Phyllostomus elongatus*	LC
Noctilionoidea	Phyllostomidae	*Phyllostomus hastatus*	LC
Noctilionoidea	Phyllostomidae	*Platyrrhinus incarum*	NA
Noctilionoidea	Phyllostomidae	*Platyrrhinus lineatus*	LC
Noctilionoidea	Phyllostomidae	*Platyrrhinus recifinus*	LC
Noctilionoidea	Phyllostomidae	*Pygoderma bilabiatum*	LC
Noctilionoidea	Phyllostomidae	*Rhinophylla pumilio*	LC
Noctilionoidea	Phyllostomidae	*Sturnira lilium*	LC
Noctilionoidea	Phyllostomidae	*Sturnira tildae*	LC
Noctilionoidea	Phyllostomidae	*Tonatia bidens*	DD
Noctilionoidea	Phyllostomidae	*Tonatia saurophila*	LC
Noctilionoidea	Phyllostomidae	*Trachops cirrhosus*	LC
Noctilionoidea	Phyllostomidae	*Trinycteris nicefori*	LC

Noctilionoidea	Phyllostomidae	*Uroderma bilobatum*	LC
Noctilionoidea	Phyllostomidae	*Uroderma magnirostrum*	LC
Noctilionoidea	Phyllostomidae	*Vampyressa pusilla*	DD
Noctilionoidea	Phyllostomidae	*Vampyrodes caraccioli*	LC
Noctilionoidea	Thyropteridae	*Thyroptera tricolor*	LC
Vespertilionoidea	Molossidae	*Cynomops abrasus*	DD
Vespertilionoidea	Molossidae	*Cynomops planirostris*	LC
Vespertilionoidea	Molossidae	*Eumops auripendulus*	LC
Vespertilionoidea	Molossidae	*Eumops glaucinus*	LC
Vespertilionoidea	Molossidae	*Eumops patagonicus*	LC
Vespertilionoidea	Molossidae	*Eumops perotis*	LC
Vespertilionoidea	Molossidae	*Molossops neglectus*	DD
Vespertilionoidea	Molossidae	*Molossops temminckii*	LC
Vespertilionoidea	Molossidae	*Molossus molossus*	LC
Vespertilionoidea	Molossidae	*Molossus rufus*	LC
Vespertilionoidea	Molossidae	*Nyctinomops laticaudatus*	LC
Vespertilionoidea	Molossidae	*Nyctinomops macrotis*	LC
Vespertilionoidea	Molossidae	*Promops nasutus*	LC
Vespertilionoidea	Molossidae	*Tadarida brasiliensis*	LC
Vespertilionoidea	Natalidae	*Natalus macrourus*	NT
Vespertilionoidea	Vespertilionidae	*Eptesicus brasiliensis*	LC
Vespertilionoidea	Vespertilionidae	*Eptesicus diminutus*	DD
Vespertilionoidea	Vespertilionidae	*Eptesicus furinalis*	LC
Vespertilionoidea	Vespertilionidae	*Eptesicus taddeii*	NA
Vespertilionoidea	Vespertilionidae	*Histiotus montanus*	LC

Vespertilionoidea	Vespertilionidae	*Histiotus velatus*	DD
Vespertilionoidea	Vespertilionidae	*Lasiurus blossevillii*	LC
Vespertilionoidea	Vespertilionidae	*Lasiurus cinereus*	LC
Vespertilionoidea	Vespertilionidae	*Lasiurus ega*	LC
Vespertilionoidea	Vespertilionidae	*Myotis albescens*	LC
Vespertilionoidea	Vespertilionidae	*Myotis dinellii*	NA
Vespertilionoidea	Vespertilionidae	*Myotis izecksohni*	NA
Vespertilionoidea	Vespertilionidae	*Myotis lavali*	NA
Vespertilionoidea	Vespertilionidae	*Myotis levis*	LC
Vespertilionoidea	Vespertilionidae	*Myotis nigricans*	LC
Vespertilionoidea	Vespertilionidae	*Myotis riparius*	LC
Vespertilionoidea	Vespertilionidae	*Myotis ruber*	NT
Vespertilionoidea	Vespertilionidae	*Rhogeessa io*	LC

Table 2. Site information: Description of the fields related with the location of each study site.

Type of information	Variables	Description	Levels	Example
SITE INFORMATION	**ID**	Identification code for each record, making it easier to connect with other ATLANTIC series data	bat1001-bat1205	bat1001
	Country	English name of the country	Brazil, Paraguay, Argentina	Brazil
	State	State, Province or Department of the study site derived based on the geographic coordinates	20	RIO DE JANEIRO
	Municipality	Municipality of the study site derived based on the geographic coordinates	119	PATY DOS ALFERES
	Study_location	Local name of the study site derived based on the information in the reference paper. There are sites with more than one survey		Parque Estadual de Porto Ferreira
	Latitude	Corrected and transformed coordinates of the latitude in decimal degrees (Datum WGS84). The precision of the reported coordinates in the reference papers were mostly inexact. We used the centroids of sampling sites as our sampling point (x, y). Correction was conducted with the help of the clues in the reference papers, such as vegetation type, approximate coordinates, trails, rivers, and reserve names. These clues were cross-validated against Google Earth satellite images.	decimal degree	-25,08685287

	Longitude	Corrected and transformed coordinates of the longitude. See above for further information.	decimal degree	-47,92796182
	Precision	Coordinate precision of the study site. Precise: the grid, transect or vegetation patch coordinates are reported. Non-precise: the coordinates of the municipality are reported, or the coordinates mismatch the written information in the reference paper.	Precise	Precise
	Reserve_Area	Reserve area reported in the reference paper, value in hectars (ha)	1 to 50650	45
	Altitude	Meters above sea level reported in the reference paper or obtained later based on the corrected coordinates		64
	Altitude1km	Altitude in meters above sea level, from the Hydro-1K dataset (United States Geological Survey – USGS, 2001. HYDRO 1K: Elevation Derivative Database. Available from: <http://edc.usgs.gov/products/elevation/gtopo30/hydro/namerica.html>) on May 5th	0 to 2043	13
	Annual_mean_temperature	Annual mean temperature. WorldClim v. 1.4., in Celsius degrees, available in http://www.worldclim.org/version1. Access on May 5th, 2017.	From 12.13-25.7	24.2
	Annual_rainfall	Annual rainfall. WorldClim v. 1.4., in mm, available in http://www.worldclim.org/version1. Access on May 5th, 2017.	From 965 to 2490	1551
	Olsong200r	Olson bioregion (Olson et al. 2001), represented by G200_REGIO column of the shapefile wwf_terr_ecos	Atlantic Forests, Cerrado Woodlands and Savannas	

	Olsoneconame	ECO_NAME column of the shapefile wwf_terr_ecos available in WWF website (Olson et al. 2001).	Serra do Mar coastal forests Atlantic Coast restingas Araucaria moist forests Alto Parana Atlantic forests Cerrado Bahia coastal forests Bahia interior forests Pernambuco coastal forests Southern Atlantic mangroves Humid Chaco Campos Rupestres	Atlantic Coast restingas

			montane savanna Southern Cone Mesopotamian savanna Caatinga Pernambuco interior forests Uruguayan savanna	
	ribeirovegtype	Type of vegetation sensu Ribeiro et al. (2009)	Dense Ombrophilous Forest Mixed Ombrophilous Forest Semideciduous Forest Deciduous Forest Savana Stepe Open Ombrop	Dense Ombrophilous Forest

			hilous Forest	
	BSRs	Type of biogeographical sub-regions (BSRs) sensu Ribeiro et al. (2009)	Serra do Mar Pernambuco Florestas de Araucaria Interior Forests Bahia	
	uc	Level of protection of the study site area. Yes: protected areas, including Botanical Parks, National, State Parks. No: study site is not located in a protected area.	Y, N	Y
	protectedtype	Type of the protected area column DESIG of shapefile available in WDPA IUCN and UNEP-WCMC (year), The World Database on Protected Areas (WDPA) [Online], [insert month/year of the version downloaded], Cambridge, UK: UNEP-WCMC. Available at: www.protectedplanet.net.	Park Protected Forest World Heritage Site Biological Reserve Indigenous land	Park

			Wildlife refuge	
			Ecological Station	
			Area of relevant ecological interest	
			Private Reserve	
			National Park	
			Natural Monument	
			National reserve	

Table 3. Reference information. Description of the fields related to the reference information and voucher collection of each study.

Type of information	**Variable**	**Description**	**Levels**	**Example**
REFERENCE INFORMATION	**ID**	Identification code for each record.	bat1001-bat1205	bat1001
	Authors	Short name of author without special characters	factor	Mello
	Type	Type of publication. Thesis refer to monographs, theses and dissertations.	Database Thesis Article	Article
	Reference	Reference in Ecology style	factor	Mello, M. A. R., and G. M. Schittini. 2007. Ecological analysis of three bat assemblages from conservation units in the lowland

				Atlantic forest of Rio de Janeiro, Brazil. Chiroptera Neotropical 11:206–210.
	Voucher_Specimens	Name of the collection where voucher specimens were deposited. It is possible to find more than one reference per study ID.	factor	Coleção Zoológica de Referência, Universidade Federal de Mato Grosso do Sul (ZUFMS), Campo Grande, MS, Brazil

Table 4. Capture information. Description of the fields related with bat capture information.

Type of information	Variables	Description	Levels	Example
CAPTURE INFORMATION	**ID**	Identification code for each record.	bat1001-bat1205	bat1001
	Year_start	Year of the beginning of the study	1991-2016	2008
	Year_finish	Year of the end of study. Many were vague.	1997-2016	2016
	Duration	Unstandardized duration of study. Several were vague.		1 year
	Season	Season reported in the reference paper	dry, wet, both	both
	Method	Capture method used for capturing bats	mist nets mist nets, active capture and harp trap mist nets and active search in roosts	mist nets
	Strata_sampling	Vertical strata location where	Understory ground nets (U)	UC

		capturing was performed	From Canopy to Understory (UC), below canopy (BC), Canopy (C)	
	Nights	Total number of capture nights	1 to 140	15
	hours_per_night	Duration of capture, i.e. number of hours mistnets were open. We reported the maximum as 12 hours also for the studies conducted during the dry season.	1 to 12	6
	number_of_mistnets	Number of mistnets used, regardless of their length, mesh, or material.	1 to 32	6
	effort_straube_bianconi	Effort accounting area of the mistnets and duration of the survey given in hours*square meters (Straube and Bianconi 2002). Since	52.5 to 534240	3300

		many studies do not report mistnet size or model, this standardized measure is common for comparing bat inventories.		
	Sampling_habitat	Brief description of the area where the mist net stations were placed. Information was obtained from the reference paper or from the author of unpublished data.	Forest trails and surroundings Forestry understorey Restinga Native vegetation trails and surroundings Interior of control forest	Forest trails and surroundings

			Edge of Control area	
			Interior of forest patch	
			Edge of forest patch	
			Capoeira	
			Interior of control forest are	
			Edge of control forest area	
			forest interior and forest edge	
			Forest and surroundings	
			Pinus forest with dense understory full of Piper	
			Riparian forest	
			Edges of primary forest and edges with sugarcane	
			Edges of forest and edges with sugarcane	
			Forest trails and edge with sugarcane	

			Seasonal Forest interior and Tree plantations	
			Seasonal Semi-Deciduous Forest and abandoned forestry	
			Coastal Atlantic Forest interior	
			Seasonal Atlantic Forest	
			Rocky Grasslands and Cerrado	
			Coastal Atlantic Forest	
			Cloud forest	
			lowland moist forests, with areas also covered by restinga and mangroves	
			Open and flooded shrubland	
			Capoeira, secondary forests, edges with surroundings including fields and periurban areas	

			Open fields, moist Chaco, Islands of Parana Paranean forest Forest trails and surroundings Restored area since 1998 up to 8m height Restored area since 1987 up to 10m Restored area since 50s up to 15m Native vegetation trails and surroundings up to 20m Regenerating vegetation up to 20m Secondary forest Open shrubland and forest patches	
	Community	Reported bat assemblage. All: when all bat assemblage was reported. Leafnosed:	all, leafnosed	leafnosed

		phyllostomid species data (leaf-nosed bats) were reported.		
	Class	Taxonomic class		Mammalia
	Order	Taxonomic order	Chiroptera	Chiroptera
	Superfamily	Taxonomic superfamily	Noctilionoidea, Vespertilionoidea, Emballonuroidea	Noctilionoidea
	Family	Taxonomic family	Phyllostomidae, Molossidae, Vespertilionidae, Emballonuridae, Thyropteridae, Natalidae, Noctilionidae, Furipteridae	Phyllostomidae
	Capture_number	Number of captures	0-5350	20
	Species	Species name		*Anoura geoffroyi*
	Status	Status in global assessment of IUCN Red List	LC, DD, NA, NT, EN	LC

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Capítulo 2

Uma nota sobre os limites territoriais da Mata Atlântica

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English version: https://github.com/LEEClab/ATLANTIC-limits/

Uma nota sobre os limites territoriais da Mata Atlântica

Mata Atlântica

A Mata Atlântica é um dos hotspots de biodiversidade mais conhecidos no planeta. Compilamos os principais limites geográficos disponíveis para a Mata Atlântica.

Longitude

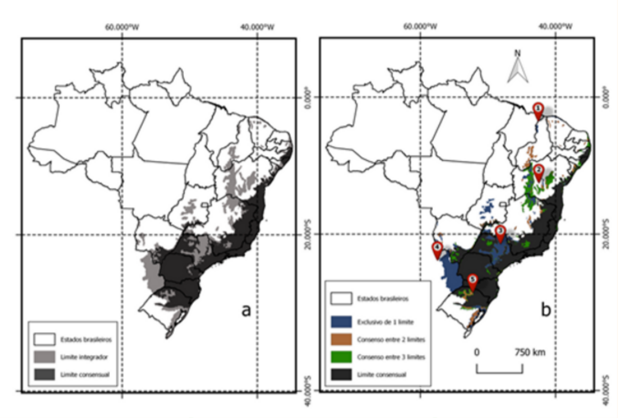
32 - 58° W

Latitude

8 - 28° S

Altitude

0 - 3.000 m



Divergências

O limite integrador abrange a união de todos os limites disponíveis, e suas principais divergências estão em **vermelho**. O limite consensual é a área em que todos os limites apontam como sendo Mata Atlântica.

A Mata Atlântica é um bioma

Bioma é uma área geográfica extensa, que apresenta uma comunidade de plantas e animais especifica, com uma fitofisionomia particular e que é influenciada diretamente pelo clima (Whittaker 1970)

Área original da Mata Atlântica Brasileira

1 milhão km2

Vegetação Nativa remanescente

16%

Fonte: https://github.com/LEEClab/ATLANTIC-limits

ABSTRACT: The geographic delimitation of a biome encompasses questions that involve environmental factors such as climate and vegetation characteristics as well as political aspects. Consequently, variation on biome delimitation is recurrent. The Atlantic Forest is one of the most important biodiversity hotspots in the world, and historically several territorial delimitations have been proposed for this biome. Here we aim on 1) discussing the four main delimitations and 2) based on the existing limits, discussing their union (Integrative limit) and Intersection (Consensual limit). The main limits present consensual and integrative areas of 1.01 and 1.62 million km^2, respectively. Five regions of divergence must be carefully evaluated. Finally, we suggest a debate about the use of limits in ecological studies and their application in conservation studies.

Palavras-chave: biogeografia histórica, bioma, distribuição geográfica, domínio, floresta tropical, hotspot de biodiversidade

Keywords: tropical forest, biome, domain, geographic distribution, biodiversity hotspot, historical biogeography

Uma nota sobre os limites territoriais da Mata Atlântica

Após as primeiras menções feitas por Whittaker (1962), o conceito de bioma foi amplamente debatido sob a perspectiva ecológica e biogeográfica. O termo surgiu como uma busca por uma unidade espacial que fosse utilizada em estudos de bio-ecologia, mas que também fosse apropriada para entender a distribuição da flora e fauna (Clements & Shelford 1939). Desde então o termo tem sido utilizado sob diferentes perspectivas, seja se referindo à flora, fauna, relevo, fitofisionomia ou a combinações desses elementos (Coutinho 2006). Os biomas podem apresentar diversas delimitações espaciais, as quais variam de acordo com interesses ambientais, ecológicos, políticos ou de gestão de seus proponentes. Este é o caso do bioma Mata Atlântica, um *hotspot* de biodiversidade que apresenta mais de 90% de sua distribuição original no Brasil, ocorrendo também em partes da Argentina e Paraguai (MITTERMEIER et al., 2004).

Ainda que diferentes limites territoriais de um mesmo bioma possam atender a diferentes objetivos, a falta de uma delimitação única pode gerar confusão. Além das questões ecológicas e ambientais, a delimitação de um bioma também tem apoio político, pois pode incorrer sobre a determinação ou limitação dos possíveis usos territoriais por diferentes atores sociais, o que é objeto de frequentes conflitos de interesses (Steinberger & Rodrigues 2010).

Neste artigo nós tratamos bioma como uma área geográfica extensa, que apresenta uma comunidade de plantas e animais específica, com uma fitofisionomia particular e que é influenciada diretamente pelo clima (Whittaker 1970). Embora a Mata Atlântica apresente diferentes fitofisionomias – como a floresta ombrófila densa, floresta ombrófila mista, florestas estacionais, restingas, formações campestres, formações litorâneas e ecótonos, a mesma é tratada como bioma por diversos autores (Morellato & Haddad 2000, Olson *et al*. 2001, IBGE 2004, Tabarelli *et al*. 2010). Essa variedade de fitofisionomias deve-se, sobretudo, ao amplo gradiente latitudinal (8 – 28° S), longitudinal (32 – 58° W) e altitudinal (0 – ~3.000 m), combinados a grandes variações climáticas, formações geomorfológicas e de tipos de solos (Oliveira-Filho & Fontes 2000, Eisenlohr *et al.* 2015). Tais variações, juntamente com as expansões e retrações geográficas sofridas, como resultado das mudanças climáticas do passado, propiciaram a evolução e especialização de diversas formações vegetacionais na Mata Atlântica (Carnaval *et al.* 2009, *Joly e*t al. 2014, Sobral-Souza *et al.* 2015, Sobral-Souza & Lima-Ribeiro 2017).

Diferentes delimitações geográficas para a Mata Atlântica decorrentes de mudanças climáticas ocorridas ao longo dos últimos 21 mil anos foram propostas (veja Sobral-Souza *et al*. 2015). A Mata Atlântica atual se estende por boa parte do litoral brasileiro, atingindo o interior austral do continente, onde abrange regiões do Paraguai e Argentina (Figura 1, Morellato & Haddad 2000, Ribeiro *et al*. 2009). Grandes compilados sobre abundância e distribuição de espécies têm sido feitos (ver a crescente série ATLANTIC de data papers em https://esajournals.onlinelibrary.wiley.com/doi/toc/10.1002/(ISSN)1939-9170.AtlanticPapers), o que nos leva a constatar que a Mata Atlântica é um dos *hotspots* de biodiversidade mais bem conhecidos do planeta. Por apresentar elevada riqueza de espécies, nível de endemismo e impacto antrópico (restam atualmente menos de 16% de cobertura de vegetação nativa, Ribeiro *et al.* 2009), a Mata Atlântica é considerada uma região prioritária para conservação da biodiversidade (Myers *et al*. 2000).

Apesar de diversos estudos terem sido realizados com o intuito de descrever a delimitação geográfica da Mata Atlântica (Oliveira-Filho & Fontes 2000, Morellato & Haddad 2000, Silva & Casteleti 2005), estabelecer os limites da Mata Atlântica não é uma tarefa trivial. Os ecótonos com os outros biomas (e.g. Cerrado, Caatinga e Pampa) podem ser graduais e de complexa classificação em determinadas regiões. Por exemplo, a transição entre a Mata Atlântica e o Cerrado pode se estender por centenas de quilômetros e ser composta por diferentes vegetações savânicas, campestres e florestais, com prevalência de espécies representativas de ambos os biomas (Oliveira-Filho & Fontes 2000, L*öbler et* al. 2015). Dessa forma, apesar de sua implicação prática para fins de conservação e desenvolvimento de políticas públicas, o estabelecimento de limites bem definidos para a Mata Atlântica pode apresentar inconsistências com o mundo real, principalmente quando se considera a complexidade de formações vegetais, clima e fauna associada aos ecótonos (Eisenlohr *et al.* 2015)

Devido à complexidade inerente à delimitação de biomas, neste estudo nós discutimos as quatro principais delimitações geográficas da Mata Atlântica. Nossos objetivos foram: 1) disponibilizar, descrever e apresentar os critérios usados em cada uma das delimitações, quantificando suas similaridades e diferenças; e 2) discutir a forma mais extensa dos limites avaliados como um Limite integrador e sua intersecção como um Limite consensual. Dessa forma, nós propomos aqui uma reflexão sobre as diferentes extensões e os conceitos utilizados para se definir a Mata Atlântica, e sobre quais as implicações para seu uso em estudos ecológicos, biogeográficos e de conservação.

Ainda que existam delimitações exclusivas às regiões da Argentina, Brasil e Paraguai (e.g. Huang *et al.* 2007, IBGE 2004), nós discutimos aqui tanto as delimitações que abrangem a Mata Atlântica nos três países nos quais ela ocorre (Figura 1, *World Wildlife Fund*, WWF 2001, Olson *et al.* 2001) quanto apenas a Mata Atlântica brasileira (MMA, IBGE, 2004, Lei da Mata Atlântica, 2006 e Ribeiro *et al.*, 2009). Para quantificar as diferenças entre os limites, nós transformamos os mapas de formato vetor para grade (*raster*) com resolução espacial de 1 km e extensão abrangendo todos os limites (latitudes e longitudes máximas e mínimas dentre os vetores). Para cada um dos limites, nós atribuímos códigos para as células dos seus respectivos arquivos *raster* separadamente. Após essa etapa, nós somamos os mapas e criamos um novo *raster* para distinguir as semelhanças e diferenças entre os limites em três diferentes níveis: (1) células com valores únicos, (2) células com valores combinados para cada dois mapas e (3) células com valores para três e/ou quatro mapas. O cálculo da área total dos limites foi baseado nos arquivos *shapefiles* com o auxílio do software R (R Core Team 2015) utilizando a projeção cônica equivalente de Albers e o datum horizontal SAD 69.

Os quatro diferentes limites e suas respectivas áreas podem ser observados na Tabela 1. Os limites, bem como informações complementares estão disponíveis em https://github.com/LEEClab/ATLANTIC-limits-shapefiles.

Tabela 1. Limites da Mata Atlântica utilizados e suas respectivas áreas, referências e fonte dos dados.

Limite	**Área total (km²)**	**Referência**	**Fonte**
MMA, IBGE (2004)	1.117.862	IBGE (2016)	http://mapas.mma.gov.br/i3geo/datadownload.htm e http://www.ibge.gov.br/home/presidencia/noticias/21052004biomashtml.shtm
Lei da Mata Atlântica (2006)	1.291.000	Decreto Federal nº 6660/2008 Lei nº. 11.428/ 2006, IBGE, Silva *et al.* (2016)	http://www.planalto.gov.br/ccivil_03/_ato2004-2006/2006/lei/l11428.htm e http://www.mma.gov.br/biomas/mata-atlântica_emdesenvolvimento
World Wildlife Fund (WWF, 2001)	1.335.416	Olson *et al.* (2001)	http://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world
Ribeiro *et al.* (2009)	1.366.000	Ribeiro *et al.* (2009)	https://github.com/LEEClab/ATLANTIC-limits-shapefiles
Limite integrador (União)	1.620.000	presente artigo	https://github.com/LEEClab/ATLANTIC-limits-shapefiles
Limite consensual (Interseção)	1.018.241	presente artigo	https://github.com/LEEClab/ATLANTIC-limits-shapefiles

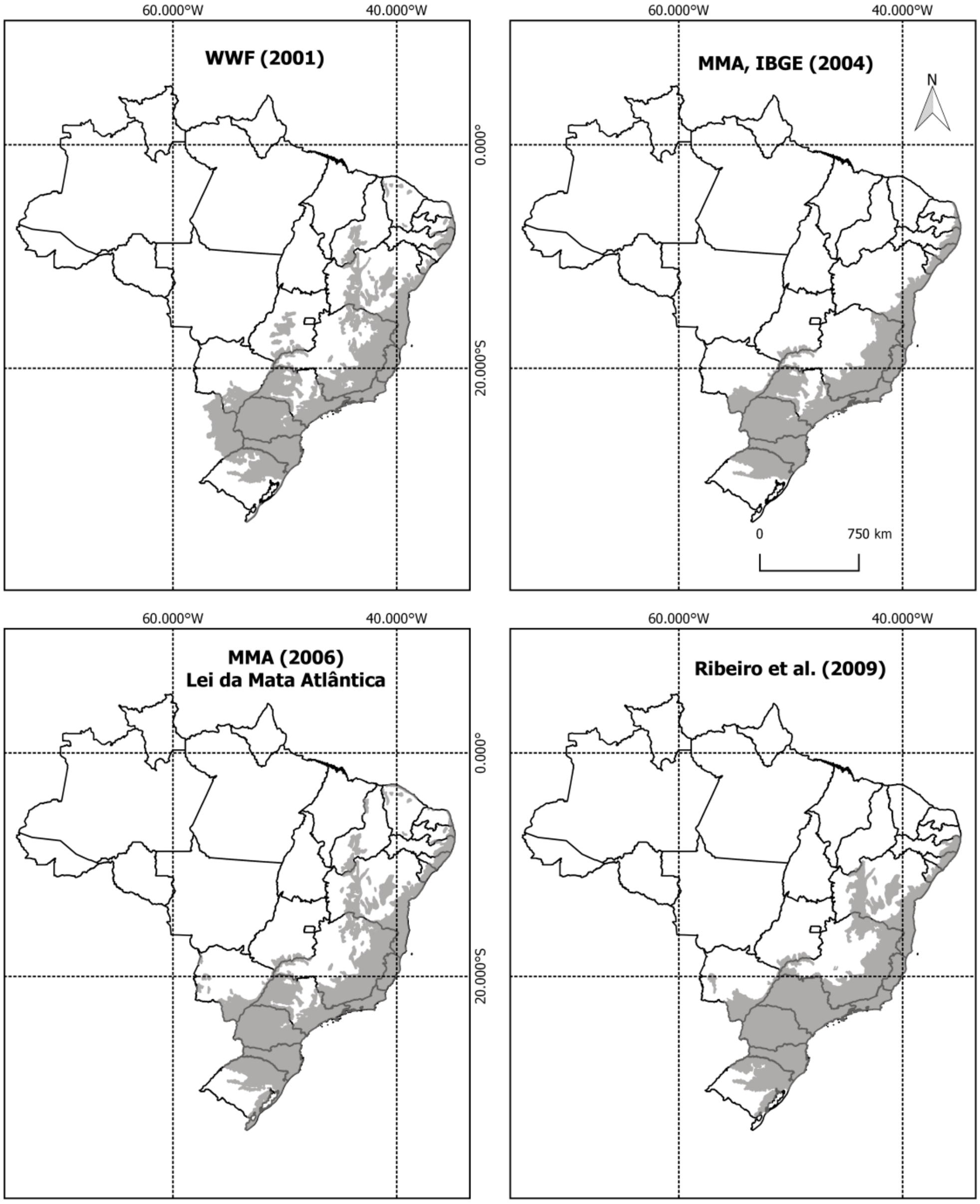


Figura 1. Quatro limites da Mata Atlântica segundo diferentes mapas amplamente utilizados e disponíveis online.

1. World Wildlife Fund (WWF, 2001) (Olson et al. 2001)

A organização não-governamental WWF estabeleceu limites unificados para os ecossistemas terrestres ao redor do mundo. O produto divide o planeta em 867 ecorregiões definidas como "*uma extensa parte de terra ou água que compartilha espécies e condições ambientais comuns*" (Olson *et al.* 2001) e 14 biomas. Os biomas e ecorregiões da WWF têm como objetivo refletir melhor a distribuição de espécies e comunidades animais e vegetais do que as unidades baseadas em modelos derivados de características bioclimáticas (como temperatura e pluviosidade, estrutura de vegetação, ou derivados de assinaturas espectrais de sensoriamento remoto), pois esses métodos não enfatizam os gêneros endêmicos. De acordo com essa definição a Mata Atlântica é classificada como parte dos biomas Floresta tropical e subtropical úmida e Floresta tropical e subtropical seca, e aqui consideramos como Mata Atlântica as classes *Atlantic Forests e Atlantic dry Forests* (coluna G200_REGIO) do arqu*ivo shapefile* de ecossistemas terrestres (*Terrestrial Ecoregions of the World,* Olson *et al*. 2001). No Brasil, o limite avança para transições com o Cerrado, como nos estados de São Paulo, Minas Gerais e Bahia, e Caatinga no nordeste brasileiro, além de adentrar vegetações florestais do Paraguai e da Argentina (Figura 1). A construção deste limite foi feita com base no conhecimento e cooperação de mais de 100 pesquisadores.

2. *MMA, IBGE (2004)* *(IBGE 2016)*

Este é o limite da Mata Atlântica formalizado pelo Instituto Brasileiro de Geografia e Estatística (IBGE), disponibilizado juntamente com o Ministério do Meio Ambiente (MMA), e definido com participação governamental, da comunidade científica e de organizações da sociedade civil atuantes no campo socioambiental. A Mata Atlântica foi delimitada em um mapa de biomas brasileiros, juntamente com os limites brasileiros da Amazônia, Caatinga, Cerrado, Pampa e Pantanal. O objetivo desse limite é servir como referência para o estabelecimento de políticas públicas diferenciadas e para acompanhamento das ações implementadas em cada um deles pela sociedade. Dessa forma, muitos remanescentes da fitofisionomia de Mata Atlântica que estão distribuídos em ecótonos com demais biomas não são considerados. Esse limite é comumente utilizado por trabalhos que comparam ou abordam diferentes biomas brasileiros. Nele, a Mata Atlântica ocupa a faixa continental atlântica que margeia a costa leste e se estende para o interior no Sudeste e Sul do Brasil, e a principal diferença em relação aos demais limites é sua abrangência mais restrita na região Nordeste (Figura 1). Dentre os critérios utilizados neste limite, destacam-se a "vegetação dominante (florestal)" e o "relevo extremamente diverso" (IBGE 2016). Trata-se do limite de menor extensão espacial dentre os quatro.

3. Lei da Mata Atlântica (2006) *(IBGE, Lei nº. 11.428/ 2006, Silva et al. 2016)*

Este limite é regulado pelo Decreto Federal nº. 6660/2008 e pela Lei da Mata Atlântica (nº. 11.428/ 2006). Além do limite do bioma, a lei divide a Mata Atlântica em biorregiões. Os principais artigos referentes ao Decreto são claros na descrição do limite, seguindo critérios do IBGE para o ano de 2006. Assim, a Mata Atlântica abrange a Floresta Ombrófila Densa, Floresta Ombrófila Mista (Mata de Araucária), Floresta Ombrófila Aberta, Floresta Estacional Semidecidual, Floresta Estacional Decidual, Campos de Altitude, Brejos Interioranos e Encraves Florestais, Refúgios Vegetacionais, Áreas de Tensão Ecológica (zonas de transições entre ambientes ou fisionomias), Áreas das Formações Pioneiras (manguezais, restingas, campos salinos e áreas aluviais), Estepes, Savanas, Savanas-Estépicas, e Vegetação Nativa de Ilhas. O Decreto nº 6.660 de 21 de novembro de 2008 estabeleceu o "Mapa da Área de Aplicação da Lei nº 11.428 de 2006", bem como regulamentou dispositivos para a determinação da utilização e proteção da vegetação da Mata Atlântica. A aplicação da lei se daria em "remanescentes de vegetação nativa no estágio primário e nos estágios secundário inicial, médio e avançado de regeneração na área de abrangência definida no caput deste artigo" (artigo 2º, parágrafo único da Lei). O limite foi gerado após longo debate entre pesquisadores, membros de órgãos governamentais e ativistas da sociedade civil com diferentes posicionamentos (STEINBERGER; RODRIGUES, 2010), e é inclusivo no que se refere ao interior da região Nordeste do Brasil, além de incluir regiões que estão no domínio do Pantanal e do Pampa de acordo com outros limites (Figura 1).

4. Ribeiro et al. (2009)

Em Ribeiro *et al.* (2009) foram analisados 94% da região de Mata Atlântica brasileira definida pela Lei da Mata Atlântica (nº. 11.428, ano de 2006), porém, para algumas regiões o estudo expandiu esses limites previstos na lei, contemplando a delimitação de regiões biogeográficas propostas por Silva e Casteleti (2005). Desta forma, o limite define as seguintes sub-regiões biogeográficas (BSRs): Araucárias, Bahia, Brejos Nordestinos, Diamantina, Interior, Pernambuco, Serra do Mar, e São Francisco (veja Figura 1 de Ribeiro *et al.* [2009]). A delimitação proposta por Ribeiro *et al.* (2009) difere das demais principalmente por incluir áreas do interior do estado de São Paulo e partes do norte do estado do Paraná, que são consideradas como áreas pertencentes ao domínio do Cerrado pelos outros três limites (Figura 1). Os autores incorporaram essas regiões pelo fato de que, além de áreas de savana do domínio do Cerrado (como, por exemplo, a Estação Ecológica de Itirapina), parte de suas formações vegetais correspondem a florestas estacionais semideciduais da Mata Atlântica, ou áreas de transição entre os dois biomas (Oliveira-Filho & Fontes 2000, Ribeiro *et al.* 2009). Na região Nordeste, o limite abrange áreas de Floresta Semidecidual da Serra do Espinhaço e Brejos Nordestinos. Na região Sul, áreas da planície costeira do Rio Grande do Sul não fazem parte da delimitação. E por fim, o mapeamento não inclui manchas pequenas de Mata Atlântica na costa brasileira até o norte de Pernambuco, Rio Grande do Norte e Ceará (Figura 1).

Comparação entre os limites

A partir dos quatro limites detalhados acima, nós propomos dois novos limites: o primeiro refere-se à união dos quatro limites – Limite integrador – e o segundo consiste na interseção dos limites – o Limite consensual da Mata Atlântica (Figura 2a). Apresentamos o resultado da sobreposição dos quatro limites na Figura 2b e Tabela 2, nas quais é possível observar as regiões exclusivas, bem como as áreas que coincidem para dois ou três limites. Enquanto a união dos limites existentes compreende uma área de mais de 1,6 milhão de km^2, a intersecção entre os limites apresenta uma cobertura de cerca de 1,08 milhão de km^2 (Tabela 1, Figura 2a). Chamamos de Limite consensual da Mata Atlântica a interseção dos limites, pois é onde os quatro limites apontam como sendo área de Mata Atlântica.

Tabela 2. Valores referentes à área territorial (km²) que incorpora similaridades e diferenças entre limites da Mata Atlântica. * O primeiro valor se refere a área total dos rasters, incluindo a Mata Atlântica internacional; ** O segundo valor foi feito após um corte de cada porção pela delimitação política atual do Brasil, com base na malha municipal brasileira de 2016, disponível em https://downloads.ibge.gov.br.

Descrição	Limites utilizados	Área (km²) total*	Área (km²) dentro do limite político atual do Brasil**
Área Exclusiva de um limite	Exclusivo do WWF	148.472	35.992
	Exclusivo do MMA	1.788	1.766
	Exclusivo da Lei da Mata Atlântica	25.197	22.912
	Exclusivo de Ribeiro *et al*. (2009)	148.268	146.977
Convergência de dois limites	WWF e MMA	1.331	1.311
	WWF e Lei da Mata Atlântica	35.839	34.642
	MMA e Lei da Mata Atlântica	21.758	21.752
	WWF e Ribeiro *et al*. (2009)	16.318	16.093
	MMA e Ribeiro *et al*. (2009)	3.177	3.156
	Lei da Mata Atlântica e Ribeiro *et al*. (2009)	27.147	26.856
Convergência de três limites	WWF, MMA e Lei da Mata Atlântica	11.994	11.980
	WWF, MMA e Ribeiro *et al*. (2009)	8.250	8.217
	WWF, Lei da Mata Atlântica e Ribeiro *et al*. (2009)	93.663	93.616
	MMA, Lei da Mata Atlântica e Ribeiro *et al*. (2009)	51.258	51.253
Limite consensual/Intersecção dos quatro limites	WWF, MMA, Lei da Mata Atlântica e Ribeiro *et al*. (2009)	1.018.241	1.018.222

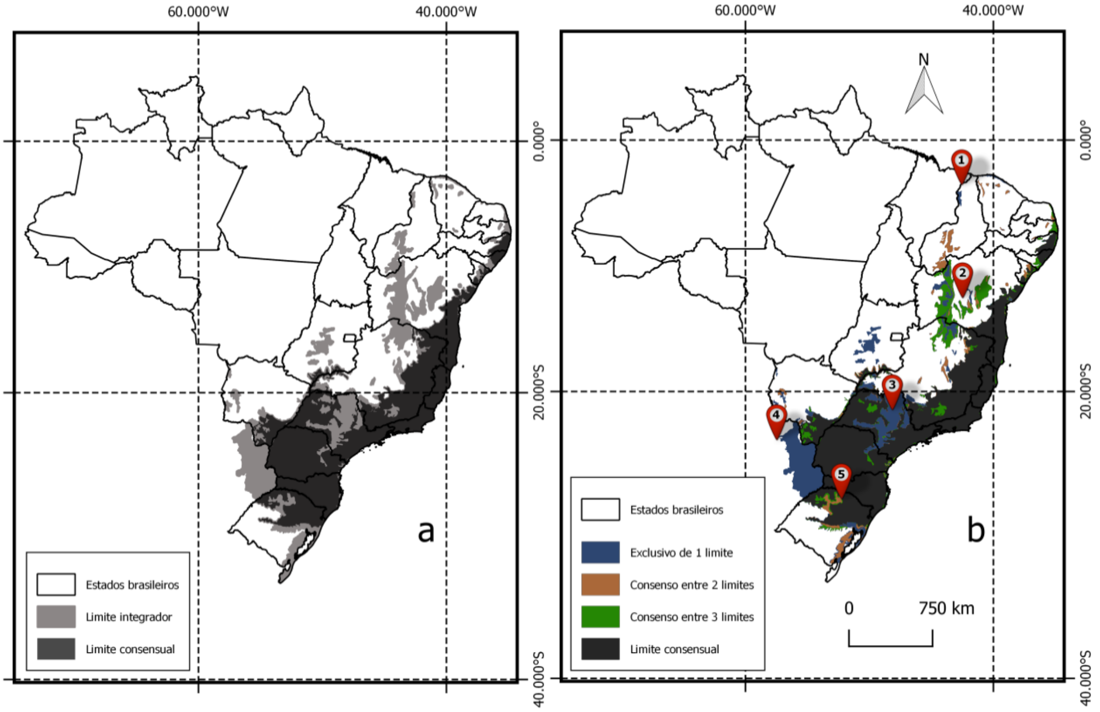


Figura 2. Similaridades e diferenças dentre os limites. a: Limite integrador (união) e consensual (interseção) da Mata Atlântica. b: Similaridades e diferenças entre os limites da Mata Atlântica internacional (WWF internacional, IGBE, Ribeiro *et al.* (2009) e Lei da Mata Atlântica). Marcadores em vermelho indicam principais divergências entre os limites.

A união dos quatro limites aqui apresentados – o Limite integrador da Mata Atlântica – pode ser considerada abrangente e inclusiva e abarca alguns padrões de biogeografia histórica. Isto significa que a inclusão de remanescentes florestais em regiões de ecótonos com outros biomas brasileiros pode ser importante para evidenciar a diversidade de plantas e animais que fizeram parte da Mata Atlântica e atualmente estão distribuídos em outros biomas. Diferentes espécies podem ter permanecido isoladas em fragmentos em regiões de ecótonos com outros biomas devido às mudanças climáticas ocorridas ao longo do tempo geológico e que levaram à expansão e ou retração das florestas Neotropicais em diferentes períodos temporais (Werneck *et al*. 2012, Sobral-Souza *et al*. 2015). Além disso, perdas recentes de biodiversidade são associadas à ação humana modificando intensamente as paisagens. Tais alterações nas paisagens devido à perda e fragmentação de habitat sofridas nos últimos séculos estão dentre os principais fatores causadores de extinções e que definem o período conhecido como Antropoceno (Dirzo *et al.* 2014). Para compreender melhor como as alterações na paisagem influenciam na distribuição e na persistência de espécies, principalmente em ecótonos da Mata Atlântica onde o processo de fragmentação está bastante avançado, é importante olhar para os remanescentes do bioma como áreas de potenciais refúgios de espécies nativas onde é importante focar esforços de monitoramento e conservação.

Ao observar a Figura 2b a partir da região norte em direção ao sul, nota-se a existência de cinco regiões que adentram outros biomas e que não são contempladas no Limite consensual da Mata Atlântica, mas onde ocorrem áreas exclusivas ou de consenso entre dois ou três limites: (1) uma região ao norte do limite e que inclui áreas de Caatinga, reconhecidas como brejos de altitude, como em Ibiapaba e Baturité no estado Ceará; (2) a região do Rio São Francisco, que compreende parte do interior de Minas Gerais e Bahia; (3) a região que engloba um grande enclave considerado como domínio de Cerrado no estado de São Paulo; (4) outra região ao sudoeste que adentra partes do Pantanal e Chaco; e, por último, (5) uma região ao sul, que permeia os Pampas. As regiões 1, 2 e 4 foram descritas como rotas de ligação entre a Mata Atlântica e a Amazônia durante o processo de expansão e retração das florestas úmidas ao longo dos ciclos glaciais e interglaciais do Pleistoceno (Sobral-Souza *et al.* 2015). A revisão de Sobral-Souza e Lima-Ribeiro (2017) reforça a ideia da persistência de manchas de Mata Atlântica nessas regiões no passado ao debater a similaridade genética e de composição de espécies entre o sul da Mata Atlântica e o oeste da Amazônia, a maior similaridade taxonômica entre matas de galeria do Cerrado e a Mata Atlântica (na porção central) e a similaridade de espécies dos brejos de altitude da Caatinga com espécies do norte da Mata Atlântica.

Em relação às ressalvas de cada limite, retomamos ressalvas levantadas por Olson *et al*. (2001), apropriadas para qualquer mapeamento biogeográfico: 1) nenhuma delimitação biogeográfica atende à todas as espécies; 2) limites raramente são abruptos, e na verdade há ecótonos e mosaicos entre eles; 3) a maior parte das "ecorregiões" (subconjuntos de biomas de acordo com a WWF ou outras delimitações baseadas em biomas, ou a própria delimitação de bioma), contém habitats que são diferentes do habitat que define o bioma. No caso do limite consensual, que é o mais restritivo da Mata Atlântica, áreas do interior de São Paulo, interior da Bahia e Goiás, além de áreas do norte do Ceará e costa sul do Rio Grande do Sul não são consideradas áreas do Bioma da Mata Atlântica, bem como a parte da Mata Atlântica no Paraguai e na Argentina. Fica além do escopo desta nota propor uma delimitação única ou mais adequada, mas ressaltamos que o Limite consensual não parece contemplar sua real extensão, sendo que reduz sua área em mais de 600.000 km^2. Seria interessante avaliar, por exemplo, a variação entre os diferentes limites em relação à proporção de áreas florestais protegidas, como já foi feito para as ecorregiões da WWF (Olson *et a.l* 2001) em Dinerstein *et al*. (2017). Neste estudo, os autores demonstram que em média apenas 12% de área está protegida quando consideram-se as florestas tropicais globalmente (Olson *et al.*2001).

Buscamos motivar uma reflexão sobre as diferenças entre os limites já propostos, para que os mesmos sejam utilizados com critérios adequados ao estudo proposto, ainda que seja para simplesmente representar uma região de estudo em um mapa ilustrativo. Após comparar os quatro principais limites disponíveis da Mata Atlântica, concluímos que não existe uma solução trivial para a escolha do limite a ser utilizado para trabalhos em diferentes escalas, seja em estudos biogeográficos, macroecológicos, ou para a investigação de processos em extensões geográficas mais restritas. A comparação dos limites realizada aqui permite que estudos ecológicos na Mata Atlântica e outros biomas tenham uma decisão da delimitação espacial em questão mais consciente por parte dos pesquisadores. O Limite integrador e o Limite consensual podem ser utilizados para investigar questões relacionadas à proposição de políticas públicas e gestão de territórios e recursos naturais, ainda que tais aplicações possam estar sujeitas a limites já implementados para aplicação de leis e tomadas de decisão, como o Limite da Lei da Mata Atlântica, pois os mesmos envolvem questões de soberania e jurisdição. Não cabe a esta nota questionar a validade dos limites existentes, mas sim gerar discussões para que estudos ecológicos e de aplicação de políticas públicas levem em consideração a complexidade da extensão da Mata Atlântica.

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Capítulo 3

Hantavirus host assemblages and human disease in the Atlantic Forest

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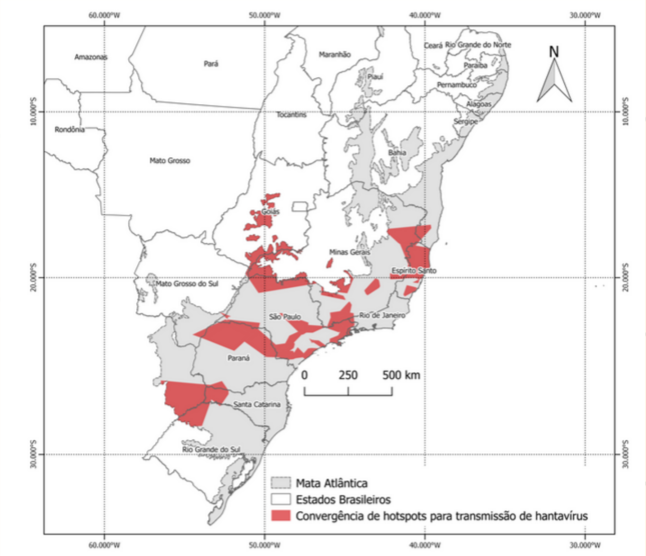
A DIVERSIDADE DE CULTIVOS E FLORESTAS, CLIMA E BIODIVERSIDADE LOCAL INFLUENCIAM NA PROPORÇÃO DE ROEDORES HOSPEDEIROS DE HANTAVÍRUS

MATA ATLÂNTICA

Medimos a proporção de roedores que podem carregar hantavírus patogênicos. Também investigamos a correspondência entre essa proporção predita por modelos espaciais e a vulnerabilidade ao hantavírus patogênico índice de infecção em humanos predita por análise multi-critério



Sabendo onde há mais roedores que podem estar infectados, podemos priorizar locais para alocação de recursos para vigilância e prevenção da hantavirose

Áreas mais importantes

- Norte do Paraná
- Sul de São Paulo
- Norte de São Paulo
- Centro de Goiás
- Oeste de Santa Catarina
- Misiones, Argentina
- Sul do Paraguai

Picos de vulnerabilidade à doença ocorrem em paisagens com menos de 15 espécies de pequenos mamíferos

Oligoryzomys nigripes
Necromys lasiurus
+
10
Espécies de roedores podem carregar pelo menos um tipo de hantavírus

LEEC unesp FAPESP

Hantavirus host assemblages and human disease in the Atlantic Forest

Abstract: Several viruses from the genus *Orthohantavirus* are known to cause lethal disease in humans. Sigmodontinae rodents are the main hosts responsible for hantavirus transmission in the tropical forests, savannas, and wetlands of South America. These rodents can shed different hantaviruses, such as the lethal and emerging *Araraquara orthohantavirus*. Factors that drive variation in host populations may influence hantavirus transmission dynamics within and between populations. Landscape structure, and particularly areas with a predominance of agricultural land and forest remnants, is expected to influence the proportion of hantavirus rodent hosts in the Atlantic Forest rodent community. Here, we tested this using 283 Atlantic Forest rodent capture records and geographically weighted models that allow us to test if predictors vary spatially. We also assessed the correspondence between proportions of hantavirus hosts in rodent communities and a human vulnerability to hantavirus infection index across the entire Atlantic Forest biome. We found that hantavirus host proportions were more positively influenced by landscape diversity than by a particular habitat or agricultural matrix type. Local small mammal diversity also positively influenced known pathogenic hantavirus host proportions, indicating that a plasticity to habitat quality may be more important for these hosts than competition with native forest dwelling species. We found a consistent positive effect of sugarcane and tree plantation on the proportion of rodent hosts, whereas defaunation intensity did not correlate with the proportion of hosts of potentially pathogenic hantavirus genotypes in the community, indicating that non-defaunated areas can also be hotspots for hantavirus disease outbreaks. The spatial match between host hotspots and human disease vulnerability was 17%, while coldspots matched 20%. Overall, we discovered strong spatial and land use change influences on hantavirus hosts at the landscape level across the Atlantic Forest. Our findings suggest disease surveillance must be reinforced in the southern and southeastern regions of the biome where the highest predicted hantavirus host proportion and levels of vulnerability spatially match. Importantly, our analyses suggest there may be more complex rodent community dynamics and interactions with human disease than currently hypothesized.

Author Summary

Hantaviruses cause disease in people, mainly following transmission from wild rodents to people through contact with infected excreta. Wild rodents use different habitats, and many survive even in anthropogenically changed environments, but to an unknown extent. The objective of our study was to understand how these rodents respond to habitat change in the landscape, to biodiversity and to climate. We measured the proportion of pathogenic hantavirus hosts in the rodent community. We then investigated the spatial correspondence between this proportion and a vulnerability to pathogenic hantavirus infection index in humans within the Atlantic Forest. We found 12 well represented species of rodents that can carry at least one hantavirus genotype. Despite high variation in the host proportion data, the peaks of human vulnerability to disease occurs at higher levels of habitat diversity in the landscape, intermediate levels of rainfall, and areas with less than 15 species in the local small mammal community. Our results suggest hantavirus surveillance and prevention measures are needed in the south and south-east regions of Brazil where highest host proportions and levels of vulnerability spatially match.

Introduction

The members of the genus *Orthohantavirus* (hereafter hantavirus) are three-segmented negative-stranded RNA viruses in the family *Hantaviridae.* More than 90 species of rodents (order Rodentia) and increasing numbers of bats (order Chiroptera) and shrews (family Soricidae) are recognized as hosts, and at least 47 rodent species are known to host pathogenic genotypes of hantavirus (MILHOLLAND et al., 2018). Hantaviruses are spread by host excreta, and it is thought that the main transmission route to humans is via inhalation of viral particles through the respiratory tract, or by direct contact with blood or saliva of infected rodents (VAHERI; VAPALAHTI; PLYUSNIN, 2008). Within natural reservoir-hosts, hantaviruses do not cause obvious disease (KALLIO et al., 2007), whereas transmission to humans can lead to hantavirus disease with severe cardiopulmonary and renal involvement (GIZZI et al., 2013; RASMUSON et al., 2011). Hantaviruses are rarely transmitted between humans and human disease is caused by at least 23 recognized viruses carried by specific rodent (LÁZARO et al., 2007). In Brazil there are three species of hantavirus causing disease among humans: *Andes orthohantavirus* (ANDV), *Rio mamore orthohantavirus* (RIOMV), and *Laguna Negra orthohantavirus* (LANV) [7]. Within ANDV three genotypes: *Araraquara orthohantavirus* (ARQV), *Juquitiba orthohantavirus* (JUQV), and *Castelo dos Sonhos orthohantavirus* (CASV); within RIOMV the genotype *Anajatuba orthohantavirus* (ANJV) (JONSSON; FIGUEIREDO; VAPALAHTI, 2010; KRUGER et al., 2015; OLIVEIRA et al., 2014; SABINO-SANTOS JR et al., 2018). Hantavirus is a putatively emerging virus in Brazil and carried by more than 16 wild rodents which are endemic in the Atlantic Forest and Cerrado biomes (SABINO-SANTOS JR et al., 2018). There is a considerable diversity of pathogenic hantavirus genotypes harbored by common wild rodents in the Atlantic Forest of South America (Fig 1). Despite being uncommon, the hantavirus cardiopulmonary syndrome (HCPS) is frequently fatal, with fatality rates reaching 66% among 20 to 34-year old patients, and 45% of infected people in southeastern Brazil (DE OLIVEIRA et al., 2015).

The relationship between biodiversity and pathogen incidence is idiosyncratic (CIVITELLO et al., 2015; KEESING et al., 2010; SALKELD; PADGETT; JONES, 2013), but host distribution combined with environmental effects are likely the main drivers for hantavirus disease risk in people (MILHOLLAND et al., 2018). Thus, investigation of the relationship between the hosts' distributions and landscape alteration is of major interest.

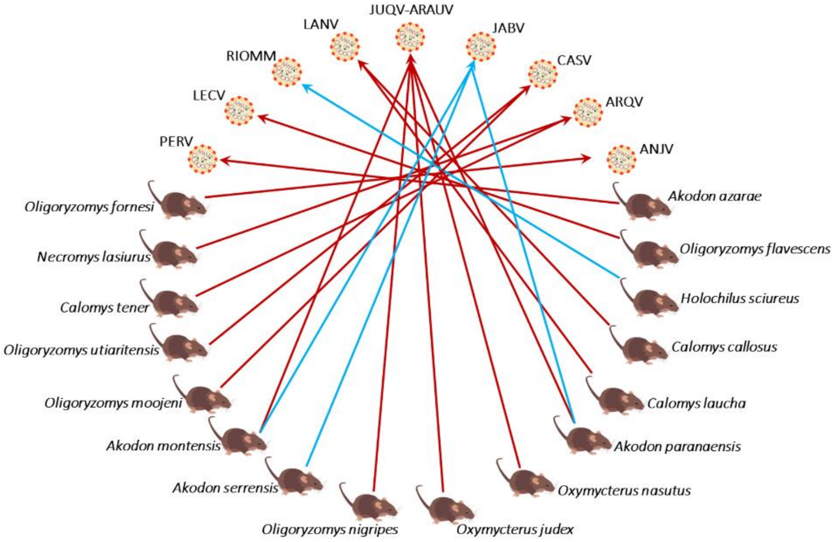


Fig 1. Interactions between hantaviruses and their hosts in South American Atlantic Forest and its boundaries. *Araraquara-Paranoa orthohantavirus* (ARQV), *Castelo dos Sonhos orthohantavirus* (CASV), *Juquitiba-Araucaria orthohantavirus* (JUQV-ARAUV*)*, *Lechiguanas orthohantavirus* (LECV), and *Pergamino orthohantavirus* (PERV) are genotypes of *Andes orthohantavirus* (ANDV); *Rio Mearim orthohantavirus* (RIOMM) and *Anajatuba orthohantavirus* (ANJV) are genotypes of *Rio Mamore orthohantavirus* (RIOMV); *Laguna Negra orthohantavirus* (LANV); *Jabora orthohantavirus* (JABV) (BRASIL, 2014; CHU; OWEN; JONSSON, 2011; DE OLIVEIRA et al., 2014; GUTERRES et al., 2015; MILHOLLAND et al., 2018; SABINO-SANTOS JR, 2015). Known-pathogenic viruses interactions have red connecting lines, others blue.

Based on a recent framework for understanding drivers of hantavirus disease outbreaks (PRIST; D´ANDREA; METZGER, 2017), an important component for rodent to human transmission is the proportion of reservoir hosts in a given community. Some ecological correlates of rodent host occurrence suggest land use change, climate, and human disturbance increases host population abundance and thus the proportion of hosts in rodent communities. Furthermore, biotic factors such as the presence of predators and/or competitors and local small mammal diversity can negatively influence reservoir host abundance. In degraded areas, habitat generalist rodents can move through agricultural matrices (PIRES et al., 2002), increasing opportunities for human-rodent contact and viral transmission. In the Atlantic Forest biodiversity hotspot, hantaviruses are mainly associated with the black-footed pygmy rice rat, *Oligoryzomys nigripes* (hosts of JUQV genotype), and the hairy-tailed bolo mouse, *Necromys lasiurus* (host of ARQV genotype). Other sigmodontine rodents (Cricetidae: Sigmodontinae) (WAGNER; ELÍA, 2016), including at least one more species of grass mouse, *Akodon montensis,* have been found infected with hantavirus and likely play a role in transmission and maintenance of hantavirus genotypes in the Atlantic Forest (CHU; OWEN; JONSSON, 2011; DE OLIVEIRA et al., 2014; FIRTH et al., 2012).

An important landscape attribute that may influence incidence of a pathogen is the arrangement of the contact areas between hosts and humans (WILKINSON et al., 2018), since this may modulate the intensity by which the hosts use and move through the matrix. Landscape structure can be evaluated in different ways – such as forest cover, edge density, isolation and connectivity – which includes landscape diversity metrics, representing the combination and juxtaposition of different land cover classes as a proxy for habitat diversity, such as forest and agricultural areas. The response of fauna to spatial heterogeneity is still not clear, however a positive association between the suitability for generalist species of rodents and landscape diversity is reported (MASSA; TETA; CUETO, 2014; SILVEIRA DOS SANTOS, 2014). Rodent reservoir hosts of hantavirus seem to be negatively influenced by native forest cover (%), such as *N. lasiurus*, which is expected to thrive on agricultural land (PRIST et al., 2017). Intermediate levels of landscape diversity may reflect a combination of different habitats that can provide suitable areas for nesting and feeding, mainly for species that are not strictly forest-dwelling. For instance, rodents can nest in sugarcane and *Eucalyptus* plantations, where hantavirus disease transmission risk may increase for people that work or pass through these locations.

Here we investigate how potential hantavirus hosts within their mammal communities respond to landscape structure, climate and biodiversity patterns. We test four main hypotheses for explaining hantavirus host proportions: 1) there is a positive correlation with the amount of agricultural matrix; 2) there is a positive relationship with the total habitat diversity of the landscape; 3) that the absence of predators and large competitors (defaunation intensity (DIRZO et al., 2014)) and 4) local small mammal diversity would both increase hantavirus host proportions in rodent communities. We used geographically weighted regressions (GW) models to test if these relationships vary in space (see methods). We also explored the correlation between our modelled predictions of hantavirus host distributions and a vulnerability index of human populations to hantavirus infection based on public health surveillance data.

Methods

Study region and hantavirus hosts

We analyzed data from areas where target rodents were captured from a set of 283 inventories located within the Atlantic Forest (MUYLAERT et al., 2018b) available in the ATLANTIC series database (BOVENDORP et al., 2017). The ATLANTIC database is the most comprehensive and reliable data set of assemblages for small mammals in the Atlantic Forest – see https://github.com/LEEClab/Atlantic_series. The data were validated through taxonomic correction of reported species, which is crucial for Cricetidae rodents, because they can be misidentified (MÜLLER et al., 2013). We evaluated the distribution of potential hosts across sampled sites and did not run models for extremely rare species (S1 Fig). We included all rodents relevant for carrying hantavirus genotypes in the analyses, even when there was no evidence for human disease transmission in the Atlantic Forest, because absence of evidence of transmission does not mean evidence of absence. We also include the interface with vegetation types adjacent with the Atlantic Forest such as boundaries with Cerrado grasslands and Chaco wetlands.

The recognized reservoir hosts of pathogenic genotypes of hantaviruses that occur in the Atlantic Forest and its boundaries (S1 Fig) are *Necromys lasiurus*, *Oligoryzomys nigripes*, *Calomys callidus* (absent in ATLANTIC database), *Calomys laucha*, *Oligoryzomys moojeni* (absent), and *Oligoryzomys fornesi* (GUTERRES et al., 2015; KRUGER et al., 2015). Hantaviruses can also infect *Akodon montesis* and *Calomys tener* (SABINO-SANTOS JR, 2015), so we also included these species in models along with: *Oligoryzomys flavescens* (DELFRARO et al., 2003), which is linked to hantavirus transmission in Argentina (SUÁREZ et al., 2003) and Uruguay; *Oligoryzomys fornesi*, the presumed reservoir of ANJV in Amazon (GUTERRES et al., 2014), but also captured in Cerrado; *Calomys laucha* and *Calomys callosus*, that are considered reservoirs of pathogenic hantavirus in Paraguay (LANV) (BRASIL, 2014); *Akodon paranaensis* (GUTERRES et al., 2015) and *Akodon cursor* (commonly confounded with other *Akodon* species), important hantavirus hosts in Paraguay (BRASIL, 2014; PADULA et al., 2007); *Akodon azarae,* which is infected with PERV in Argentina, but with unknown pathogenicity in Brazil (BRASIL, 2014); *Oxymycterus nasutus*, a host for JUQV-ARAUV genotypes (DE OLIVEIRA et al., 2014); and *A. serrensis*, a host of JABV that can occur in high altitude grasslands and in Montane forests (TEIXEIRA et al., 2014).

Mapping procedure

Each landscape was mapped in land use and land cover classes with the most appropriate Google image from the start of sampling in QGIS v. 2.0 (QGIS DEVELOPMENT TEAM, 2015). Classes of land use were water, initial or medium growth forest, wetland, old growth forest, Cerrado, soil, soy, pasture, citrus, coffee, maize, sugarcane, other cultured crops, tree plantation (*Eucalyptus*), buildings (rural and urban), cloud and others (such as mining areas). Whenever there was doubt on visual interpretation of classes, we used SatVeg time series of spectral signatures to differentiate agricultural uses (https://www.satveg.cnptia.embrapa.br). The mapping and analyses were performed at a 1-km buffer radius from the centroid of the 283 sampling sites, with the minimum resolution for land use and cover analysis of 5 m in order to guarantee a map scale of 1:10,000. We calculated the area and perimeter of polygons using R (R CORE TEAM, 2016). We calculated the amount of each class divided by the area of buffer times 100 – i.e. % –, and edge density as the sum of the polygon's perimeter for each class divided by landscape area (m/m^2). Although we could not assess the accuracy of sampling site coordinates, the centroid of each landscape represented the most accurate measure of location coordinates from the dataset.

Landscape heterogeneity was used as a proxy for habitat diversity, and was calculated based on the presumed capacity of target rodent hosts to use resources outside forest fragments, in open agricultural areas, and other native vegetation areas (PRIST; D´ANDREA; METZGER, 2017). Shannon diversity index from Vegan package v. 2.4.2 (OKSANEN et al., 2011) was used to calculate habitat diversity in each landscape. The calculation included the amount of each one of the agricultural and native land cover classes mapped, and were also based on the 1 km buffer radius from the centroid of the 283 sampling sites. This extent has been shown to be relevant in landscapes with varying amounts of habitat for small mammal fauna (BANKS-LEITE et al., 2014; MELO et al., 2017). We did not include patch area effects in our models, since the major predictor of woodland small mammal species is habitat amount (MELO et al., 2017). Rainfall and average temperature were extracted from WorldClim's mean of monthly precipitation (in mm) and average monthly temperature (C°*10) (http://www.worldclim.org/), considering the average for area from each landscape unit.

Defaunation intensity

We conducted a literature search for studies of medium and large-sized mammals in the same or nearby localities in which we had found the assemblage of small mammals to assess their presence or absence. We also searched for papers from gray literature, and included inventories of medium and large mammals (LIMA et al., 2017). More information on calculations is provided in Bovendorp et al. (BOVENDORP et al., 2018). To calculate defaunation intensity for each site, we overlapped extent of occurrence maps from IUCN Red List website (IUCN, 2016) for 33 species of medium and large sized mammals belonging to Carnivora (23 species); Artiodactyla (nine species); and Perissodactyla (one species). The large mammal species used here were selected due their potential direct competition with and predation on small mammals. Ungulates can modify small mammal habitats by trampling and competing for food with small mammals while carnivores prey on small mammals (GALETTI et al., 2017; GALETTI; BOVENDORP; GUEVARA, 2015; KEUROGHLIAN; EATON, 2009). This information was used to calculate the defaunation intensity of medium and large bodied mammal for each site in our dataset using the defaunation index (GIACOMINI; GALETTI, 2013). We used the occurrence data to generate an expected medium and large mammal community. We calculated the defaunation index (DI) as follows

$$\text{DI=1} - \frac{\sum_{j}^{N} \text{BWES}_j}{\sum_{i}^{N} \text{BWES}_i}$$

where *N* is the total species richness in the community; *j* is the total species richness in the actual community composition; *i* is the total species richness in the potential community composition; *BWES* is the average body mass for each species of medium and large mammals. DI ranged from 0 (no defaunation) to 1 (completely defaunated).

Collinearity evaluation

We assessed the collinearity of the following predictors through Kendall's correlation (τ) analysis: small mammal local richness, defaunation index, temperature, rainfall, edge density of sugarcane, tree plantation, maize, pasture, and forest, land cover of sugarcane, tree plantation, maize, pasture, old growth forest, and habitat diversity. We considered suitable covariates to have pairwise τ values <±0.4 and with p-values >0.05 (S2 Fig). Rainfall was negatively correlated with temperature (τ = -0.46, p <0.05), and we kept rainfall as a predictor. Land cover of old growth-forest was negatively correlated with habitat diversity (τ = -0.69, p <0.05), so we kept habitat diversity. Regarding agricultural matrices, we kept the amount of pasture, sugarcane, tree plantation and maize. Edge density for most land cover types were correlated with land cover, so we kept land cover as the main predictor and dropped edge density from the set of predictors, as land cover is a more intuitive metric.

Model selection

After the selection of least correlated predictors, we checked for remaining collinearity by using the variance inflation factor (VIF). We found a small value (1.96) and proceeded with the following variables in the model selection procedure: small mammal local richness, defaunation index, rainfall, land cover of sugarcane, tree plantation, maize, pasture, and habitat diversity. Prior to analysis, we standardized covariates to zero (Z-score).

Spatial pattern can be a crucial determinant for species distribution, and should be incorporated as a potential factor influencing aspects of community composition and within a variety of contexts, especially when numerous sites across a biome are considered. For that reason, we conducted a comparison between models with and without geographically weighted terms. We iterated a forward algorithm for selecting geographically weighted models (GW models, (GOLLINI et al., 2015; LU et al., 2014)) based on our hypotheses via calibrating all the possible bivariate GW models by: 1) sequentially regressing a single predictor against each dependent variable; 2) finding the best performing models (minimum AICc values), and permanently including the corresponding predictor in subsequent models; 3) sequentially introducing a predictor from the remaining group predictors to construct new models with the permanently included independent variables, to determine the next permanently included variable from the best fitting model that has the minimum AICc value; and 4) repeating step 3 until all the variables are permanently included in the model. After that we selected the plausible models from where the algorithm kept the AICc values lowest. Local regressions for all covariates (a complete GW model, when all covariates are non-stationary predictors) might not be always meaningful or add relevant explanation (balanced with model complexity and parsimony). This means that not all factors meaningfully vary in space. When a covariate effect does not spatially vary in models, we call it a global (fixed) covariate, because it will have one slope (β) for the entire regression, no matter the spatial coordinate. Local regression coefficients provide local estimates for each response variable. When part of the model varies in space, we call it a mixed model with local and global covariates. After evaluating the lowest AICc model, we tested the hypothesis of non-stationarity for each model covariate via a Monte Carlo procedure ($N = 999$). When p-values were <0.05, we consider the term as varying in space (non-stationary) and re-run the mixed geographically weighted model maintaining as fixed the coefficients that were not significantly non-stationary. Thus, the mixed GW model is an intermediate between a global (fixed) model and a complete GW model. This step guaranteed parsimony for final model interpretation and generalization of predicted effects for the proportions. Thus, our final best supported model types were based on Monte Carlo estimated p-values.

Model calibration

We built models for each target species and category using GW model (GOLLINI et al., 2015; LU et al., 2014). These models allow us to explore responses influenced by regions, and where the residual variation tends to be less spatially autocorrelated (FORTIN et al., 2012). The GW models generate a formula for every sampling unit of the dataset incorporating the response and local predictors falling within a pre-defined bandwidth with a Gaussian function for the spatial decay in similarity. This can complicate generalization but can also be useful to address uncertainty or dynamic patterns. We defined the optimal distance using a calibration procedure. Since the Atlantic Forest is a large biome with more than 1 million km^2 (MUYLAERT et al., 2018b), but we have sparse and irregular sampling sites, we chose an adaptive bandwidth for each response variable (species and category, S1 Table), which suits irregular sample configurations. Adaptive bandwidths can ensure sufficient local information for each local calibration. During calibration we used Albers equivalent projection with datum SAD69 (EPSG 102033).

Known hosts, viral potential pathogenicity, and species

We used capture number and hantavirus host proportion in a community as proxies for local abundance of host species, and thus the model error terms and link function distribution were declared linear. Mean correlation between species abundance and their proportion was high, validating the use of proportion as proxies for abundance for each species (Kendall's τ = 0.62, se = 0.06, S1 Table). We calculated the proportion of hosts of potentially pathogenic hantavirus genotypes by summing the capture number of all potential host species dividing this by the total number of captures. We had categories of the proportions of hosts of ARQV, JUQV and LANV through summing their respective hosts values. We also divided all hosts between those for which the viral pathogenicity is known and all hosts, including those for which pathogenicity is unknown.

Since sampling effort is an important attribute for determining the number of captures in rodents (BOVENDORP; MCCLEERY; GALETTI, 2017), we included it in our models as a fixed effect. We could not run different sets of models for the subset of data from pitfall traps, live-traps, and when both were used, since the sample sizes for those methods greatly varied, with 13 sites using pitfalls, 211 used live traps and 59 both. Thus, we ran models for the 283 sites altogether regardless of capture method, but accounting for effort. We did not run models for extremely rare species, since model convergence is limited.

Reservoir host and vulnerability to hantavirus infection in humans

After evaluating models for each host type, we checked the nexus between predicted host proportion and local vulnerability to hantavirus infection using geostatistics. The local vulnerability to hantavirus infection index was calculated through a multi-criteria analysis using public health surveillance data developed by de Oliveira et al. (DE OLIVEIRA et al., 2015). This index classified the municipality as low (value = 1) to high (value = 5) in terms of vulnerability, based on weighted known risk factors from the literature: the human disease incidence of HCPS, economic gains from agriculture, municipal human development index and degree of urbanization. We computed values of vulnerability using NNJoin in QGIS v. 2.18. We compared the vulnerability index with generated rodent reservoir-hosts maps to investigate the nexus of rodent peak values and disease risk levels. Similarities between higher quantiles of predicted host proportions and higher quantiles of estimated vulnerability were estimated between layers generated by Getis Ord Gi (DEKA; MORSHED, 2018) geostatistics. We generated a hotspot map for the predicted proportion of hosts with potential to carry pathogenic hantavirus genotypes (reservoir hosts) and another hotspot map for the vulnerability to infection. We considered as clusters locations that matched high-high and low-low neighbor values within 95% confidence intervals for local G values. For those analyses we used the R-package "spdep" (BIVAND et al., 2018). To improve visualization, we used a Voronoi polygon transformation of the sampling locations. Different coding styles can be used to minimize topology-induced heterogeneity on heatmaps. For instance, style "W" (leverage on low connected sites), or "C" emphasis on hubs. Here we used style "S", which balances possible biases from those two (TIEFELSDORF; GRIFFITH; BOOTS, 1999).

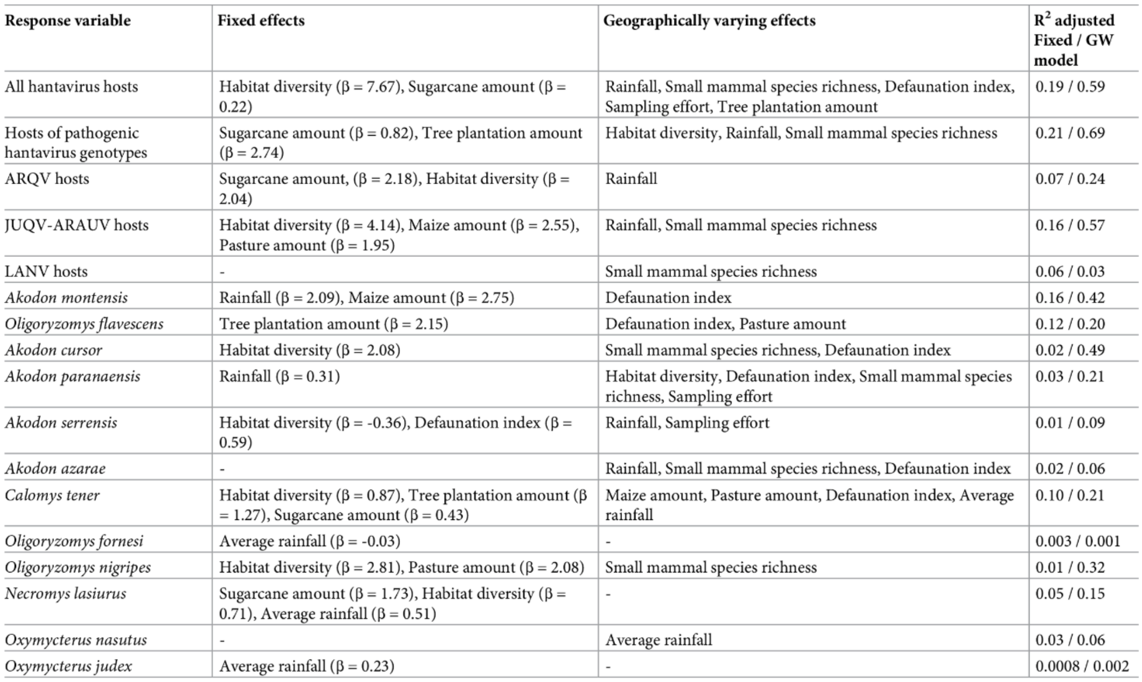
After building the hotspot maps, we tabulated the matching values. Then, we plotted a smoothed graph with the main spatial predictors of host proportion in the community (for pathogenic genotypes) and the vulnerability clustering levels (coldspots, hotspots and neutral spots of vulnerability to hantavirus disease).

Finally, maps were made using QGIS v. 2.18 with the layer sources being 1) Atlantic Forest limits from Muylaert et al. (MUYLAERT et al., 2018b) available at https://github.com/LEEClab/ATLANTIC-limits., and: 2) Bazilian states from the Instituto Brasileiro de Geografia e Estatística (IBGE) archive for 2015, available at ftp://geoftp.ibge.gov.br/organizacao_do_territorio/malhas_territoriais/malhas_municipais/municipio_2015/Brasil/BR/.

Results

The best supported model types for each species and group can be found in Table 1. The summary of the best-supported models and input data can be found in S2 Table. For the group of hosts that can potentiality carry pathogenic hantavirus genotypes the most plausible was a spatially weighted model with an adjusted $R^2 = 0.21$. Habitat diversity, rather than habitat type, most strongly influenced the proportion of pathogenic hantavirus hosts in the community. The median slope values for explaining the proportion of pathogenic hantavirus hosts spatially were 7.61 for habitat diversity, 4.08 for rainfall and 1.65 for small mammal diversity. The amount of forestry ($\beta = 0.82$) and sugarcane ($\beta = 2.74$) in the landscape had fixed positive effects (Fig 2).

Table 1. Optimum model covariates for each rodent host group and virus genotype in the Alantic Forest. Best supported model types for each of the response variables are given, selected based on a Monte Carlo procedure (999 randomizations). Fixed effects do not vary geographically, and estimates are shown. Geographically varying estimates are provided in S2 Table. R^2 adjusted values represent the value for a fixed model and a GW model, respectively.



Response variable	**Fixed effects**	**Geographically varying effects**	**R^2 adjusted Fixed / GW model**
All hantavirus hosts	Habitat diversity (β = 7.67), Sugarcane amount (β = 0.22)	Rainfall, Small mammal species richness, Defaunation index, Sampling effort, Tree plantation amount	0.19 / 0.59
Hosts of pathogenic hantavirus genotypes	Sugarcane amount (β = 0.82), Tree plantation amount (β = 2.74)	Habitat diversity, Rainfall, Small mammal species richness	0.21 / 0.69
ARQV hosts	Sugarcane amount, (β = 2.18), Habitat diversity (β = 2.04)	Rainfall	0.07 / 0.24
JUQV-ARAUV hosts	Habitat diversity (β = 4.14), Maize amount (β = 2.55), Pasture amount (β = 1.95)	Rainfall, Small mammal species richness	0.16 / 0.57
LANV hosts	-	Small mammal species richness	0.06 / 0.03
Akodon montensis	Rainfall (β = 2.09), Maize amount (β = 2.75)	Defaunation index	0.16 / 0.42
Oligoryzomys flavescens	Tree plantation amount (β = 2.15)	Defaunation index, Pasture amount	0.12 / 0.20
Akodon cursor	Habitat diversity (β = 2.08)	Small mammal species richness, Defaunation index	0.02 / 0.49
Akodon paranaensis	Rainfall (β = 0.31)	Habitat diversity, Defaunation index, Small mammal species richness, Sampling effort	0.03 / 0.21
Akodon serrensis	Habitat diversity (β = -0.36), Defaunation index (β = 0.59)	Rainfall, Sampling effort	0.01 / 0.09
Akodon azarae	-	Rainfall, Small mammal species richness, Defaunation index	0.02 / 0.06
Calomys tener	Habitat diversity (β = 0.87), Tree plantation amount (β = 1.27), Sugarcane amount (β = 0.43)	Maize amount, Pasture amount, Defaunation index, Average rainfall	0.10 / 0.21
Oligoryzomys fornesi	Average rainfall (β = -0.03)	-	0.003 / 0.001
Oligoryzomys nigripes	Habitat diversity (β = 2.81), Pasture amount (β = 2.08)	Small mammal species richness	0.01 / 0.32
Necromys lasiurus	Sugarcane amount (β = 1.73), Habitat diversity (β = 0.71), Average rainfall (β = 0.51)	-	0.05 / 0.15
Oxymycterus nasutus	-	Average rainfall	0.03 / 0.06
Oxymycterus judex	Average rainfall (β = 0.23)	-	0.0008 / 0.002

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Proportions of JUQV-ARAUV hosts were influenced by average rainfall (β_{min} = -9.41, β_{median} = -13.40, β_{max} = 16.88), small mammal species richness (β_{min} = -14.44, β_{median} = -1.56, β_{max} = 10.65), habitat diversity (β = 4.14), maize (β = 2.55), and pasture (β = 1.95) amounts. Proportions of ARQV hosts were influenced by sugarcane amount (β = 2.18), habitat diversity (β = 2.04), and average rainfall varying spatially (β_{min} = -3.7, β_{median} = 0.71, β_{max} = 3.44). The proportion of LANV hosts in community vary from negative to positive rainfall influence (β_{min} = -0.27, β_{median} = 0.001, β_{max} = 0.03).

Species varied in response to environmental and biotic preditors. *Oligoryzomys flavescens*, *O. nigripes* and *A. montensis* were positively influenced by rainfall and tree plantations. Maize and defaunation intensity also influenced *A. montensis* positively. *Necromys lasiurus* was positively influenced by sugarcane and habitat diversity, but was not affected by rainfall. *Akodon* species varied in their responses to predictors and, with the exception of *A. azarae*, all were best supported by mixed models. *Akodon montensis* proportions were explained by rainfall, maize, and defaunation. *Akodon cursor* and *A. paranaensis* proportions were influenced by defaunation intensity, habitat diversity and small mammal species richness. *Akodon paranaensis* and *A. serrensis* were also influenced by sampling effort, mostly negatively along a spatial gradient (β_{median} for *A. paranaensis* = -0.006; *A. serrensis* = -0.23). Defaunation affected *A. cursor*, *A. montensis* and *A. paranaensis* differently across space, from negative influence to positive influence (S3 Fig).

For *A. cursor* we see the same for northern and coastal areas, but a stronger positive effect in southeastern coastal areas, where more intensively defaunated areas tend to have higher predicted proportions of *A. cursor* in the community. For *A. montensis*, defaunation had a positive effect on their proportion in southeastern areas, and a negative effect in northern and coastal areas. *Akodon paranaensis*, a species restricted to southern areas, seems to be negatively influenced by defaunation intensity in its core range. Rainfall positively influenced *A. paranaensis* proportions in the community ($\beta = 0.31$).

Oligoryzomys flavescens was influenced by tree plantation ($\beta = 2.15$), pasture amount ($\beta_{median} = 0.04$, $\beta_{max} = 5.58$) and defaunation intensity ($\beta_{median} = -0.21$, $\beta_{max} = 0.23$). *Oligoryzomys nigripes* was influenced mostly by small mammal species richness, pasture amount and habitat diversity. *Calomys tener* was influenced by habitat diversity (0.87), tree plantation (1.27), sugarcane (0.43), maize (β_{min}-1.45, β_{median}= -0.41, β_{max} = -0.22), and pasture (β_{min} = -2.48, β_{median} = -0.45, β_{max}= 0.06) amounts, defaunation intensity (β_{min} = -2.79, β_{median} = -0.38, β_{max} = -0.02), and average rainfall (β_{min} = -2.36, β_{median} = 0.36, β_{max} = 1.25). *Oxymycterus nasutus* (linked to JUQV-ARAUV genotype), *A. azarae* (linked to PERV genotype) and the group of LANV hosts (*C. laucha* and *C. callosus*) were best explained by GW models.

When evaluating all hosts together, regardless of virus genotype they might host, habitat diversity, average rainfall, and small mammal species richness are the best predictors, varying spatially. The best-supported model for all hosts was a semi-parametric model, where the fixed effect was sugarcane, which positively influences host proportion (β = 0.22). Sampling effort consistently had a negative influence on hantavirus host proportion, emphasizing the nature of these rodents being common in degraded areas and being easily captured (even with little capturing effort) throughout the Atlantic Forest. The exception was in southern areas, where higher capturing effort led to the highest predicted proportions of hosts in the community (β_{min} = -6.79, β_{mean} = -3.40, β_{max} = 20.39).

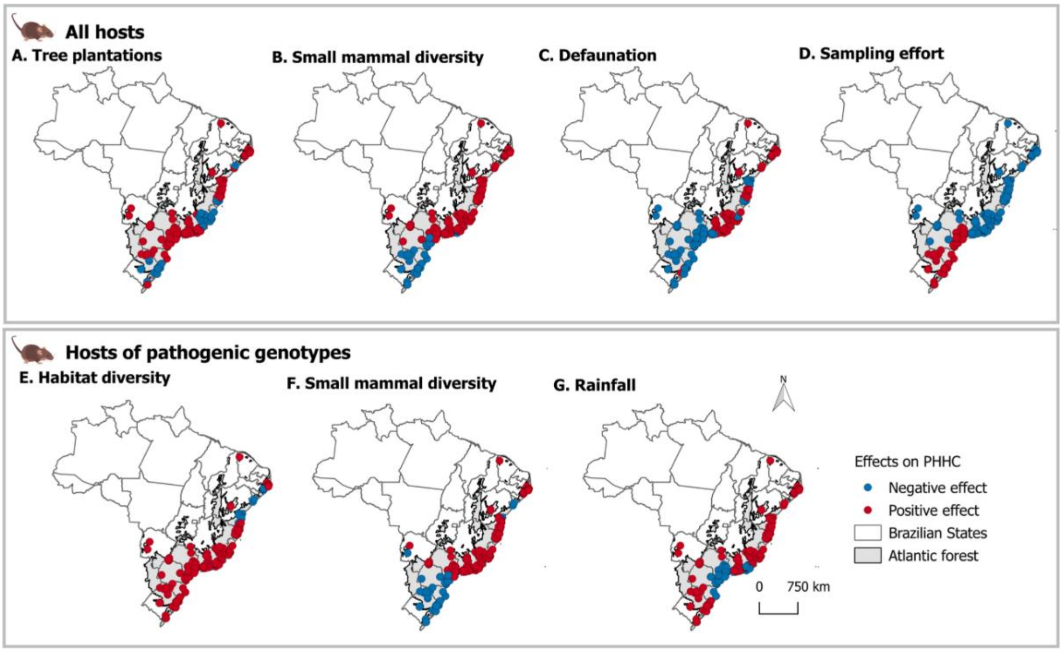


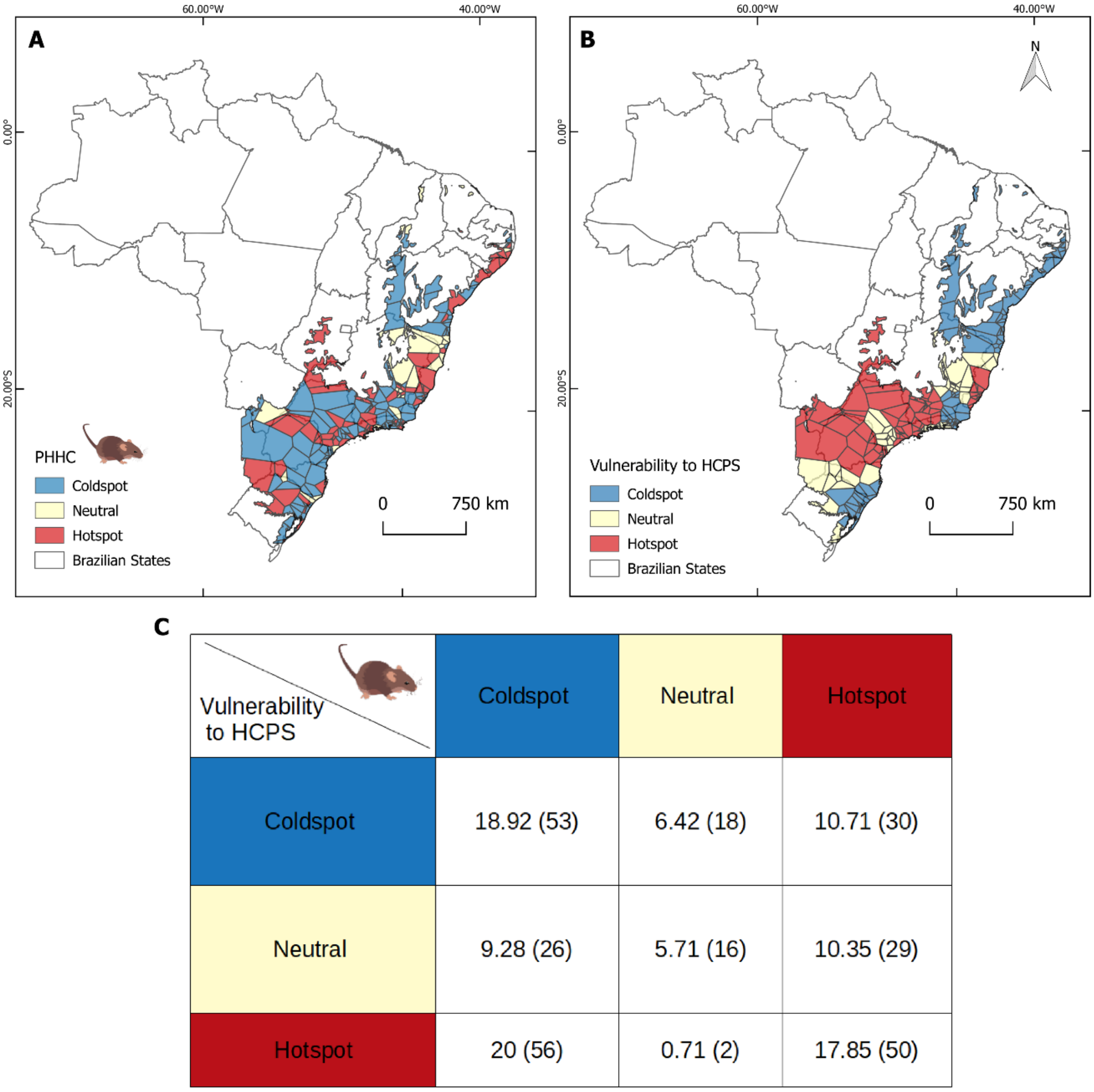
Fig 2. Predicted rodent hantavirus host proportion (PHHC) in the Atlantic Forest rodent community using selected mixed geographically weighted models. A-D: best supported predictors and their spatially varying values for known hosts of hantavirus genotypes (%); E-G: best supported predictors and their spatially varying values for hosts of pathogenic hantavirus genotypes.

Rainfall was an important predictor for *O. nasutus* and *A. azarae* (always positive, but varying in space), and small mammal species richness was the main predictor of these species. Defaunation had a negative influence on *A. azarae* proportions ($\beta_{min} = -0.25$, $\beta_{median} = -0.11$, $\beta_{max} = 0.06$). We could not fit models for *C. laucha, C. callosus, O. fornesi*, and *H. sciureus* separately because of the scarcity of capture data (less than five observations). *Necromys lasiurus* and *O. judex* proportions were best explained by fixed models, but with low adjusted R^2 of respectively 0.05 in fixed effect model versus 0.15 in GW model, and 0.008/0.002. Despite increased adjusted R^2 for the GW models, the observed spatial variation might be due to random noise and the low number of observations of this species (S1 Fig, and see estimated p-values at S2 Table). *Akodon montensis, C. tener, O. nasutus, O. judex,* and *O. nigripes* can be found in native vegetation areas but also on abandoned pastures and *Eucalyptus* forests [48]. *Necromys lasiurus* populations are positively influenced by habitat heterogeneity and a weak but positive effect of rainfall ($\beta = 0.51$) and sugarcane ($\beta = 1.73$). *Necromys lasiurus* proportions in the community peaked at intermediate to high levels of habitat heterogeneity at landscape scale. Local rodent diversity was not associated with *N. lasiurus* proportions.

Reservoir host and vulnerability to hantavirus infection in humans

We found significant clustering for low and high values of hantavirus host proportions and for the vulnerability index for hantavirus infection leading to HCPS (Fig 3). There was a 17% match between both hotspot maps, and 20% of non-correspondent coldspots and hotspots between maps. Both maps had similar total numbers of hotspot sites ($N_{\text{Vulnerability}} = 109$, $N_{\text{Hosts}} = 110$), but the host map had a higher number of neutral sites ($N_{\text{Vulnerability}} = 37$, $N_{\text{Hosts}} = 71$).

When we visualize the direct effects of habitat diversity, rainfall and small mammal richness on host proportion there is overdispersion (Fig 4), likely because the effect of predictors varies along the environmental and spatial gradients. However, it enables us to explore how host proportions change at different vulnerability clustering levels (hotspots, coldspots and neutral spots). In general, for hotspots the host proportion in community increased with habitat diversity and was higher in areas with intermediate values of rainfall. The highest proportions of hantavirus hosts were found in areas with low to mid-levels of rainfall (between 1500 and 2000 mm). For comparison purposes, the average rainfall in Brazil is 1761 mm (FAO, https://data.worldbank.org/indicator/AG.LND.PRCP.MM). Also, the host proportions in hotspots seem to increase in areas where small mammal richness is below 15 species.



Vulnerability to HCPS	Coldspot	Neutral	Hotspot
Coldspot	18.92 (53)	6.42 (18)	10.71 (30)
Neutral	9.28 (26)	5.71 (16)	10.35 (29)
Hotspot	20 (56)	0.71 (2)	17.85 (50)

Fig 3. Hotspot maps. A. Predicted pathogenic genotype hantavirus host proportions in the community (PHHC). B. Human vulnerability to hantavirus disease (HCPS) of municipalities within the Atlantic Forest. For comparison we used Voronoi polygon optimization based on coordinates of 280 sampling sites. **C.** Spatial matching (%) of hotspots and coldspots of both variables. Number of Voronoi polygons in each class is in parentheses.

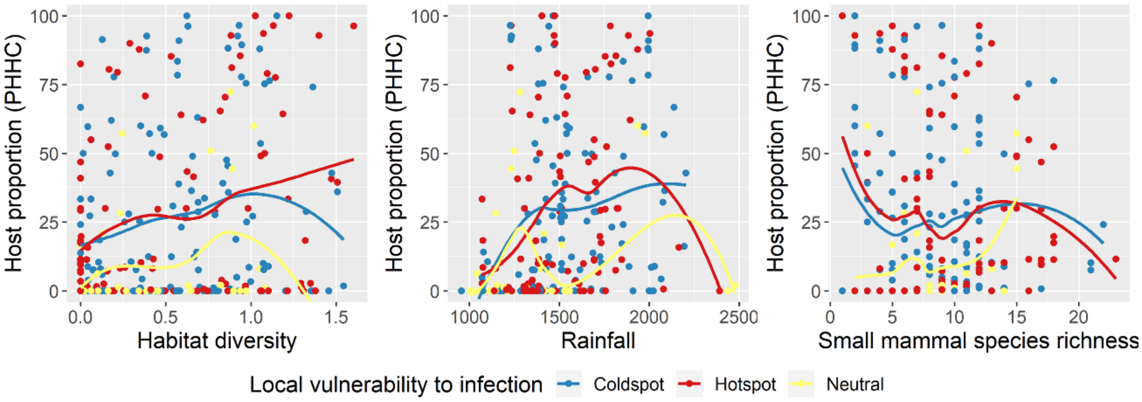


Fig 4. Best supported predictors from geographically weighted models explaining hosts of potentially pathogenic hantavirus genotypes proportions in rodent communities (PHHC) in the Atlantic Forest. The colored loess lines indicate the level of spatial clustering of vulnerability to hantavirus infection in humans.

Discussion

In this study we link biodiversity and hantavirus host proportions in local assemblages across the entire Atlantic Forest biome. Landscape level amounts of sugarcane and tree plantation positively influenced hosts of potentially pathogenic hantavirus genotypes (Hypothesis 1). Our models suggest an overall positive influence of habitat diversity and rainfall on pathogenic host proportions in the community (Hypothesis 2). Moreover, we discovered that the hantavirus host proportions in rodent communities are positively influenced by local species numbers in most of the Atlantic forest (Hypothesis 3), but that local species richness seems to be a diluting force in southern communities. Defaunation intensity had a geographically varying influence for known hantavirus hosts but did not seem to influence the proportion of the hosts for pathogenic viruses in local rodent communities (Hypothesis 4).

A recent model developed for predicting hantavirus case probability in the Atlantic Forest and Cerrado concluded that native forest cover did not predict case probability, but that sugarcane and social development index did (PRIST et al., 2016). Sugarcane amount was a good predictor of the proportion of hosts of potentially pathogenic hantavirus genotypes, such as *C. tener* and *N. lasiurus*. In a local study in the state of São Paulo, landscapes with higher amounts of sugarcane plantation had a higher prevalence of rodent hosts (SABINO-SANTOS JR, 2010). Landscape degradation negatively influences rodent diversity (ESTAVILLO; PARDINI; DA ROCHA, 2013), while sugarcane areas tend to have higher species dominance, particularly for habitat generalist species (SABINO-SANTOS JR, 2015). Anthropogenic landscape matrix use can differ among rodent species (ASSIS, 2014), where generalist hosts might use sugarcane plantations and other agricultural land types as corridors, for nesting and/or as foraging sites (PREVEDELLO; FORERO-MEDINA; VIEIRA, 2010), in contrast to forest specialist species (UMETSU; PARDINI, 2007). From our results, increased habitat diversity influences hantavirus host proportion non-linearly.

Here we used the proportion of rodents in the community as a measure of rodent density. We lack long-term sampling data for most species within the studied biome, which would allow measurement of both infection dynamics and host demography. However, we assume that a higher host proportion in the community can be a proxy for important areas for hantavirus disease, despite us not having the infection rates from the captured rodents. Although many rodent hosts are common—and this should lead to a balance in host proportions in similar communities across space—rodent prevalence might be very low (DE OLIVEIRA SANTOS et al., 2018; RABONI et al., 2012), and density can influence the infection dynamics of hantaviruses (LUIS; KUENZI; MILLS, 2018). However, other components that vary temporally, such as contact rates, density dependent infection transmission, and transmissibility (LUIS et al., 2010; LUIS; KUENZI; MILLS, 2018) were not assessed, limiting our power to infer transmission risk.

Here we show that landscape diversity has a positive influence on potentially pathogenic hantavirus host proportions in the Atlantic Forest rodent community, likely in part due to the increased availability of agricultural areas and other native habitat types, such as Cerrado, but this varies in space. Hosts are present on most of the gradient of habitat diversity, but peak with intermediate levels of rainfall, with a decreasing trend in their proportion where there is higher species richness (Fig 4).

The remaining fauna in degraded landscapes has the key characteristic of being miniaturized. Small rodents are less conspicuous, less hunted, have rapid reproduction cycles or large population sizes. The downsized fauna has the potential of performing important ecological processes, including ecosystem services and disservices, but with rapid change in its quality and quantity. Despite being known as "generalists", hosts of known hantavirus genotypes were influenced by defaunation intensity, with the relationship varying across the Atlantic Forest. *Akodon montensis*, *O. flavescens*, *A. cursor*, *A. paranaensis*, and *C. tener* were most influenced. Defaunation intensity positively affected *A. serrensis* and mostly positively affected *A. cursor*. Thus, the absence of predators and herbivores as competitors is beneficial for some hantavirus hosts. We still do not know to what extent this can also affect viral prevalence. Orrock et al. (ORROCK; ALLAN; DROST, 2011) found that predator richness reduces *Sin Nombre orthohantavirus* (SNV) prevalence among rodents, suggesting that the conservation of predators and biological diversity may have benefits on human health via the control of infectious diseases prevalence in wildlife. Although it is tempting to suggest that in our results the hotspots of hantavirus disease vulnerability in the Atlantic Forest may result from a lack of a complex network of interacting species (including predators), the mismatches of hotspots prevents us from making a definitive conclusion (Fig 3, Fig 4). The increased presence of small mammals reservoirs would tend to increase viral presence (GOODIN et al., 2006; MARTIN et al., 2012; PRIST; D´ANDREA; METZGER, 2017), and thus the risk of disease transmission. As our results show, hantavirus host proportion peaks when agricultural expansion is accentuated (Fig 2A), mostly in southern regions. In the southern region of Brazil, where the presence of rodents in grain crops and storage areas is frequent, hantavirus disease cases are the second highest nationally (PEREIRA et al., 2012). Since *N. lasiurus* often has high infection rates (SABINO-SANTOS JR, 2010; SUZUKI et al., 2004) we suggest that increased surveillance may be effective in southeastern areas, where they are present in the highest predicted proportions. Local rodent diversity was not associated with *N. lasiurus*, suggesting that landscape alteration is more important than other rodent species dominance effects in determining abundance. Indeed, in southeastern Brazil, it has been observed that *N. lasiurus* is the most abundant rodent in non-native grassland crops of *Brachiaria decumbens*, where the original vegetation was Cerrado (SABINO-SANTOS JR, 2010). A more detailed long-term period of monitoring is required to test those associations in detail (SUZUKI et al., 2004).

Our study has some additional limitations. First, it was developed with secondary data and has spatial gaps that can lead to uncertainty regarding habitat selection. Low capture efforts were sufficient to detect most of the species in our dataset, but some species are inherently rare in the Atlantic Forest, such as open area specialist rodents which are more common in Central Brazil in a typical savanna-like biome. Surveys were conducted with different sampling efforts, and this was taken into consideration in our models as a fixed variable. Seasonality seems to be an important factor influencing rodent abundance, as well as viral prevalence, and this was not accounted for in our study. For instance, Luis et al. (LUIS et al., 2010) demonstrated that seasonality has a great influence on the abundance of *Peromyscus maniculatus*, the sigmodontine rodent host of SNV in Montana, USA; likewise, the abundance of small wild mammals is highly associated with the dry season in an agricultural system within the Atlantic Forest (D'ANDREA et al., 2007). Importantly, novel questions arise from our results, especially relating to the coexistence between host species in a certain assemblage. How rodents share space and resources, and whether infection spillover risk reaches a threshold are open questions.

There was a weak correspondence between our model of hantavirus host proportions and observed hantavirus infection rates in people, however our hotspot analysis points towards important zones, such as north of the State of São Paulo and southern interior regions, in which spillover to humans is most likely to occur if no prevention is applied. Since 1993 almost 2,000 hantavirus cases have been reported across most Brazilian states. Santa Catarina State, in southern Brazil presents the second highest incidence of the disease. Southeastern Atlantic Forest is the most vulnerable area within the biome in Brazil. This information helps to inform surveillance and prevention of hantavirus disease risk and contributes to the understanding of potential factors influencing disease transmission risk.

Overall, we found that there is a strong effect of space and land use change influencing hantavirus host assemblages at the landscape level across the entire Atlantic Forest. In the central-north areas of the State of São Paulo, one of the hotspots for hantavirus disease (Fig 3B), the most common hosts are *N. lasiurus, O. nigripes* and *A. montensi*s (SUZUKI et al., 2004). Rodents with diet plasticity such as *N. lasiurus* [69,70] and the ability to adapt to disturbance in native ecosystems can rapidly decrease the distance, and thus increase interactions, between humans and the wildlife hosts. This may have further implications, since it increases the probability of human contact with infected rodent excreta.

Hantavirus disease risk is detected in areas populated more densely by reservoir-hosts, as described here in the areas of hotspots convergence between vulnerability to disease and host proportion in community. However, the presence of hosts acts as a simple proxy for the distribution of their pathogens [72] and our results show that defaunation leads to greater dominance of hantavirus hosts in communities of the northern parts of Atlantic Forest, while small mammal richness is associated to reduced dominance of hosts of pathogenic hantavirus genotypes in southern regions. These findings do not inevitably mean more disease risk for people in northern areas (Fig 4), because the prevalence of infection is not necessarily proportional to the community structure. Thus, we should further evaluate infection dynamics in maintenance communities. For example, one study identified a high abundance and broad distribution of suitable hosts with no detection of infection in Rio de Janeiro (DE OLIVEIRA SANTOS et al., 2018). Investigating the effects of other biotic factors on virus prevalence across different host populations would also help us to understand whether hantavirus pathogenic genotypes are subject to a dilution effect (LUIS; KUENZI; MILLS, 2018). Importantly, if there is a dilution effect, then conservation efforts will work synergistically to maintain biodiversity and reduce disease prevalence.

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Supporting Information

Table S1. Correlation between the proportion of hantavirus host in a community (PHHC) and number of captures. All correlations were significant (p <0.05) and positive and thus we used proportion in community as the response variable. The adaptive bandwidth used for geographically weighted models and semi parametric models (mixed) are shown. Adaptive bandwidths are the number of neighbors included for local spatial regressions.

Response variable (PHHC)	**Kendall's correlation**	**Optimum adaptive bandwidth**
Assemblage of Hosts of potentially pathogenic hantavirus genotypes: *Necromys lasiurus, Oligoryzomys nigripes, Akodon montensis, Calomys tener, Oligoryzomys fornesi, Oxymycterus nasutus, Oxymycterus judex, Calomys callosus, Calomys laucha, Oligoryzomys flavescens*	0.42	25
Assemblage of All Hosts: *Necromys lasiurus, Oligoryzomys nigripes, Akodon montensis, Calomys tener, Akodon paranaensis, Akodon cursor, Akodon serrensis, Oligoryzomys fornesi, Oxymycterus nasutus, Oxymycterus judex, Holochilus sciureus, Calomys callosus, Calomys laucha, Akodon azarae, Oligoryzomys flavescens*	0.37	27
Assemblage of Hosts of AQAV: *Necromys lasiurus, Calomys tener*	0.58	52
Assemblage of Hosts of JUQV ARAUV: *Oligoryzomys nigripes, Akodon montensis, Oxymycterus nasutus, Oxymycterus judex, Akodon paranaensis*	0.29	25
Assemblage of Hosts of LANV: *Calomys laucha, Calomys callosus*	0.46	182

Response variable (PHHC)	**Kendall's correlation**	**Optimum adaptive bandwidth**
Akodon azarae	0.76	182
Akodon cursor	0.33	27
Akodon montensis	0.51	25
Akodon paranaensis	0.64	39
Akodon serrensis	0.6	55
Calomys tener	0.5	53
Necromys lasiurus	0.45	66
Oligoryzomys flavescens	0.79	53
Oligoryzomys nigripes	0.27	39
Oxymycterus judex	0.41	281
Oxymycterus nasutus	0.8	182

Table S2 (.XLS). Best supported models and their statistical descriptors.

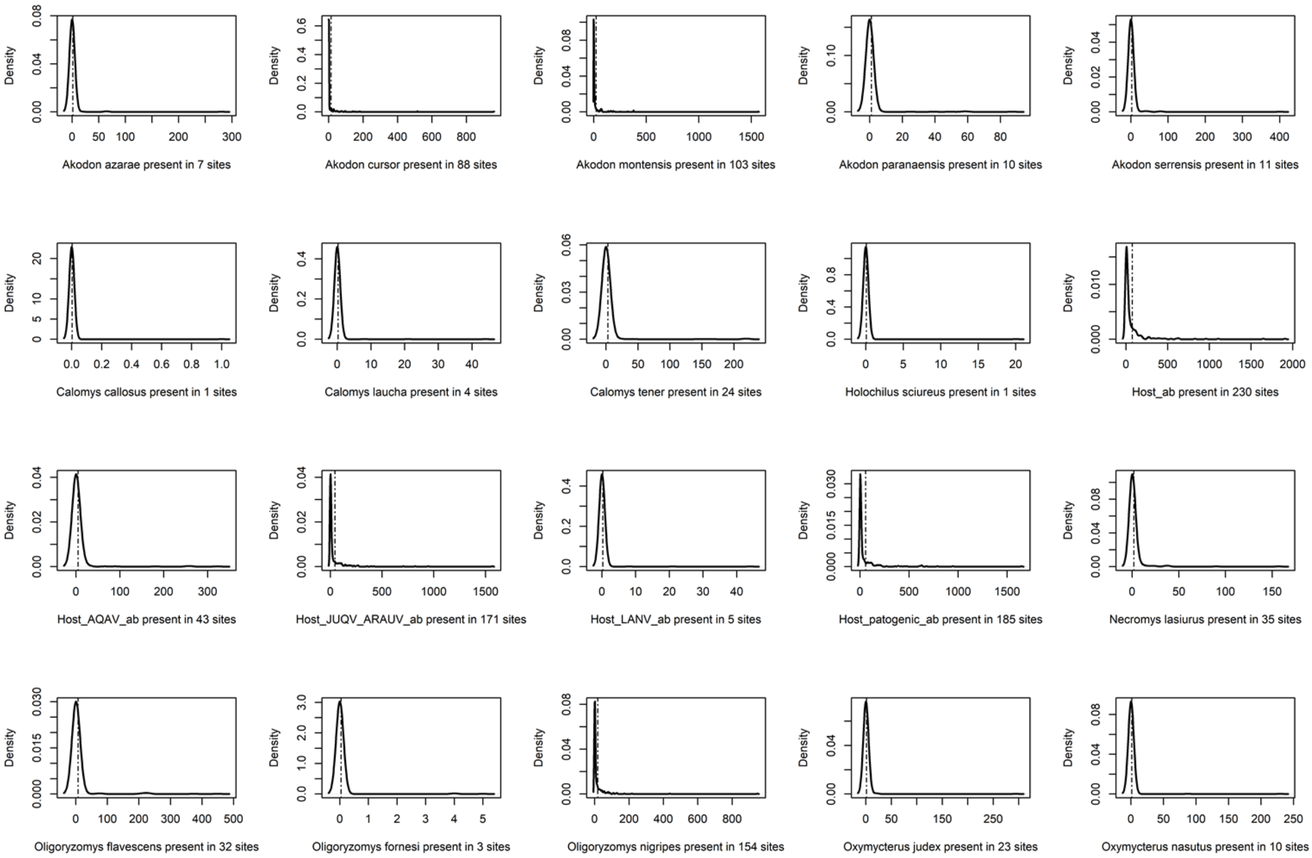

Fig S1. Capture distribution of the main potential hosts of hantavirus within Atlantic Forest sites. Number of captures are in y axes; dashed lines show the mean value of captures and at the bottom how many sites the species was present.

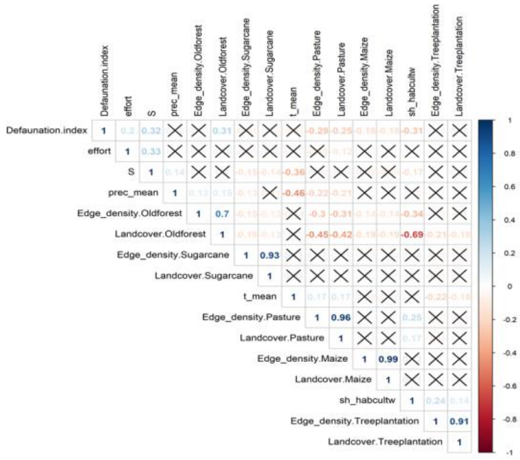

Fig S2. Model predictors selection based on Kendall's τ using observational data from Atlantic Small mammal dataset. Crosses indicates non-significant correlations (p<0.05). We only used predictors with correlations lower than 0.4 in magnitude in the same model. S = small mammal local species richness, prec_mean = average rainfall, t_mean = average temperature.

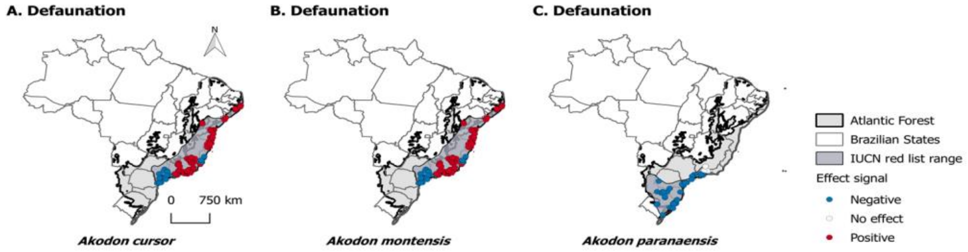

Fig S3. Fig. Geographically weighted effect of defaunation intensity of medium and large sized mammals on known geographic ranges of extant *Akodon* species proportion in the rodent community within Atlantic Forest. A. *Akodon cursor*, B. *Akodon montensis* and C. *Akodon paranaensis* proportions as a function of defaunation. Ranges were downloaded from IUCN red list website [44].

Capítulo 4

Spatial temporal dynamics of hantavirus cardiopulmonary syndrome transmission risk in Brazil

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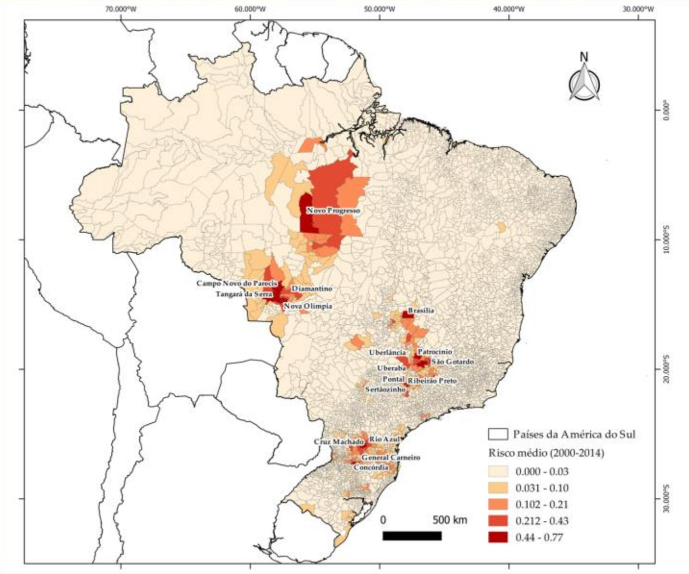
Mapa de risco para a hantavirose no Brasil

A hantavirose é causada pelos hantavírus, vírus que são transmitidos para o ser humano a partir do contato com excretas de certos **roedores infectados** (hospedeiros do vírus)

Mapas de risco podem ser usados para ajudar a alocar medidas preventivas em saúde pública



Áreas nativas, milharais e canaviais aumentam o risco de hantavirose, principalmente por promover a interação entre as pessoas e roedores

O planejamento do uso da terra deveria considerar medidas que evitem o aumento do risco de doenças

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Article

Spatiotemporal Dynamics of Hantavirus Cardiopulmonary Syndrome Transmission Risk in Brazil

Renata L. Muylaert [1,2,*], Gilberto Sabino-Santos Jr [3,4,5], Paula R. Prist [6], Júlia E. F. Oshima [1], Bernardo Brandão Niebuhr [1,7,8], Thadeu Sobral-Souza [9], Stefan Vilges de Oliveira [10], Ricardo Siqueira Bovendorp [11], Jonathan C. Marshall [2], David T. S. Hayman [2] and Milton Cezar Ribeiro [1]

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Abstract: Background: Hantavirus disease in humans is rare but frequently lethal in the Neotropics. Several abundant and widely distributed Sigmodontinae rodents are the primary hosts of *Orthohantavirus* and, in combination with other factors, these rodents can shape hantavirus disease. Here, we assessed the influence of host diversity, climate, social vulnerability and land use change on the risk of hantavirus disease in Brazil over 24 years. Methods: Landscape variables (native forest, forestry, sugarcane, maize and pasture), climate (temperature and precipitation), and host biodiversity (derived through niche models) were used in spatiotemporal models, using the 5570 Brazilian municipalities as units of analysis. Results: Amounts of native forest and sugarcane, combined with temperature, were the most important environmental factors influencing the increase of disease risk. Population at risk (rural workers) and rodent host diversity also had a strong positive effect on disease risk. Conclusions: Land use change—especially the conversion of native areas to sugarcane fields—can have a significant impact on hantavirus disease risk, likely by promoting the interaction between the people and the infected rodents. Our results demonstrate the importance of understanding the interactions between landscape change, rodent diversity, and hantavirus disease incidence, and suggest that land use policy should consider disease risk. Meanwhile, our risk map can be used to help allocate preventive measures to avoid disease.

Keywords: land use change; emerging diseases; public health; polygon-based analysis; approximate Bayesian inference; latent Gaussian models; integrated nested Laplace approximations; zero inflation

1. Introduction

Land use change can influence the spread and distribution of infectious diseases, especially emerging zoonotic ones [1], such as hantavirus disease, caused by a nearly globally distributed set of *Orthohantavirus* genotypes (hereafter hantavirus) [2] (family *Hantaviridae* [3,4]). In Brazil, hantavirus disease is manifested in humans as a cardiopulmonary syndrome (HCPS) [5], and it is considered a problem due to its high mortality rates [6]. The risk factors for human hantavirus infection include direct exposure to rodent hosts' blood, saliva and excreta [7], which is a consequence of contact during agricultural or leisure activities [8,9].

There is evidence that agriculture expansion—particularly of sugarcane plantations— influences hantavirus disease risk in southeastern Brazil [10]. Sugarcane, planted pasture, and *Eucalyptus* plantations may increase HCPS outbreaks [11]. Maize plantations were linked to hantavirus disease in previous works [12,13]. Human occupied areas in proximity to native vegetation, however, also tend to present a higher disease risk because they benefit rodent hosts and allow higher probability of local human encroachment and contact [14,15].

There were notable changes in Brazilian land use from 1940 until recently [13]. Besides deforestation, there was an increase in sugarcane and maize plantations, expansion of soybean areas, and intensification in the use of pre-existing pasture areas. These changes may have expanded the distribution of rodent host species, as several of them can utilize multiple habitats [16], and consequently increased human exposure to hantaviruses.

Hantavirus disease in different localities is apparently caused by only one virus that infects people in each region and the virus is typically linked to a main opportunistic host species. If there is only one competent host species, greater species richness possibly dilutes transmission to humans by increasing non-competent host contacts. In this one-species, one-host situation, the dilution effect will reduce the chance of transmission through non-competent host contacts.

Therefore, the dilutive effect on the predominant viral lineage increases with the abundance and number of other hosts to reduce the chance of viral transmission. Contrastingly, if multiple competent hosts exist, increased diversity may increase risk. The virus-host species specificity paradigm does not seem to be completely true for hantaviruses in South America [17]. There are at least three *Orthohantavirus* species known to have the potential to cause disease in humans in Brazil (*Andes orthohantavirus*—ANDV, *Laguna Negra orthohantavirus*—LANV, and *Rio Mamoré orthohantavirus*—RIOMV, a LANV variant) and they can be detected in more than 20 rodent species in South America, with considerable range overlap between some of them [17]. Therefore, it is necessary to investigate several rodent species beyond the known individual reservoir host species [10,18]. Mapping the areas where hantavirus host species are distributed and may concentrate different hantavirus genotypes is a priority for disease surveillance [9]. There have been recent attempts to understand HCPS distribution regionally [19] and nationally [12], including using expert opinion approaches to develop and analyze vulnerability measures [6,20]. However, to our knowledge, investigations modeling the disease risk for large regions are still missing in the Neotropics, particularly for Brazil. These studies are important to help understand the drivers increasing hantavirus risk and to guide educational and preventive measures.

The transmission dynamics of hantaviruses to humans and disease surveillance is a complex process, especially in the hyper-biodiverse South America [21], for which case notifications depend on several steps. The rodent host needs to occur in a certain location, and, for the infection to exist, rodent populations may need to be above a certain abundance threshold [11]. Then excreted virus particles in substrates (e.g., soil) must be aerosolized under specific environmental conditions, infecting humans through inhalation of viral particles. Thereafter, susceptible humans must develop disease and present themselves to clinics with clinical signs and symptoms that must be diagnosed as hantavirus, prior to a compulsory report being provided to the Ministry of Health.

We believe that areas with higher numbers of at-risk people (adults working in rural areas) in the State of São Paulo [6] have higher disease risk due to the increased probability of exposure to pathogens. We expect that increased proportions of rural workers increases hantavirus disease risk. We also expect that areas of moderate to high levels of rainfall have increased hantavirus disease incidence as an indirect effect on host species population growth (an increase in density—bottom up regulation [11]). Rodent populations benefit from mild temperatures [22] and virus viability in the environment seems to be higher in mild temperatures (virus is inactivated after 24 h in temperatures ≥ 37 °C) [23].

Here, we aimed to (1) generate disease risk maps using the presence and the number of notified hantavirus disease cases over a 24 year data series as response variables, and the following hypothesized risk factors as predictor variables

(Figure S1): social vulnerability, climate, land use change, and biodiversity; and (2) evaluate the ability of the best supported model to predict new confirmed cases in humans, using subsets of our data series. Our expectations were that land use change—especially the agricultural expansion of sugarcane and maize—and social vulnerability are the main predictors of disease risk. We also expect that host diversity positively influences the probability of disease cases in humans. This is the first study, to our knowledge, that considers all these components together. We consider that this is an important step to be taken to investigate HCPS dynamics, since the spatiotemporal analysis can elucidate how multiple factors modulate the distribution of the disease.

2. Materials and Methods

2.1. Hantavirus Disease Cases and Population Data

Data on human notified cases from 1993 to 2016 were provided by the Ministry of Health (http://www2.datasus.gov.br/DATASUS/index.php?area=0203&id=29878153). From 1993–1999, all cases were reported as notified (not necessarily laboratory confirmed). After 2000, notified and laboratory confirmed cases were available, and we used this second set of data here. A zero inflated modelling approach was used using two response variables: (1) the presence and (2) the counts of positive cases in a municipality in one year, using the data from Brazilian Ministry of Health for the period. Geographical precision of cases is reported at the municipality level because of the privacy policy for infected people. We used as the spatial reference the polygons of 5570 Brazilian municipalities taken from 2015 (after removing two lakes) from the Instituto Brasileiro de Geografia e Estatística available at (ftp://geoftp.ibge.gov.br/organizacao_do_territorio/malhas_territoriais /malhas_municipais/municipio_2015/Brasil/BR/).

All covariates were aggregated to the municipality level. We extracted data directly from Brazilian government databases (rural workers data) or applied zonal statistics for other data sources (Table S1), using the average or amount (%) for the environmental predictors and counts of species for the biodiversity component The selected indicator for social vulnerability was "population at risk", which was the number of rural workers 18 years old or older. Population censuses were conducted at three time periods (1991, 2000, and 2010). Since we had three censuses per municipality in the study time period, we used the function approxExtrap to estimate population growth by using linear interpolation of the number of rural workers. All covariates were centered to zero, by subtracting the mean from each value and dividing by the standard deviation.

2.2. Potential Host Richness

We define hosts as the rodent species which may contribute to the maintenance of hantavirus infection. We selected the following species after evaluating the availability of occurrence data for modeling: *Akodon cursor*, *Akodon montensis*, *Calomys tener*, *Holochilus sciureus*, *Necromys lasiurus*, *Oligoryzomys eliurus* [24], *Oligoryzomys fornesi*, *Oligoryzomys microtis*, *Oligoryzomys nigripes*, and *Oxymycterus dasytrichus*. We used as predictors the count of unique host species (host richness) per municipality.

We spatially predicted the occurrence of the main hantavirus hosts in Brazil using Ecological Niche Models (ENMs) [25]. The list of target species used the most recent reviews on rodent host data [17,21]. Rodent species occurrence data was mined from PREDICT (https://www.usaid.gov/news-information/fact-sheets/emerging-pandemic-threats-program), Species Link (http://www.splink.org.br/), Vert Net (http://vertnet.org/), Cerrado small mammals [26], and Atlantic small mammals [27]. Data mining was finished on August 10, 2018. We filtered the number of records to one per cell (1/km^2) for each species. We calculated habitat suitability for each rodent species that we managed to have enough records ($n = 10$) after applying a geographical filtering. The modelling spatial extent was defined as the region that includes all Brazilian biomes: Amazônia, Cerrado, Atlantic Forest, Caatinga, Pampa, and Pantanal. We added a buffer of 220 km around the species occurrence points found for each species to avoid problems on the border of predictions [28]. Climate predictors were downloaded as raster files delimited by the area of each species occurrence plus a 220 km buffer. Climate predictors for the ENM were selected with a factorial analysis of Worldclim 2.0 climatic variables (http://www.worldclim.org/bioclim) over the extent regions (~1 km spatial resolution). We built ENMs using four algorithms [29]: SVM [30], Bioclim [31], MaxEnt [32], and Gower distance [33], since ensemble forecasting approaches produce stronger predictions and are considered a useful framework to account for uncertainties in model projections [12]. Resampling of data points was conducted with bootstrapping with a convergent threshold of 10^{-5} considering 10,000 background points. To evaluate model performance, we randomized the occurrence data into 75%:25% train:test samples to calculate the True Skill Statistics (TSS) and the Area Under the Operator Curve (AUC) [34] for each model. We used expert opinion for selecting the most realistic maps, using the weighted suitability based on the best-supported models (TSS > 0.5).

Threshold values were calculated to transform each of the model predictions (probabilities, distances, or similar values) to a binary score (presence or absence of each species). We generated the maps based on maximum specificity and sensitivity thresholds at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) was highest. After selecting the best supported ENMs we plotted the binary maps based on 1) the lowest presence threshold (LPT) of observed presences and 2) on the 10th percentile of the LPTs, and asked for expert opinion. After selecting the best maps for each species, we calculated the sum of presences of each host per pixel summing the binary maps. The overlay of species layers resulted in a final map of host–species richness. Then, we derived zonal statistics based on the host species map for the Brazilian municipalities' shapefile, calculating the predicted host richness per municipality.

2.3. Land Use and Climate

For calculating the amount (%) of pasture and grasslands we used the compiled Brazilian Historical Agricultural Land Use database [13] (see data sources at Table S1), which covers most of the time series (1993–2014). From this dataset we extracted sugarcane, maize, planted pasture, and native pasture land-use classes per municipality per year. Forest and forestry amount per municipality were calculated with Mapbiomas collection 2 for 2000–2016 (www.mapbiomas.org). We made a mosaic raster from Mapbiomas 2 using the codes 1 to 8 as "native forests", which produced binary maps of forests from 2000 to 2016. We did the same for forestry (mostly *Eucalyptus* and *Pinus* plantations) using the code 9. Then, we extracted the amount (%) of each of those land use classes in each municipality. Rainfall data was extracted from Climate Hazards Group Infrared Precipitation with Stations (CHIRPS) [35], and surface temperature data from NOAA Merged Land Ocean Global Surface Temperature Analysis Dataset [36]. We calculated average annual rainfall (mm) from monthly data, and for temperature we used average annual temperature (°C*10). Zonal statistics for municipalities were calculated from custom functions available at https://github.com/LEEClab/GeneralizedZonalStats. We used the WGS 84 coordinate reference system throughout and kept the original spatial resolution of data (Table S1).

2.4. Spatiotemporal Models

We evaluated the distribution of hantavirus disease cases across space and time to select the most appropriate likelihood distributions used in the models. We did that by calculating the proportion of zeros in the dataset. To our knowledge, transmission between humans has not been reported for hantavirus genotypes from Brazil [37]. The absence of human-to-human transmission helps keep the disease rare. Modeling a rare and emergent disease is challenging, but given the size of the dataset and number of cases ("successes"), it is possible to fit comprehensive models to it. For instance, Prist et al. [10] had 1.6% "events" in São Paulo State and it was possible to infer risk with considerable accuracy. We decided to use data from 2000 onwards, from where the consistency of case presences (more than 1%) allowed us to model the events. The presence of cases in a municipality from 2000–2014 (i.e., 15 years) in 5570 municipalities is equivalent to 1.1%, where a case was present 958 times over 83,550 observations. We used the "zeroinflatedpoisson0" distribution for the zero truncated model

[38]. We used data from 2000–2014 to fit the model and data from 2015–2016 for checking the correspondence between predictions and observed data not included in the model.

We decided to use a zero inflated approach, considering two models: (1) a model containing a binomial distribution to estimate the probability of having any case in a municipality (risk), using presence or absence of cases as response variable; and (2) a zero-truncated Poisson model for the count data, where we only use as the input data observations in municipalities where the number of cases were different from 0 as response variable. The covariates used in both models were the same (see Figure S1). We verified the model sensitivity using the most recent covariate data and new case data, corresponding to 2015–2016. Prior to model building, we checked for correlation between model predictors and variance inflation factors (Figure S2). We ran models with the components based on Figure S1. We set model parameters with non-informative priors for all covariates.

Municipalities or political limits could be used in our analyses, but careful interpretation of model predictions should be made because of the bias of using municipality limits at data boundaries. A stratified spatial autocorrelation Moran's I for each year was applied for data exploration (Table S2). Then, we created a default neighbor list object and graph from the polygon's shapefile containing the spatial interaction among the municipalities. We used a second-order random walk as the temporal term (rw2) and a Besag iCAR spatial model, which is able to cope with irregularly spaced data [39]. To reduce model complexity and avoid computational limitations, interaction terms were not included.

We inspected the model fit [39] using uncertainty calculations and the conditional predictive ordinate (CPO) values as a measure of model adequacy. CPO is a type of cross-validation procedure that ranges from 0 to 1 for each observation. If CPO values were inadequate, an optimization of the model was conducted to improve estimates using inla.cpo. The uncertainty in risk predictions was calculated based on the amount of variation of 95% highest and lowest credible intervals from the posterior mean. All model response variables used were related to data from 2000–2014. After diagnosing the spatiotemporal models (a model containing a Bernoulli component and a model containing a truncated Poisson component), we applied them to new data for covariates from 2015–2016. This allowed us to assess the model validation [40].

For the spatial analysis and raster processing we used Python 2.7 [41], GRASS GIS 7.2 [42] and QGIS 2.18 [43]. For ENMs' development we used the package *dismo* [44] and for spatiotemporal model building we used the package INLA 19.01.24 [45,46] in R 3.5.1 [47]. Code developed for data analyses are available at a public repository (https://github.com/renatamuy/Muylaert_et_al_2019). Coefficient plots were created using coefINLA (https://github.com/hesscl/coefINLA).

3. Results

3.1. Hantavirus Disease Cases and Population Data

Overall, in the time period investigated, there was intense land use change in Brazil and also an increase in the number of HCPS cases (Figure 1, Figure S3). Cases were reported in all major regions of the country, but most cases were reported in central and south Brazil (Figure 2a), where host richness values were also high (Figure 3). Population at risk (the number of rural workers) positively influenced both number of HCPS cases in a municipality and disease risk (Figure 4, Figure 5).

Table S5 shows the average and range values for each fixed covariate. There was a clear increase of sugarcane, a decrease in number of rural workers through time (rural exodus), and a slight increase in forestry and decrease of pasture and maize amounts. The amount of forest also varied through time, as did temperature and rainfall. The least dominant culture was forestry, never reaching more than 2% on average, while pasture reached more than 20% on average, considering all municipalities in the country.

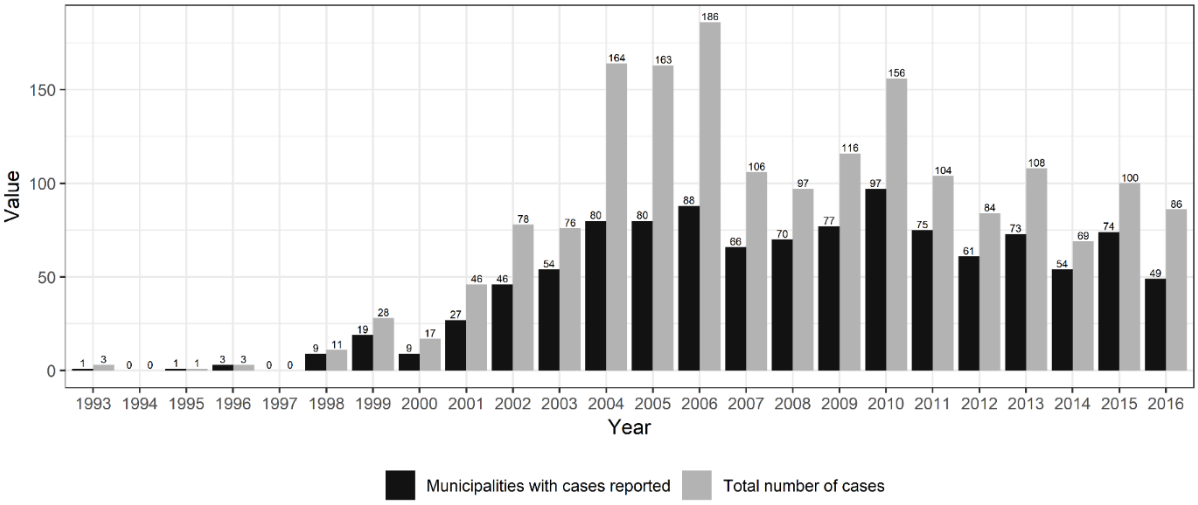
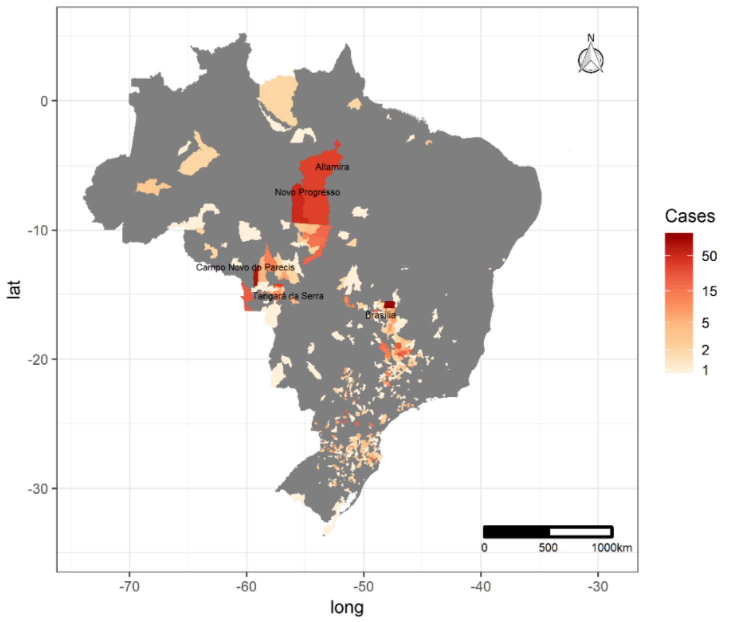


Figure 1. Hantavirus disease cases in Brazil. Data were downloaded from www.datasus.gov.br. Data from 2016 was updated in January 2019.

(a) Cases (1993-2016)



(b) Risk

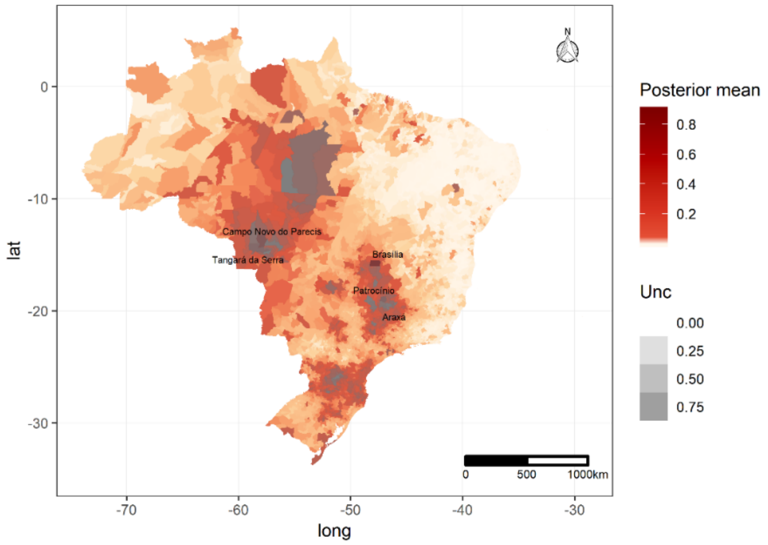
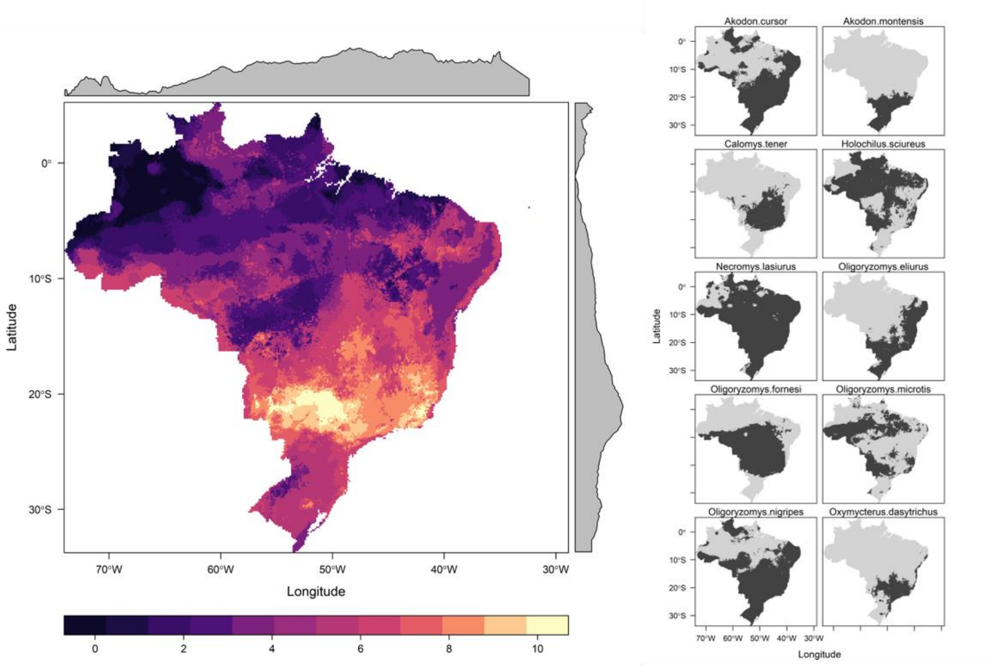


Figure 2. Hantavirus disease distribution in Brazil. (**a**) Observed values from 1993–2016, highlighting the municipalities with largest number of cases. Grey areas are municipalities with no notified cases; (**b**) Expected values for the probability of hantavirus disease in humans, predicted by a spatiotemporal model containing forest, climate, and social vulnerability, with uncertainty as transparency levels (Unc) based on the variation of credible intervals. The top five municipalities in terms of risk per year are highlighted. See the risk map without the uncertainty layer in Figure S4.



(a) (b)

Figure 3. Distribution of potential hantavirus hosts in Brazil: (**a**) Richness of potential hantavirus hosts in Brazil. Lighter colors represent more hosts. The grey areas represent variation in pixel counts per latitude and longitude. (**b**) Binary maps generated by Ecological Niche models with the black areas indicating higher habitat suitability for each modeled rodent species.

Figure 4. Scatterplot with the number of HCPS cases observed and predicted by a zero truncated Poisson model. Each point represents the number of hantavirus disease notified cases in a municipality in one year.

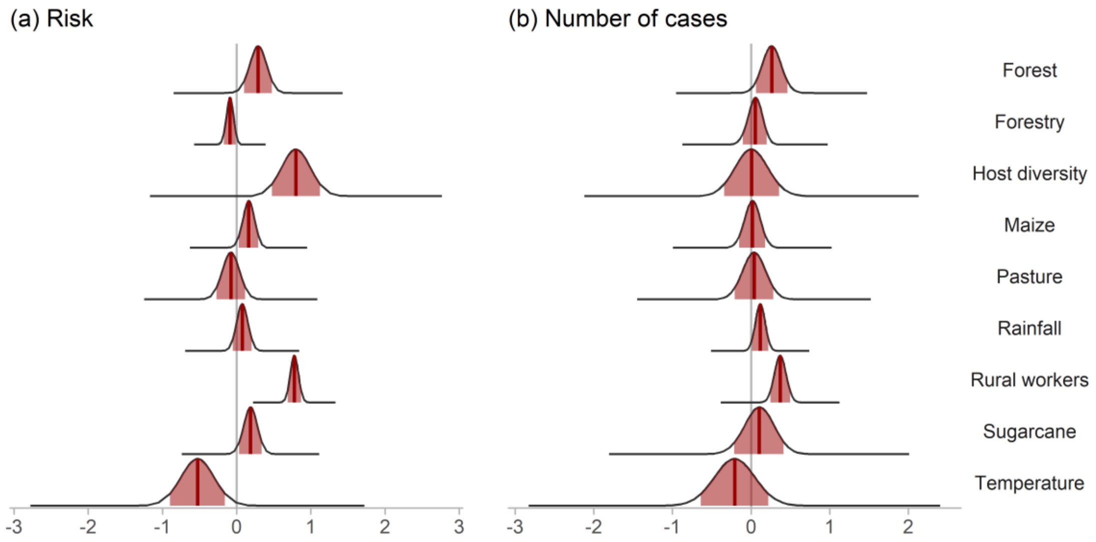


Figure 5. Posterior distributions of the effect sizes with the median (dark red line) and 95% credible intervals (light red shade) of each covariate on the (**a**) probability of cases and (**b**) positive counts of cases in a zero-truncated Poisson model, according to different predictors from two spatiotemporal models in Brazil from 2000–2014.

Among all predictors the variance inflation factor values were below 2 for the entire period and for the period selected for modelling (Figure S1). From the two models (Figure 4, Figure 5), CPO values ranged from zero to 0.99, with a mean of 0.98 for the binomial model. CPO values for the truncated Poisson model ranged from zero to 0.96, with a mean of 0.36, indicating a “low” adjustment. Hence, we optimized the zero truncated Poisson model to improve the CPO values, resulting in a new mean of 0.58 (min = 0, max = 0.96).

3.2. Potential Host Richness

The following bioclimatic variables were used in the ecological niche models (Table S3): Mean Diurnal Range (bio02), Isothermality (bio3), mean temperature of warmest quarter (bio10), precipitation of driest quarter (bio17), and precipitation of the warmest quarter (bio18). We were able to run models for 10 species relevant for hantavirus infection [48]: two rodents of the genus *Akodon* (hosts of *Juquitiba orthohantavirus* and *Juquitiba-like orthohantavirus* [17], *Pergamino orthohantavirus* and *Jabora orthohantavirus* [48])—*Akodon cursor* and *Akodon montensis* [49]; one species of genus *Calomys* (hosts of *Laguna Negra orthohantavirus*, *Andes orthohantavirus* and *Andes-like orthohantavirus*, [17]): *Calomys tener*; one species of the genus *Holochilus* (*Rio Mearim orthohantavirus* in Brazil [50]), *Holochilus sciureus*; *Necromys lasiurus* (*Araraquara orthohantavirus*—ARQV, and *Juquitiba orthohantavirus* [17]); *Oligoryzomys eliurus* (part of the *Oligoryzomys* complex hosting ANDV) [24,51]; *Oligoryzomys fornesi* (*Anajatuba orthohanavirus* [24]); *Oligoryzomys microtis* (*Rio Mamore orthohantavirus* [24]), *Oligoryzomys nigripes* (*Juquitiba orthohantavirus* [17]); and *Oxymycterus dasytrichus* (ANDV clade, data not published [52,53]), for which antibodies against ARQV nucleoprotein were found, implying that this rodent can become infected. We did not have enough data to model *C. laucha* or *C. callosus*, the hosts of LANV, and they were excluded from the analysis. The summary of adequate ensemble models can be viewed in Table S4. Three expert researchers agreed on the 10 percentile maps as being the most accurate for all modelled species (Figure 3). Peaks of host richness values occur in central and southeastern Brazil (Figure 3). Host richness had a positive effect on disease probability (Figure 5a) but not on the number of cases (Figure 5b).

3.3. Land Use, Population and Climate

Increased maize, forest, and sugarcane amounts had a positive effect on disease probability. Temperature had a negative effect on case probability (Figure 5a). For the case counts, the predictors rainfall, forest, and number of rural workers had a positive effect, and no covariate presented a relevant negative effect (Figure 5b). When we evaluated all components, the effect of forest amount and rural workers consistently positively influenced both disease risk and number of cases in a municipality.

3.4. Spatiotemporal Models

There was spatiotemporal variation in HCPS risk during the period modelled (GIF S1). The coefficient values for each predictor in both models are in Table S6. Note that many municipalities in southeastern Brazil were not at risk (clear areas in Figure 2b, Figure S4), while some municipalities in the northeast with no cases reported were indicated as areas at risk. Figure 5 shows the effect of each covariate on the case probability (disease risk) and number of cases. Overall, four spatial higher risk conglomerates can be recognized, being two in the northwest, one in central southeastern areas and one in the south (Figure 2b).

The mean estimated probability parameter for zero (absence of HCPS cases) was estimated as $\pi_{zero} = 0.99$, which is very high [39], but not surprising considering hantavirus disease rarity [11]. The time trend for the binomial model had a precision for year $\tau = 34.38$ ($sd = 29.71$) (Figure S4a). For the temporal term random effect in the case count model (Figure S5a), the predicted effect on the number of cases seems to decrease with time ($Precision\ for\ year\ \tau = 179.33, sd = 431.74$) . The estimated time trend predicted when using new data for the covariates from 2015 to 2016 did not differ from the overall trend (Figure S5b, Figure S6b). There was a non-linear temporal trend, with a slight increase in temporal correlation along the time series. Regarding spatial effects, the neighbor list object with 5570 regions had 32,546 non-zero spatial links, and 5.84 average number of links per municipality. The spatial random fields for the binomial model are shown in Figure S7 ($mean\ precision\ for\ u_i = 0.19$, $\sigma_i = 0.017$), and for the case counts, $mean\ precision\ for\ u_i = 0.5$, and $\sigma_i = 0.09$) . The predictions of the zero truncated model had a Pearson´s correlation 0.48 with the observed number of cases when we considered the period from 2000–2016, omitting the data from 2016 in the model (Figure 4). The higher risk biomes in terms of disease risk were Cerrado, Amazônia, and Atlantic Forest (Figure S8).

We provide the list of municipalities and their overall risk based on our model predictions in Table S7. Based on the observed number of cases, the largest outbreaks occurred in Brasília (2004, *n* = 28), Feliz Natal (2010, *n* = 19), and Altamira (2006, *n* = 17). The mean risk considering the entire country in the period modeled (2000–2014) was low (mean = 0.01) and the maximum risk reached 0.92 in Brasília in 2010. Considering a threshold of 5% for a relevant risk per municipality averaged over period modelled, 11.59% municipalities would be at risk. A threshold of 10% would include only 306 municipalities (5.4%). A high threshold for a risk value (>50%) would include only 11 municipalities, which (with the short State name and biome in parenthesis) are: Brasília (DF, Cerrado), Campo Novo dos Parecis (MT, Cerrado), Patrocínio (MG, Cerrado), Araxá (MG, Cerrado), Tangará da Serra (MT, Cerrado), Cruz Machado (PR, Atlantic Forest), Sertãozinho (SP, Cerrado), São Gotardo (MG, transition between Cerrado and Atlantic Forest), Novo Progresso (PA, Amazon), Ibiá (MG, Cerrado) and Ribeirão Preto (SP, Cerrado). According to our predictions, the risk increases over the years, reaching the maximum risk values in 2015 and 2016, with the maximum values occurring in Brasília, despite it not having the maximum number of cases in the period.

4. Discussion

This is the first study predicting hantavirus disease risk and number of cases in humans for the whole of Brazil using landscape, social, climate and biodiversity variables. A key finding of our results is that the amount of forest cover and the rural population at risk positively affect both disease risk and the number of cases. Our results also demonstrated that maize, sugarcane, and temperature can affect hantavirus cardiopulmonary syndrome risk. Our risk map identified that 11% of the country municipalities have a level of risk equal or higher than 5% per year, with 11 municipalities showing a very high risk (>50% risk). High-risk areas were mostly found in Cerrado and Atlantic Forest, followed by Amazon municipalities. This risk increased through time, confirming the emerging characteristic of HCPS in Brazil. The positive influence of both the amount of forest and the number of rural workers seems to explain the high number of cases occurring per year in the central and northern areas of Brazil.

From our hypotheses for explaining disease risk, we found the expected results regarding host diversity, rural workers, sugarcane, and maize amounts. Still, we detected results that differed from expected for temperature, rainfall, forest, pasture and forestry (Figure S1). According to our results, host diversity had a positive effect on the risk of pathogen transmission, but not on the number of human cases.

Disease risk is a complex and local phenomenon that is linked to multiple aspects, including the composition of reservoir host assemblages [54]. In a highly diverse community of rodent species, whose distributions overlap with a great number of other rodent species, a high viral diversity is expected [55]. HCPS in Brazil is caused by ARQV, JUQV, CASV, LANV, RIOMV and ANJV [21]. Different genotypes and strains, such as JUQV, ARQV and CASV belong to ANDV clade, while LANV, ANJV and RIOMV belong to LANV clade [21]. However, despite the diversity, the "viral load" in the communities may be very low, if there is "dilution" through high viral host species' contacts limiting viral transmission among heterogeneously susceptible host species, lowering overall transmission risk to humans. There is some evidence that mammalian biodiversity is the best predictor of zoonotic disease diversity at a large scale, but not of specific diseases [25], and here we show this effect must be further investigated, because we found a positive effect of host diversity on HCPS risk. We hypothesize that this happened because a high diversity of hosts is related to a greater diversity of viruses circulating in the same region and, despite the low viral load—if there is a certain threshold rodent population abundance in order to maintain the virus in the environment—disease risk could be increased. However, if more than one main rodent species can effectively transmit viral lineages, the mechanism for the dilution effect (heterogeneous host susceptibility) will be less strong, and local susceptible host abundance will be less affected by species diversity, limiting the impact of species diversity on disease risk. Further, hantavirus particles may remain infectious for weeks, depending on temperature, humidity, and association with protective proteins [23], thus limiting the impact of increasing host diversity on intra-species transmission.

Our results show that the effect size of the population at risk is the highest among the risk factors for disease risk. This finding corroborates the occupational nature of hantavirus disease in Brazil and that rural activities define the risk, as has been reported for other regions [21]. The positive effect of rural worker population sizes on disease risk was expected and found for the Atlantic Forest biome [10], but not previously for Cerrado areas [10,56]. Notwithstanding overall rural worker populations decline through time, the disease risk still increased and was positively influenced by the rural worker populations in municipalities. This fact highlights the need for better prevention measures in situ.

In a multicriteria analysis using expert knowledge, it was pointed out that areas such as Mato Grosso state (MT) had increased disease vulnerability, and the risk might be increasing in areas of previous disease "absence", such as the northern region of Brazil [6]. Indeed, we verified that the overall risk increased with time (Figure S5a) although we notice a trend towards a reduction in the overall number of cases over time. This indicates a geographical expansion of the disease, which is increasingly detected in more municipalities.

The positive effect of forest amount on disease risk was not expected, but should be further investigated, since when we look at the entire country we have different host species with different habits and habitat requirements [19,20]. It is notable how the disease reports increased in northern areas of Brazil recently, in areas that have high native forest cover. In this area, the effect of forest amount on hantavirus disease risk was positive and consistent. Those areas with increased risk might be where there is contact between forested areas and rural areas where both rodents and workers transit through.

We also found a positive effect of sugarcane expansion on disease risk, but not for the total number of cases. Sugarcane expanded a lot from 2000–2010 (Figure S3), but so did machinery technology and the cessation of pre-harvest fires in some locations [57]. Moreover, worker conditions are expected to vary across different states, and the positive effect of sugarcane and host richness seem to be concentrated in Atlantic Forest and Cerrado areas in southeastern Brazil (Figure S8), while other conditions impose more influence in the total number of disease cases in the rest of the country, such as the amount of forest, rainfall and rural population numbers. Another hypothesis is that there is a time lag between the effects of sugarcane expansion and the influence of land use alteration on the number of cases, meaning there will be a detectable problem in the future if prevention measures are not applied. The potential effect of pasture on hantavirus disease risk through the availability of grasses, such as brachiaria, for rodent hosts that can locally benefit from that may be present, but it was not detected in our study. Confounding associations, such as the presence or intensity of land use for cattle production, could limit the local suitability for hosts along with our ability to make inferences regarding risk from pasture areas. More local analyses may find disease risk is increased in these areas.

With respect to the long-term data, we had intrinsic limitations to model risk due to the rarity of notified cases in the first years of the time series (1993–1999). Moreover, we had the limitation of linearity among sparse data. It is important to investigate the possible non-linearity of effects, since we have many areas composed almost entirely by rural work forces in the Northeast of Brazil that have never had hantavirus disease cases notified and clearly are not suitable for the known hosts of hantavirus (Figure 3). Therefore, the large effect of the rural population at risk must be carefully interpreted, bearing in mind that there are localities in Brazil that lack the hosts, and thus might make the probability of the disease non-realistic.

Regarding spatial clustering of high-risk areas, we highlight that we found spatial random effects higher than 8%. Those areas are municipalities where attention has been given to hantavirus disease surveillance. Detecting these effects becomes even more important to support government strategies that focus on the control of the disease in Brazil and to elucidate if current government action measures are being effective to prevent the hantavirus expansion. Despite the increase in disease risk, it seems that the trend in outbreaks (i.e., case counts) decreased through time, which could be a consequence of specific applications of site monitoring or improvement of working conditions and guidance on safety at work (personal protective equipment, mechanization or improvement in working protocols). We did not include those variables in our models, but there are government efforts to prevent hantavirus disease in Brazil, such as the "Manual of surveillance, prevention and control of hantavirus cardiopulmonary disease" published in 2014 [12] and local monitoring from federal and state government Institutes, such as FIOCRUZ and Adolfo Lutz.

In conclusion, we showed that host diversity, social vulnerability, climate, and land use change influence hantavirus disease risk in Brazil. The expansion of sugarcane and maize plantations lead to an increase in HCPS disease risk, with additive positive effects from social vulnerability (despite an evident rural exodus trend) and native forest amount in a municipality. Confirmed cases are useful to understand the disease transmission risk of this relatively rare disease because case occurrences are provided by Brazilian Ministry of Health in unified databases of communicable diseases. Despite compulsory but suboptimal notification and diagnostic difficulties for HCPS, these datasets are the most reliable data available. Modeling approaches that maximize the predictive efficiency while reducing the computational time or field sampling effort are desired to predict emerging diseases. We recommend that HCPS mitigation and surveillance strategies need to be applied to prevent future outbreaks in the following highest-risk municipalities and their surroundings: Brasília, Campo Novo dos Parecis, Patrocínio, Araxá, Tangará da Serra, Cruz Machado, Sertãozinho, São Gotardo, Novo Progresso, Ibiá and Ribeirão Preto.

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Supplementary Materials

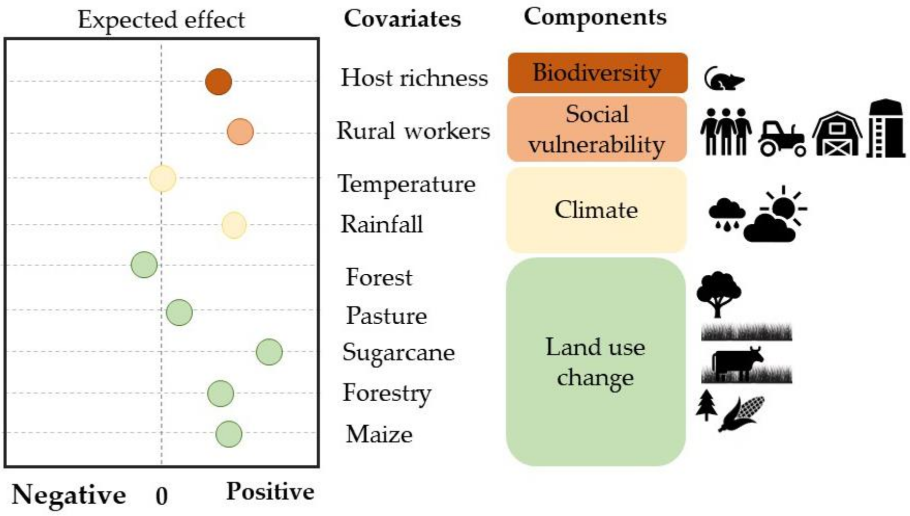


Figure S1. Coefficient plot based on our working hypothesis for hantavirus disease risk in Brazil. Negative coefficients represent a decrease in risk, positive values represent an increase in risk. Expected effect sizes were inferred from previous findings (DE OLIVEIRA et al., 2015; LEITE et al., 2018; PRIST et al., 2016; PRIST; D´ANDREA; METZGER, 2017).

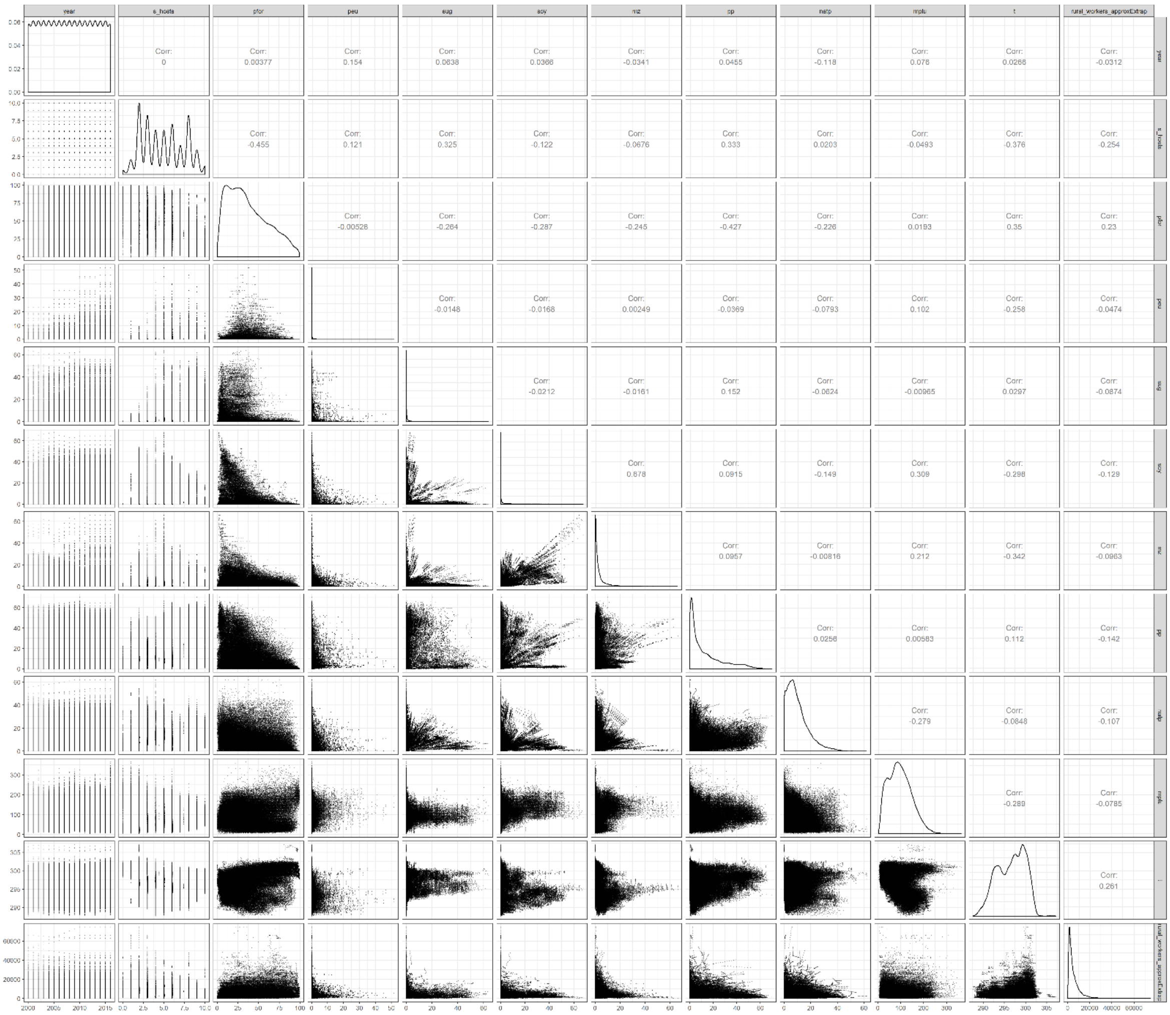


Figure S2. Pair plots and correlation between predictors used to model hantavirus disease risk in Brazil. Values correspond to Pearson´s correlation coefficients.

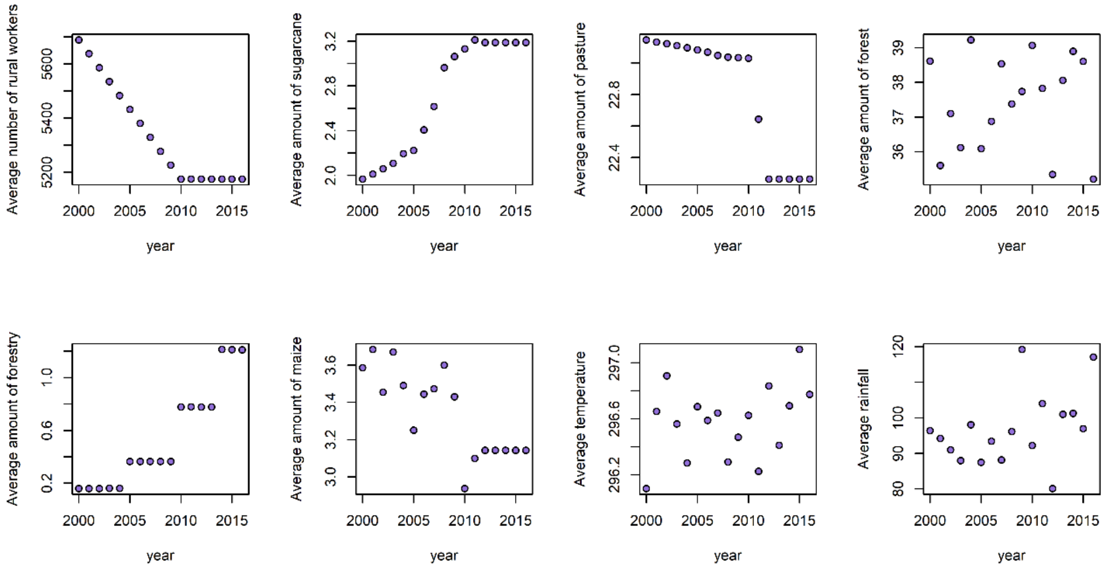


Figure S3. Fixed covariate values averaged over municipalities. We used the covariates in the modeling procedure of hantavirus disease numbers and the probability of cases in Brazil from 2000-2016. Host richness was considered constant through time.

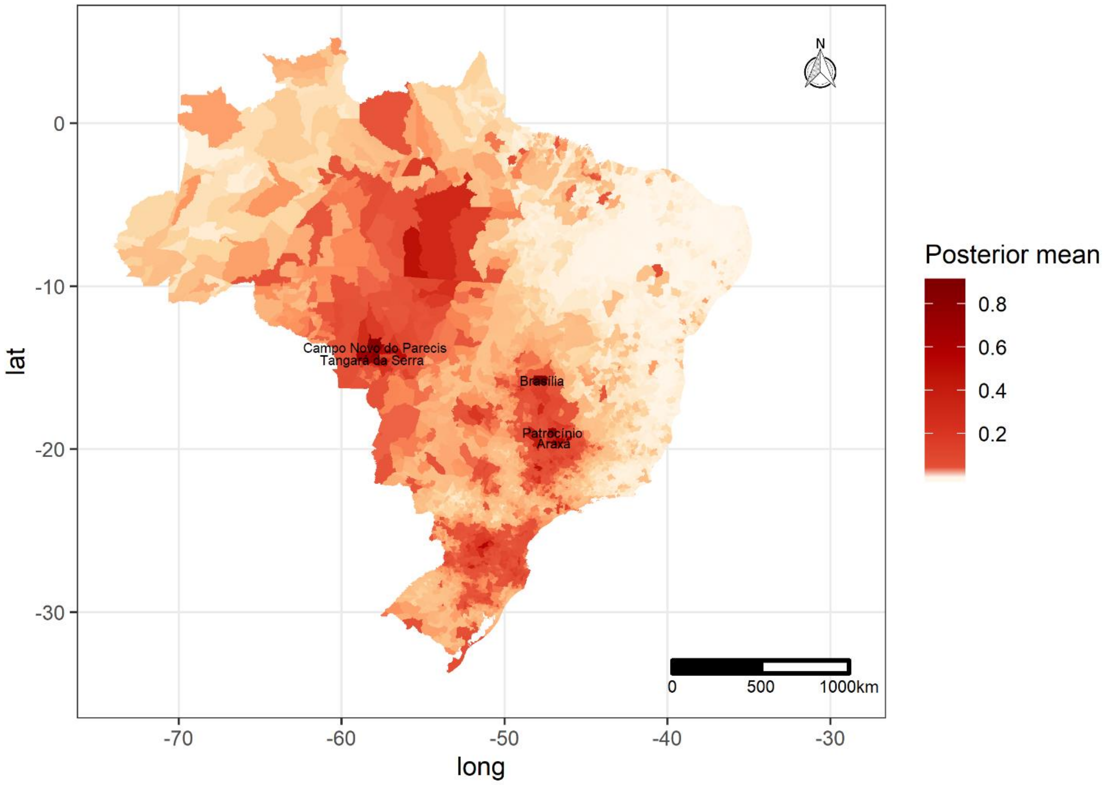
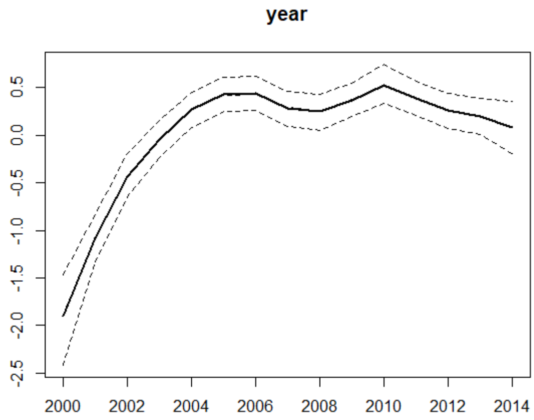
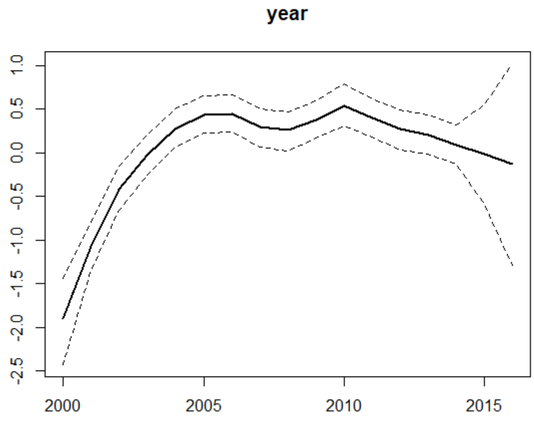


Figure S4. Hantavirus disease distribution in Brazil. Current expected values for the probability of hantavirus disease in humans, predicted by a spatio-temporal model containing forest, climate, and population at risk. Top five municipalities in terms of risk per year are highlighted. See the risk map with the uncertainty layer in Figure 3.

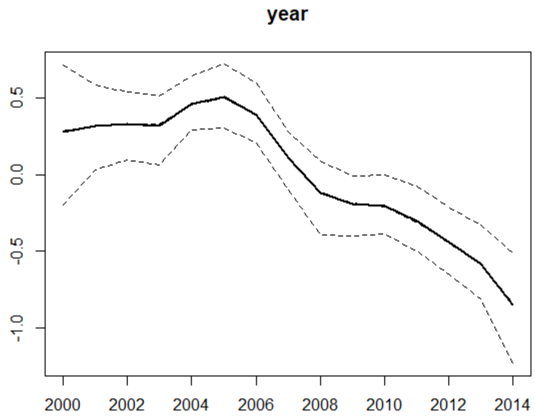


(a)

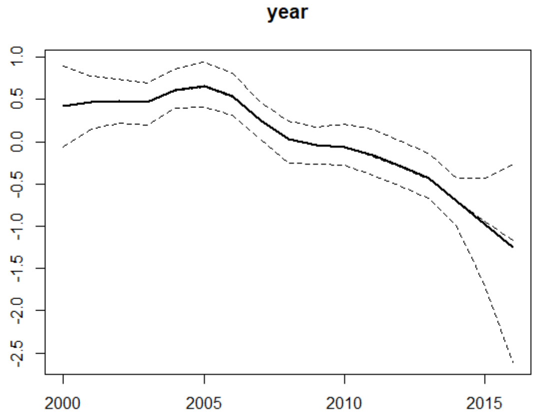


(b)

Figure S5. (a) Time trend for a binomial model estimating the probability of hantavirus disease cases in humans as a function of biodiversity, climate, social vulnerability and landscape change between 2000 to 2014 in Brazil. The y axis represents random effect values and the predictor is each year**.** (b) Predictions for 2015 and 2016 using new data for covariates and NA data for response variable. Dashed lines correspond to 95% credible intervals or the posterior mean.



(a)



(b)

Figure S6. (a) Time trend for a zero truncated Poisson model estimating the number of cases in humans as a function of biodiversity, climate, social vulnerability and landscape change between 2000 to 2014 in Brazil. The y axis represents random effect values and the predictor is each year**.** (b) Predictions for 2015 and 2016 using new data for covariates and NA data for response variable. Dashed lines correspond to 95% credible intervals or the posterior mean.

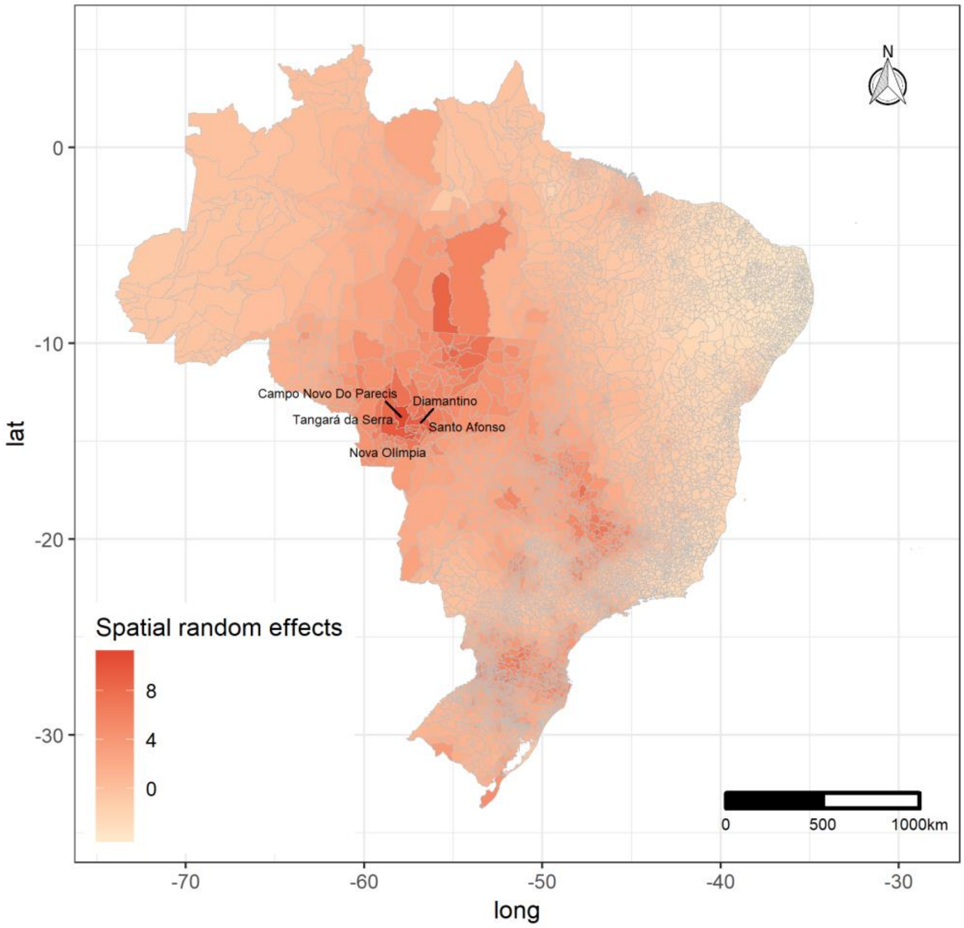


Figure S7. Municipalities showing positive effects of the spatial random field on hantavirus disease risk. The municipalities in labels are the ones with top five higher spatial random effect values.

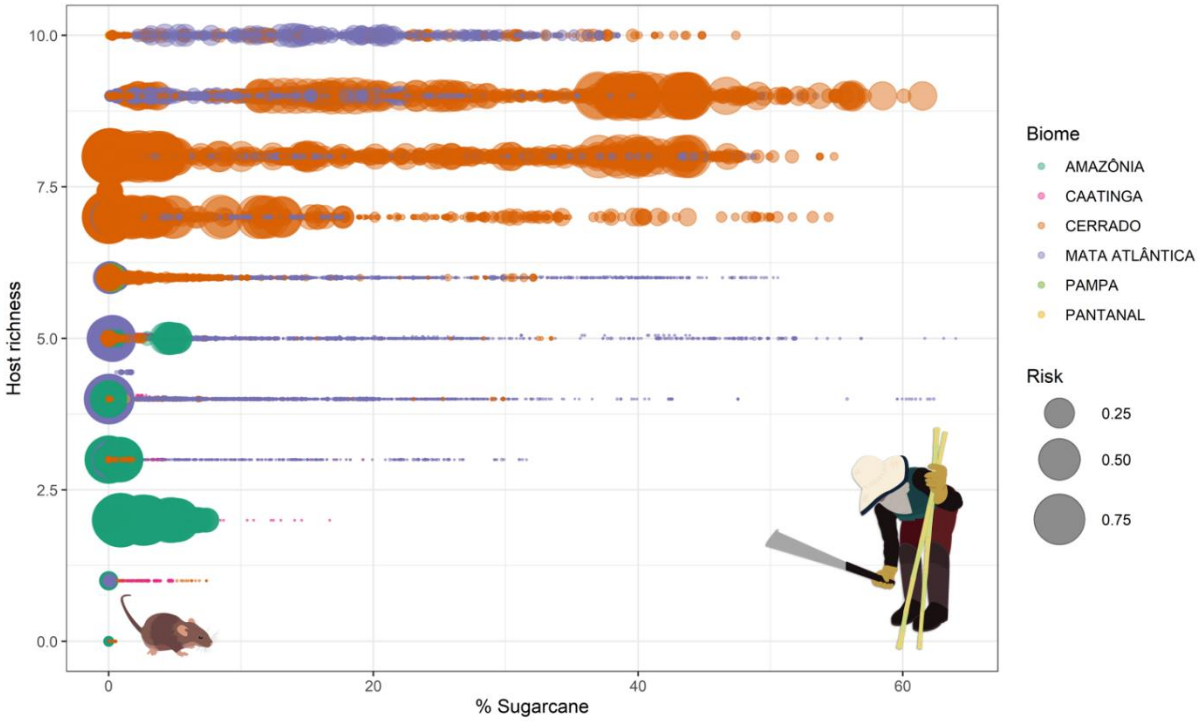


Figure S8. The number of species of hosts and the sugarcane amount in the municipality. The bubble size is proportional to the average predicted HCPS risk. Points are colored according to biome.

Table S1. Data sources used in the spatial-temporal modelling procedure.

Variable	**Time span**	**Spatial resolution in decimal degrees (Metric)/ Cartographic scale (Metric)**	**Source**	**Source URL**
Surface Temperature	2000-2016	0.5 (50 km)	NOAA NCEP	iridl.ldeo.columbia.edu/SOURCES/.NOAA/, http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.CPC/.GHCN_CAMS/.gridded/.deg0p5/.temp/
Rainfall	2000-2016	0.05 (5 km)	CHIRPS	http://chg.geog.ucsb.edu/data/chirps/, https://pubs.usgs.gov/ds/832/
Agricultural land use	2000-2014	0.01 (1 km)	Dias et al 2016 GCB	biosfera.dea.ufv.br/pt-BR/banco/uso-do-solo-agricola-no-brasil-1940-2012---dias-et-al-2016
Native habitat pasture	2000-2014	0.01 (1 km)	Dias et al 2016 GCB	biosfera.dea.ufv.br/pt-BR/banco/uso-do-solo-agricola-no-brasil-1940-2012---dias-et-al-2016
Native habitat forests and forestry	2000-2016	0.0003 (30 m)	Mapbiomas 2	http://mapbiomas.org/pages/database/mapbiomas_collection
Political divisions	2015	1:500000 (2.5 km)	IBGE	ftp://geoftp.ibge.gov.br/organizacao_do_territorio/malhas_territoriais/malhas_municipais/
Hantavirus cases in humans	1993-2017	1:500000 (5 km)	M Health	datasus.gov.br
Census	1991, 2000, 2006, 2010	1:500000 (5 km)	IBGE	https://downloads.ibge.gov.br/downloads_estatisticas.htm, ATLAS ONU, ftp://ftp.ibge.gov.br/Estimativas_de_Populacao/, ftp://ftp.ibge.gov.br/Censos/
Biome limits	2004	1:250000 (2.5 km)	MMA	http://mapas.mma.gov.br/i3geo/datadownload.htm, https://drive.google.com/file/d/0Byp5eRWoQ-Pka0hITTVDVWVfSFU/view?ts=5984ccbf

Table S2. Spatial auto-correlation tests for the distribution of hantavirus disease cases in humans in Brazil. Using 5% as alpha error level, we observe some clustering in 2006 and 2013. sd= standard deviation. In 1994 and 1997 no cases were notified.

Year	Observed	Expected	sd	P value
1993	-0.0001	-0.0002	0.0001	0.4953
1995	-0.0002	-0.0002	0.0001	0.4571
1996	-0.0003	-0.0002	0.0046	0.9864
1998	0.0008	-0.0002	0.0051	0.8494
1999	-0.0008	-0.0002	0.005	0.8988
2000	0.001	-0.0002	0.0046	0.806
2001	0.0041	-0.0002	0.0053	0.4121
2002	0.0034	-0.0002	0.0053	0.4963
2003	0.0035	-0.0002	0.0055	0.5015
2004	0.0018	-0.0002	0.0042	0.6334
2005	0.0028	-0.0002	0.0052	0.5711
2006	0.0119	-0.0002	0.0052	0.0207
2007	0.0006	-0.0002	0.0054	0.8872
2008	0.0052	-0.0002	0.0049	0.2795
2009	0.0022	-0.0002	0.0052	0.6422
2010	0.0024	-0.0002	0.0047	0.5884
2011	0.0052	-0.0002	0.0054	0.3223
2012	0.0073	-0.0002	0.0055	0.1729
2013	0.0109	-0.0002	0.0052	0.0332
2014	0.0044	-0.0002	0.0055	0.4026
2015	0.0032	-0.0002	0.0054	0.5332
2016	0.0019	-0.0002	0.0051	0.6759

Table S3. Rodent host selected predictors in models based on climate. Factorial analysis showing which factors contribute more for the variation in multivariate axes over the extent. This analysis helps select the most meaningful variables for explaining the environmental gradient that possibly correlates with species distribution. Factorial analysis uses correlation among input variables to sort related variables into "Factors". From this analysis you can pick the ones that contribute more for each factor as a suitable variable describing the climatic patterns from all variables that are available to use. Selected variables in boldface.

Bioclimatic variable	**MR1**	**MR2**	**MR3**	**MR6**	**MR4**	**MR5**
BIO1 = Annual Mean Temperature	0.94	-0.06	0.23	-0.15	0.18	-0.06
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))	-0.13	-0.40	-0.05	**0.89**	0.00	0.13
BIO3 = Isothermality (BIO2/BIO7) (* 100)	0.56	0.14	0.30	-0.26	**0.66**	-0.04
BIO4 = Temperature Seasonality (standard deviation *100)	-0.64	0.12	-0.43	0.16	-0.51	0.07
BIO5 = Max Temperature of Warmest Month	0.88	-0.17	0.17	0.32	-0.12	-0.20
BIO6 = Min Temperature of Coldest Month	0.79	0.12	0.24	-0.44	0.28	-0.17
BIO7 = Temperature Annual Range (BIO5-BIO6)	-0.42	-0.25	-0.19	0.74	-0.42	0.09
BIO8 = Mean Temperature of Wettest Quarter	0.87	-0.13	0.13	-0.11	0.11	0.15
BIO9 = Mean Temperature of Driest Quarter	0.83	0.03	0.28	-0.21	0.23	-0.26
BIO10 = Mean Temperature of Warmest Quarter	**0.97**	0.01	0.11	-0.15	-0.06	-0.12
BIO11 = Mean Temperature of Coldest Quarter	0.88	-0.07	0.31	-0.16	0.30	-0.10
BIO12 = Annual Precipitation	0.22	0.55	0.77	-0.07	0.09	0.14
BIO13 = Precipitation of Wettest Month	0.29	0.04	0.93	-0.07	0.11	0.02
BIO14 = Precipitation of Driest Month	-0.06	0.95	0.11	-0.17	0.10	0.09
BIO15 = Precipitation Seasonality (Coefficient of Variation)	0.19	-0.87	-0.01	0.13	0.15	-0.11
BIO16 = Precipitation of Wettest Quarter	0.30	0.07	0.94	-0.05	0.10	0.05
BIO17 = Precipitation of Driest Quarter	-0.06	**0.97**	0.13	-0.17	0.09	0.10
BIO18 = Precipitation of Warmest Quarter	-0.26	0.36	0.15	0.19	-0.04	**0.79**
BIO19 = Precipitation of Coldest Quarter	0.22	0.48	0.45	-0.37	0.12	-0.27

Table S4. Performance of suitable niche models for explaining host occurrence in Brazil. After model selection (TSS>0.5) we used expert opinion to validate the 10-percentile threshold for observed presence data to infer host presence.

Species	Mean AUC	Mean TSS	SD AUC	SD TSS	Hantavirus genotypes
Akodon cursor	0.82	0.62	0.11	0.18	JUQV JUQV like
Akodon montensis	0.92	0.79	0.07	0.14	ARQV JABV
Calomys tener	0.88	0.77	0.08	0.14	ARQV
Holochilus sciureus	0.55	0.34	0.21	0.26	RIOMM
Necromys lasiurus	0.7	0.41	0.07	0.11	ARQV
Oligoryzomys eliurus	0.55	0.35	0.23	0.27	CASV
Oligoryzomys fornesi	0.82	0.64	0.13	0.24	ANJV
Oligoryzomys microtis	0.52	0.32	0.26	0.29	RIOMV
Oligoryzomys nigripes	0.86	0.67	0.07	0.12	JUQV, ARQV
Oxymycterus dasytrichus	0.85	0.7	0.14	0.23	JUQV

Table S5. Fixed covariate averages for 5570 municipalities of Brazil from 2000-2016.

Year	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Rural workers	5688.8	5637.44	5586.09	5534.73	5483.38	5432.02	5380.67	5329.31	5277.96	5226.61	5175.25	5175.25	5175.25	5175.25	5175.25	5175.25	5175.25
min	62	62	61	61	61	61	61	61	60	60	60	60	60	60	60	60	60
max	66055	65730	65405	65080	64755	64430	65928	68128	70327	72526	74725	74725	74725	74725	74725	74725	74725
Sugarcane (%)	1.97	2.01	2.06	2.11	2.19	2.22	2.41	2.61	2.96	3.06	3.13	3.21	3.19	3.19	3.19	3.19	3.19
min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max	64	63.09	61.66	60.25	60.48	60.69	60.96	61.32	61.88	62.05	62.34	56.18	56.1	56.1	56.1	56.1	56.1
Pasture (%)	23.15	23.13	23.12	23.11	23.1	23.08	23.07	23.05	23.04	23.03	23.03	22.64	22.26	22.26	22.26	22.26	22.26
min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max	86.9	85.76	86.54	87.7	88.86	90.03	91.33	92.5	93.69	95.94	101	91.91	83.93	83.93	83.93	83.93	83.93
Forest (%)	38.61	35.6	37.1	36.12	39.23	36.09	36.87	38.54	37.38	37.74	39.07	37.83	35.34	38.06	38.9	38.61	35.21
min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max	99.55	99.31	99.32	99.41	99.41	99.56	99.56	99.54	99.55	99.2	99.16	99.53	99.53	99.48	99.36	99.47	99.01
Forestry (%)	0.16	0.16	0.16	0.16	0.16	0.36	0.36	0.36	0.36	0.36	0.78	0.78	0.78	0.78	1.21	1.21	1.21
min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max	23.17	23.17	23.17	23.18	23.18	35.38	35.37	35.36	35.4	35.38	45.29	45.34	45.26	45.18	51.79	51.78	51.75
Maize	3.59	3.69	3.45	3.67	3.49	3.25	3.44	3.47	3.6	3.43	2.94	3.1	3.14	3.14	3.14	3.14	3.14
min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max	55.66	57.83	56.7	61.71	60.76	47.44	53.23	58.26	62.86	62.12	54.89	62.87	65.96	65.96	65.96	65.96	65.96
Temperature (10*°C)	296.1	296.65	296.91	296.56	296.28	296.69	296.59	296.64	296.29	296.47	296.62	296.22	296.84	296.41	296.69	297.1	296.77
min	287.68	288.78	288.65	288.18	287.77	288.41	288.39	288.17	287.8	288.04	288.03	287.79	288.76	287.7	288.82	288.81	287.87
max	306.5	306.89	306.89	306.8	306.82	306.82	306.41	306.63	306.27	307.11	306.36	306.38	306.61	306.69	305.98	306.35	306.44
Rainfall (mm/month)	96.37	94.14	90.97	87.93	98.01	87.44	93.43	88.15	96.11	119.23	92.19	103.95	80.08	100.98	101.21	96.9	117.05
min	12	8	10	11	10	8	6	8	8	15	10	9	4	9	8	7	8
max	296	267	326	265	266	280	332	288	314	330	324	283	286	302	304	285	364

Table S6. Model estimates from the selected predictors of hantavirus disease in humans in Brazil. Those values are related to Figure 5 in the main text. PA = presence/absence of cases, Cases = number of cases.

Response variable	Component	Coefficient	Model	Mean	95% Credible interval
	-	Intercept	Binomial with logit link	-8.347	-8.875 to -7.893
PA	Biodiversity	Host richness	Binomial with logit link	0.797	0.413 to 1.185
PA	Social	Population at risk	Binomial with logit link	0.777	0.668 to 0.886
PA	Climate	Rainfall	Binomial with logit link	0.071	-0.075 to 0.216
PA	Climate	Temperature	Binomial with logit link	-0.528	-0.968 to -0.088
PA	Land use change	Forest	Binomial with logit link	0.29	0.064 to 0.514
PA	Land use change	Pasture	Binomial with logit link	-0.08	-0.31 to 0.147
PA	Land use change	Sugarcane	Binomial with logit link	0.182	0.002 to 0.361
PA	Land use change	Forestry	Binomial with logit link	-0.082	-0.168 to -0.0006
PA	Land use change	Maize	Binomial with logit link	0.159	0.002 to 0.310
Cases	-	Intercept	Zero-Truncated poisson with log link	-0.988	-1.726 to -0.304
Cases	Biodiversity	Host richness	Zero-Truncated poisson with log link	0.005	-0.410 to 0.426
Cases	Social	Population at risk	Zero-Truncated poisson with log link	0.366	0.219 to 0.513
Cases	Climate	Rainfall	Zero-Truncated poisson with log link	0.111	-0.007 to 0.229
Cases	Climate	Temperature	Zero-Truncated poisson with log link	-0.208	-0.716 to 0.299
Cases	Land use change	Forest	Zero-Truncated poisson with log link	0.262	0.023 to 0.502
Cases	Land use change	Pasture	Zero-Truncated poisson with log link	0.036	-0.249 to 0.320
Cases	Land use change	Sugarcane	Zero-Truncated poisson with log link	0.102	-0.279 to 0.474
Cases	Land use change	Forestry	Zero-Truncated poisson with log link	0.04	-0.111 to 0.181
Cases	Land use change	Maize	Zero-Truncated poisson with log link	0.015	-0.19 to 0.217

Table S7. Average hantavirus disease risk in municipalities of Brazil with risk equal to or greater than 5%, in decreasing order, considering a Bernoulli model for the period from 2000-2014 for all 5570 municipalities of Brazil. Municipality contains the Municipality code followed by municipality name without special characters. Risk was rounded to 3 decimal places. Data for all municipalities per year can be downloaded at https://github.com/renatamuy/Muylaert_et_al_2019

Municipality	Risk
530010 Brasilia	0.771
510263 Campo Novo do Parecis	0.749
314810 Patrocinio	0.727
310400 Araxa	0.671
510795 Tangara da Serra	0.643
410680 Cruz Machado	0.616
355170 Sertaozinho	0.602
316210 Sao Gotardo	0.579
150503 Novo Progresso	0.555
312950 Ibia	0.521
354340 Ribeirao Preto	0.506
420430 Concordia	0.493
510623 Nova Olimpia	0.481
510350 Diamantino	0.479
317020 Uberlandia	0.441
317010 Uberaba	0.439
412200 Rio Azul	0.439
354020 Pontal	0.436
410850 General Carneiro	0.426
410290 Bituruna	0.381
316510 Sao Tomas de Aquino	0.351
520480 Campo Alegre de Goias	0.333
150060 Altamira	0.330
314980 Perdizes	0.324
411390 Mallet	0.312
420770 Ipumirim	0.311
412820 Uniao da Vitoria	0.309
510642 Peixoto de Azevedo	0.305
411020 Inacio Martins	0.304
420160 Arroio Trinta	0.293
354890 Sao Carlos	0.293
520110 Anapolis	0.289
510805 Terra Nova do Norte	0.287
420240 Blumenau	0.285
315550 Rio Paranaiba	0.276
421930 Videira	0.265
311150 Campos Altos	0.255
411070 Irati	0.254
510726 Santo Afonso	0.253
411440 Mangueirinha	0.251
315050 Pimenta	0.250
510787 Sapezal	0.233

510170 Barra do Bugres	0.232
411930 Pinhao	0.229
420900 Joacaba	0.229
420070 Alfredo Wagner	0.227
410940 Guarapuava	0.220
350320 Araraquara	0.218
412030 Porto Vitoria	0.213
522185 Valparaiso de Goias	0.212
314800 Patos de Minas	0.205
351930 Ibate	0.203
420985 Lindoia do Sul	0.203
510558 Marcelandia	0.201
510730 Sao Jose do Rio Claro	0.199
352370 Itirapua	0.199
411760 Palmas	0.197
410645 Coronel Domingos Soares	0.196
421590 Sao Bonifacio	0.195
316810 Tapira	0.193
521190 Jatai	0.193
420850 Ituporanga	0.193
421260 Peritiba	0.191
420127 Arabuta	0.190
150680 Santarem	0.189
350560 Barrinha	0.189
420300 Cacador	0.188
421003 Luzerna	0.188
420980 Leoberto Leal	0.179
421780 Taio	0.178
316220 Sao Joao Batista do Glaria	0.177
314790 Passos	0.174
420860 Jabora	0.170
421935 Vitor Meireles	0.169
353430 Orlandia	0.168
510190 Brasnorte	0.168
410400 Campina Grande do Sul	0.168
412060 Prudentopolis	0.167
311510 Cassia	0.167
421750 Seara	0.165
412560 Sao Mateus do Sul	0.163
510320 Colider	0.162
520620 Cristalina	0.162
421875 Tunapolis	0.159
431680 Santa Cruz do Sul	0.159
421450 Rio do Campo	0.158
421570 Santo Amaro da Imperatriz	0.158
353060 Mogi das Cruzes	0.158
521250 Luziania	0.157
355030 Sao Paulo	0.156
351090 Cassia dos Coqueiros	0.154
420765 Ipora do Oeste	0.152
421360 Porto Uniao	0.152

351460 Dumont	0.150
421370 Pouso Redondo	0.149
420680 Ibicare	0.145
420810 Itaiopolis	0.145
421670 Sao Jose do Cedro	0.145
420757 Iomere	0.142
521975 Santo Antonio do Descoberto	0.141
316680 Serra do Salitre	0.141
421920 Vidal Ramos	0.140
510340 Cuiaba	0.139
510600 Nortelandia	0.136
510560 Matupa	0.135
420090 Angelina	0.134
510345 Denise	0.133
316470 Sao Sebastiao do Paraiso	0.133
421470 Rio dos Cedros	0.130
313750 Lagoa Formosa	0.130
421020 Major Gercino	0.128
420670 Herval d'Oeste	0.127
430510 Caxias do Sul	0.126
421220 Papanduva	0.126
315150 Piumhi	0.125
315770 Santa Juliana	0.125
312890 Guimarania	0.125
421430 Rancho Queimado	0.125
420010 Abelardo Luz	0.124
351310 Cravinhos	0.124
520549 Cidade Ocidental	0.124
421960 Xavantina	0.122
420420 Chapeco	0.122
315690 Sacramento	0.119
421500 Rio Negrinho	0.119
510626 Novo Mundo	0.119
310740 Bom Despacho	0.119
421340 Ponte Serrada	0.117
510619 Nova Santa Helena	0.116
420190 Aurora	0.115
510885 Nova Marilandia	0.115
310070 Agua Comprida	0.115
510410 Guaranta do Norte	0.114
520840 Goianapolis	0.114
311930 Coromandel	0.111
313160 Irai de Minas	0.111
350590 Batatais	0.111
314650 Pains	0.109
353010 Mirandopolis	0.109
421085 Mirim Doce	0.108
520870 Goiania	0.107
421567 Santa Terezinha	0.107
420260 Bom Retiro	0.105
354760 Santa Rosa de Viterbo	0.104

351860 Guariba	0.104
421410 Presidente Nereu	0.103
431238 Monte Belo do Sul	0.103
420640 Guaraciaba	0.102
420775 Iraceminha	0.102
314320 Monte Santo de Minas	0.102
520510 Catalao	0.101
430440 Canela	0.101
420780 Irani	0.100
310510 Bambui	0.100
150730 Sao Felix do Xingu	0.100
421480 Rio do Sul	0.099
421420 Quilombo	0.099
412080 Quatro Barras	0.097
314700 Paracatu	0.097
420740 Imbuia	0.097
421540 Salto Veloso	0.097
421390 Presidente Castello Branco	0.096
421530 Salete	0.095
510130 Arenapolis	0.095
310420 Arcos	0.093
421850 Treze Tilias	0.093
315300 Pratinha	0.091
412175 Reserva do Iguacu	0.091
412150 Reboucas	0.091
420380 Canoinhas	0.091
430480 Carlos Barbosa	0.091
421490 Rio Fortuna	0.089
411870 Paulo Frontin	0.089
421180 Ouro	0.087
410570 Clevelandia	0.087
421005 Macieira	0.087
355150 Serrana	0.086
420490 Descanso	0.086
312120 Delfinopolis	0.085
410445 Cantagalo	0.085
431805 Sao Domingos do Sul	0.084
312070 Cruzeiro da Fortaleza	0.084
421440 Rio das Antas	0.084
352740 Lucelia	0.083
431440 Pelotas	0.083
311240 Capetinga	0.082
510890 Nova Maringa	0.082
353630 Patrocinio Paulista	0.081
420760 Ipira	0.081
521230 Leopoldo de Bulhoes	0.080
421050 Maravilha	0.079
510622 Nova Mutum	0.079
411820 Paranagua	0.079
420400 Catanduvas	0.079
421940 Witmarsum	0.079

522045 Senador Canedo	0.078
420630 Guabiruba	0.078
520030 Alexania	0.078
420768 Ipuacu	0.078
421190 Palhoca	0.078
421725 Sao Pedro de Alcantara	0.078
312970 Ibiraci	0.078
352930 Matao	0.078
420120 Antonio Carlos	0.078
421890 Urubici	0.077
420970 Lebon Regis	0.077
522119 Terezopolis de Goias	0.076
411860 Paula Freitas	0.076
431290 Nova Bassano	0.076
110030 Vilhena	0.075
420920 Lacerdopolis	0.075
420510 Dona Emma	0.074
520580 Corumba de Goias	0.074
521010 Ipameri	0.074
420315 Calmon	0.074
421210 Palmitos	0.073
351440 Dracena	0.073
421150 Nova Trento	0.073
313030 Iguatama	0.073
421460 Rio do Oeste	0.072
420270 Botuvera	0.072
311980 Corrego Danta	0.071
420540 Florianopolis	0.071
510268 Campos de Julio	0.071
420040 Agua Doce	0.071
421580 Sao Bento do Sul	0.071
420610 Grao Para	0.070
412700 Teixeira Soares	0.070
520815 Gameleira de Goias	0.070
510336 Conquista D'Oeste	0.070
352510 Jardinopolis	0.070
353050 Mococa	0.069
410950 Guaraquecaba	0.069
421507 Riqueza	0.069
420915 Jose Boiteux	0.068
412510 Sao Joao do Triunfo	0.068
420675 Ibiam	0.068
311995 Corrego Fundo	0.068
353360 Nuporanga	0.068
510525 Lucas do Rio Verde	0.068
430320 Cacique Doble	0.068
410965 Honorio Serpa	0.067
421400 Presidente Getulio	0.066
420330 Campo Alegre	0.066
510675 Pontes e Lacerda	0.065
350940 Cajuru	0.065

312125 Delta	0.065
420180 Atalanta	0.064
510830 Uniao do Sul	0.064
431030 Ilopolis	0.064
310190 Alpinopolis	0.064
421660 Sao Jose	0.063
412550 Sao Jose dos Pinhais	0.063
420435 Cordilheira Alta	0.063
421680 Sao Jose do Cerrito	0.063
430210 Bento Goncalves	0.063
420890 Jaragua do Sul	0.063
431730 Santa Vitoria do Palmar	0.062
351480 Eldorado	0.062
432260 Venancio Aires	0.062
352760 Luis Antonio	0.061
354650 Santa Ernestina	0.061
351620 Franca	0.061
352890 Mariapolis	0.061
353640 Pauliceia	0.061
520551 Cocalzinho de Goias	0.061
311430 Carmo do Paranaiba	0.060
420060 aguas Mornas	0.060
510050 Alto Paraguai	0.060
421630 Sao Joao Batista	0.060
412760 Tijucas do Sul	0.060
420550 Fraiburgo	0.060
420590 Gaspar	0.059
431880 Sao Lourenco do Sul	0.059
430450 Cangucu	0.059
520355 Bonfinopolis	0.059
313880 Luz	0.059
420030 Agronomica	0.059
431410 Passo Fundo	0.059
352970 Miguelopolis	0.059
421060 Massaranduba	0.059
410480 Cascavel	0.059
350925 Cajati	0.059
310410 Arceburgo	0.058
316294 Sao Jose da Barra	0.058
312860 Guarda-Mor	0.058
420910 Joinville	0.057
352430 Jaboticabal	0.057
510792 Sorriso	0.057
353310 Nova Guataporanga	0.057
520025 Aguas Lindas de Goias	0.057
421970 Xaxim	0.056
352600 Junqueiropolis	0.056
522060 Silvania	0.056
430790 Farroupilha	0.056
510370 Feliz Natal	0.056
420450 Corupa	0.055

432290 Viadutos	0.055
430165 Barao	0.055
353490 Pacaembu	0.055
431442 Picada Cafe	0.055
430910 Gramado	0.055
420243 Bocaina do Sul	0.055
420080 Anchieta	0.055
410130 Antonio Olinto	0.055
521730 Pirenopolis	0.054
314310 Monte Carmelo	0.054
315640 Romaria	0.054
353160 Monte Castelo	0.054
420470 Cunha Pora	0.054
420360 Campos Novos	0.053
354290 Ribeirao Bonito	0.053
350100 Altinopolis	0.053
421170 Orleans	0.053
355090 Sao Simao	0.053
510590 Nobres	0.052
410960 Guaratuba	0.052
353950 Pitangueiras	0.052
421030 Major Vieira	0.052
430700 Erechim	0.051
354490 Sales Oliveira	0.051
510515 Juina	0.051
354090 Pradopolis	0.050
510455 Itauba	0.050
420110 Anitapolis	0.050
130290 Maues	0.050
431971 Sao Valentim do Sul	0.050

Discussão Geral

Nesta tese busquei investigar a biodiversidade na Mata Atlântica e processos ecológicos envolvendo mamíferos e hantavírus, promovendo o uso de dados abertos (*Open data*). Um banco de dados massivo foi organizado durante a tese, contribuindo para o estudo da biodiversidade com a série ATLANTIC de *data papers* (Capítulo 1). Também contribuímos para o uso de dados abertos discutindo os limites territoriais na Mata Atlântica (Capítulo 2). Investiguei os fatores que levam a um aumento na quantidade de roedores transmissores de hantavírus, e como esses efeitos são modulados pelo espaço (Capítulo 3). Por fim, investiguei quantitativamente e de forma inédita a emergência da hantavirose no Brasil utilizando modelos espaço-temporais. A seguir discutimos os principais resultados dos capítulos gerados e sua interconexão, sugerindo também as potenciais vias de futuras investigações perante as limitações encontradas.

Open Data e *Open Science*

Foi importante para o desenvolvimento da tese que a distribuição de mamíferos fosse averiguada. Fizemos isso utilizando a ATLANTIC SERIES, bem como outras bases (*species link* e o GBIF). A ATLANTIC SERIES gerou diversos *data papers*, além do primeiro capítulo desta tese sobre os morcegos da Mata Atlântica (MUYLAERT et al., 2017a). Essas iniciativas de *open data* levaram a mobilização de grandes grupos de pesquisadores que compilaram mais de 100 anos de dados sobre a biodiversidade da Mata Atlântica em menos de quatro anos, beneficiando a ciência e a aplicação do conhecimento científico para medidas de conservação da biodiversidade e criando oportunidades de aplicação em diversos estudos ecológicos (BOGONI et al., 2018; BOVENDORP et al., 2018; MARJAKANGAS et al., 2018), incluindo um artigo científico sobre boas práticas em compartilhamento de dados (ARREGOITIA, 2018). A ATLANTIC SERIES dá suporte a diversas novas pesquisas, tendo os ATLANTICS sido os mais citados dentre os *data papers* da *Ecology* recentemente (ATLANTIC-MAMMAL TRAITS, GONÇALVES et al., 2018; ATLANTIC BIRDS, HASUI et al., 2017; ATLANTIC BATS MUYLAERT et al., 2017; e ATLANTIC CAMTRAPS LIMA et al., 2017). É importante que se dê continuidade ao projeto ATLANTIC no sentido de manter as bases de dados acessíveis e com curadoria que permita que as mesmas não fiquem obsoletas rapidamente. Diversos projetos "param no tempo" quando seus responsáveis terminam uma etapa de financiamento. Isso é algo que precisa ser discutido para que os *data papers* sejam atualizáveis. Essas atualizações também precisam ser discutidas para serem feitas não apenas em repositórios como GitHub, mas também no servidor dos periódicos nos quais são publicados.

O desenvolvimento da coleção ATLANTIC me levou a investigar os limites territoriais da Mata Atlântica sob uma perspectiva operacional (Capítulo 2). Sentimos a necessidade de discutir mais amplamente a delimitação de uma área de investigação, pois dependendo do limite adotado, a Mata Atlântica (limite consensual *versus* limite integrador) pode ter meio milhão de km^2 de diferença (equivalente a área de duas Nova Zelândias ou de dois Estados de São Paulo). Espero que com a publicação do artigo (MUYLAERT et al., 2018c) eu tenha auxiliado as pessoas de diferentes meios que trabalham com ciências ambientais a se comunicar melhor sobre a Mata Atlântica, ressaltando também a importância de descrever a fonte e as características dos dados utilizados em análises espaciais.

Eco-epidemiologia: hantavirose em foco

Grande parte dos casos de hantavirose ocorrem na Mata Atlântica. E a distribuição de uma zoonose é intrinsecamente condicionada pela distribuição dos hospedeiros do patógeno causador. No Capítulo 3, verifiquei 17% de correspondência espacial entre a alta ocorrência dos roedores reservatório e locais que concentram alta vulnerabilidade à hantavirose. Ambas as informações de *hotspots* (I. *hotspots* de proporção de roedores e II. *hotspots* de vulnerabilidade à doença) foram geradas por métodos diferentes e a partir de dados diferentes. A partir de modelos espacialmente explícitos, pude verificar que as quantidades de cana-de-açúcar e de silvicultura na paisagem levam a um aumento na quantidade de hospedeiros de hantavírus na comunidade biológica. Além disto, a diversidade da paisagem, precipitação e biodiversidade local também são *drivers* importantes para explicar a % de roedores hospedeiros de hantavírus. Por fim, a intensidade da defaunação não influenciou na proporção de hospedeiros de genótipos de hantavírus patogênicos, indicando que áreas não defaunadas também podem ser *hotspots* para surtos de hantavirose. Isso abre margem para futuros estudos sobre regulação *top down* de roedores e zoonoses por carnívoros. Desta forma, há uma demanda de estudos sobre cascatas tróficas que façam uma ponte com epidemiologia.

Descobrimos que há uma convergência parcial entre a proporção de roedores no local e a vulnerabilidade à hantavirose associada espacialmente. Regiões nas quais a convergência é positiva (*hotspots*), irrelevante (*neutral spots*) ou baixa (*coldspots*) podem apontar caminhos para estudos observacionais, ou estudos do tipo tratamento-controle que levem em conta o contexto de comunidade de roedores *versus* o contexto de *spillover*. Sabemos que nem sempre é possível testar todos os roedores para sorologia visando detectar infecção por hantavírus. Também sabemos que em alguns casos a prevalência do vírus pode ser muito baixa ou até nula, ainda que haja diversos registros de um hospedeiro competente ocorrendo em uma dada localidade (ver DE OLIVEIRA SANTOS et al., 2018). Portanto, estratégias que levem a priorização de locais para investigação e vigilância eco-epidemiológica podem ser altamente desejáveis. Ressalta-se que estimativas de proporção de roedores, como a que utilizei, possuem erros associados pois partem de um experimento observacional e não de amostragens sistematizadas. Entretanto, nossos resultados corroboram o que esperava-se do ciclo de transmissão do hantavírus no Novo Mundo, no qual o aumento de produtividade primária proveniente de habitat nativos e de diferentes culturas (p.ex. cana-de-açúcar ou silvicultura) beneficiam hospedeiros de hantavírus (PRIST; D´ANDREA; METZGER, 2017).

No Capítulo 3 analisei dados gerados pelo ATLANTIC SMALL MAMMALS (BOVENDORP et al., 2017) para modelar a proporção de roedores hospedeiros. Já no Capítulo 4 utilizei dados de todas as bases que pudemos encontrar para modelar a ocorrência das espécies de hospedeiros, visando gerar uma camada de riqueza de roedores hospedeiros. No Capítulo 4, ressaltou-se a característica ocupacional da hantavirose, já relatada, mas que nunca teve seu efeito quantificado para todos os municípios do país. Descobrimos que uma paisagem patogênica ideal para *spillover* de hantavírus, considerando que, no Brasil, os municípios apresentam uma área média 1527 km^2, teria entre 20-30% de cobertura florestal, aliada a uma cobertura de cana-de-açúcar que beira 40% da área do município, bem como uma diversidade considerável de roedores reservatórios. Chequei então que uma combinação entre uma quantidade considerável de floresta nativa (entre 20%-30%), embebida em regiões de intenso cultivo de cana-de-açúcar ou milho, de preferência com muitos trabalhadores rurais, levou a um aumento no risco de hantavirose. Uma potencial limitação da nossa modelagem foi considerar os municípios como unidades espaciais equivalentes que interagem com a vizinhança. A área de Rio Claro (SP) de aproximadamente 500 km^2, e a área de Altamira (PA), o maior município do Brasil, é 319 vezes maior, com quase 160 mil km^2. Não levei em conta efeitos de área nos nossos modelos, apenas a vizinhança entre municípios. Também não considerei contextos socioeconômicos intrínsecos de regiões políticas ou biomas diferentes. Entretanto, é notável que os fatores de risco para hantavirose em um município do Norte do país são muito menos relacionados à quantidade de cana-de-açúcar do que à quantidade de floresta nativa, pois tanto a paisagem quanto os roedores hospedeiros são diferentes na Amazônia em comparação com *hotspots* de risco no sudeste do Brasil (interface Cerrado e Mata Atlântica), onde há menos floresta e muito mais áreas de plantação de cana-de-açúcar.

O hantavírus vive em um micro-habitat e ele precisa ser mantido vivo para conseguir perdurar e circular em novos ambientes ou hospedeiros, seja por *spillover* ou não. O roedor hospedeiro é a parte principal desse micro-habitat, e por isso entender a ocorrência do hospedeiro pode esclarecer mecanismos de transmissão de patógenos. De modo geral, meus resultados indicam que a riqueza de roedores reservatório potenciais influencia positivamente no risco de hantavirose, e o papel individual de cada espécie pode ser investigado em futuros estudos. É interessante e inédita a descoberta de que o adensamento da ocorrência de reservatórios é propício para aumentar o risco de transmissão da doença. Áreas de co circulação viral devem ser melhor investigadas, e principalmente áreas de interface entre Mata Atlântica e Cerrado, e no arco do desmatamento da Amazônia, nas quais a conversão recente de terras pode levar a um aumento de risco, criando paisagens patogênicas mais favoráveis. No futuro, estudos podem incorporar variáveis que não incluímos no nosso modelo, mas que podem ser importantes fatores que influenciam de *spillover*, por exemplo a mecanização e a forma de colheita. Uma hipótese sobre o impacto da mecanização seria que o requerimento/estímulo ao uso de EPIs (equipamentos de proteção individual), bem como a diminuição natural do contato direto entre o cortador de cana e o ar circundante (já que os trabalhadores estariam na interface máquina-plantação). Tais modificações trariam uma melhoria na qualidade de vida dos trabalhadores rurais e seria detectada uma queda no risco ao longo do tempo.

Meu modelo espaço-temporal apontou municípios com risco altíssimo de transmissão dessa doença que devem ser devidamente monitorados (Tabela 1). Acredito que este ranqueamento pode direcionar ações de monitoramento do Ministério da Saúde, do público local e dos pesquisadores que se interessem por doenças emergentes. A severidade da doença nessas municipalidades de alto risco pode variar, pois as mesmas encontram-se em diferentes contextos socioambientais, porém compartilham de algumas similaridades de características de paisagem e climáticas. Por fim, a relação entre biodiversidade e a transmissão de hantavírus explorada nesta tese nos leva a novos questionamentos empolgantes sobre co circulação viral, fontes-sumidouro de vírus patogênicos, dinâmica populacional de roedores e sistemas de trabalho rural no Brasil. Espero que os resultados aqui encontrados sirvam para uma melhora na descrição e compreensão destes fenômenos.

Município	Rank
Brasília – DF	1
Campo Novo do Parecis – MT	2
Patrocínio – MG	3
Araxá – MG	4
Tangará da Serra – MT	5
Cruz Machado – PR	6
Sertãozinho –SP	7
São Gotardo – MG	8
Novo Progresso – PA	9
Ibiá – MG	10
Ribeirão Preto – SP	11
Concórdia – SC	12
Nova Olímpia – MT	13
Diamantino- MT	14
Uberlândia – MG	15
Uberaba – MG	16
Rio Azul – PR	17
Pontal – SP	18
General Carneiro – PR	19
Bituruna –PR	20

Tabela 1. Municípios de maior risco médio de hantavirose no Brasil considerando o período de 2000-2016. O risco se refere à probabilidade de ocorrência da doença em humanos para cada município.

Conclusões

Capítulo 1 (MUYLAERT et al., 2017a)

- A Mata Atlântica abriga pelo menos 8% da diversidade global de morcegos;
- Cinco espécies ocorrem em mais da metade das comunidades amostradas: *Artibeus lituratus*, *Carollia perspicillata*, *Sturnira lilium*, *Artibeus fimbriatus*, *Glossophaga soricina*, e *Platyrrhinus lineatus*;
- Dos morcegos insetívoros, o gênero mais frequentemente amostrado com redes-de-neblina é *Myotis*;
- A riqueza amostrada varia positiva e linearmente quanto maior for o esforço amostral, não tendo atingindo assíntota para nenhum valor de esforço. Isso indica que há uma riqueza inexplorada de espécies na Mata Atlântica que pode ser encontrada ainda com redes-de-neblina, mas também utilizando outros métodos de captura, como bioacústica e amostragem direta em abrigos.

Capítulo 2 (MUYLAERT et al., 2018c)

- A área total do bioma Mata Atlântica varia de 1,11 km^2 a 1,62 km^2 (limite integrador), sendo a área consensual entre os quatro principais limites utilizados 1,01 km^2 (limite consensual);
- A partir das definições de limites territoriais revisadas, pesquisadores podem tomar decisões mais conscientes em relação a qual limite utilizar em novas pesquisas;
- Existem cinco regiões de maior divergência entre limites, que trazem oportunidades de novos estudos: 1) regiões de brejos de altitude no Ceará, 2) áreas do interior de MG e Bahia na Bacia do São Francisco, 3) Enclaves de Cerrado em São Paulo, 4) Interfaces com Pantanal e Chaco, e 4) Interfaces com os Pampas.

Capítulo 3 (MUYLAERT et al., 2019)

- Na Mata Atlântica há fortes influências espaciais e da composição da paisagem na proporção de hospedeiros de hantavírus;
- A correspondência espacial entre os pontos quentes de roedores hospedeiros de hantavírus potencialmente patogênicos e pontos quentes de vulnerabilidade local à hantavirose foi de 17%, enquanto os pontos frios corresponderam em 20% das localidades;
- Meus resultados sugerem que medidas de vigilância e prevenção de hantavirose são necessárias nas regiões sul e sudeste do Brasil, onde as maiores proporções de roedores hospedeiros e níveis de vulnerabilidade coincidem espacialmente;
- Encontrei 12 espécies bem representadas de roedores que podem hospedar pelo menos um genótipo de hantavírus;
- As coberturas (%) de área destinada à plantação de cana-de-açúcar e de silvicultura na paisagem influenciaram positivamente os hospedeiros dos genótipos de hantavírus potencialmente patogênicos;
- Os modelos gerados sugerem uma influência positiva geral da diversidade de habitat e das chuvas nas proporções de roedores hospedeiros na comunidade;
- As proporções de hospedeiros hantavírus em comunidades de roedores são influenciadas positivamente pelo número total de espécies local na maior parte da floresta Atlântica, mas que a riqueza de espécies local parece ser uma força diluidora nas comunidades do sul da Mata Atlântica;
- A intensidade da defaunação teve uma influência geograficamente variável para hospedeiros conhecidos de hantavírus, mas não pareceu influenciar a proporção de hospedeiros de hantavírus patogênicos;
- Apesar da alta variação nos dados da proporção de hospedeiros em diferentes comunidades, os picos de vulnerabilidade humana à hantavirose ocorrem em níveis mais altos de diversidade de habitat na

paisagem, níveis intermediários de precipitação e áreas com menos de 15 espécies na comunidade de pequenos mamíferos.

Capítulo 4

- A população em risco (trabalhadores rurais) e a diversidade de roedores hospedeiros foram os fatores mais importantes que influenciaram o aumento do risco de hantavirose em humanos;
- A quantidade de floresta nativa, de plantações de cana-de-açúcar e milho nos municípios também tiveram um efeito positivo no risco de hantavirose;
- Quanto maior a temperatura média anual do município, menor é o risco de hantavirose;
- Trabalhadores rurais em áreas de plantações de cana-de-açúcar e milharais próximas a florestas nativas são expostos a um maior risco de hantavirose, provavelmente por haver um aumento na probabilidade de interação entre as pessoas e roedores infectados;
- O planejamento de uso da terra deve considerar o risco de doenças;
- O mapa de risco gerado nesta tese pode ser usado para ajudar a alocar medidas preventivas para evitar hantavirose.

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Comunicação Científica

Lista de links para matérias relacionadas a cada capítulo

Capítulo 1

YouTube – ATLANTIC BATS:

https://youtu.be/C1PLD7fZe7c

Revista Pesquisa FAPESP – As metamorfoses da Mata Atlântica: https://revistapesquisa.fapesp.br/2018/05/23/as-metamorfoses-da-mata-atlantica/

Capítulo 2

Portal eFlora - Um limite da Mata Atlântica para chamar de seu: https://www.efloraweb.com.br/um-limite-da-mata-atlantica-chamar/

Podcast Unesp – Pesquisadora da Unesp publica estudo sobre limites geográficos da Mata Atlântica:

https://podcast.unesp.br/radiorelease-08012019-pesquisadora-da-unesp-publica-estudo-sobre-limites-geograficos-da-mata-atlantica

Portal Unesp – Redescobrindo os limites da Mata Atlântica: Artigo propõe um limite integrador para uso em estudos sobre conservação da biodiversidade:

https://www2.unesp.br/portal#!/noticia/33763/redescobrindo-os-limites-da-mata-atlantica

Capítulo 3

Destaques Notícias Unesp – Desvendando as ameaças de hantavírus: http://unan.unesp.br/destaques/33415/desvendando-as-ameacas-de-hantavirus

Capítulo 4

Destaques Notícias Unesp – Modelo matemático prevê áreas de risco de hantavirose no Brasil: https://www2.unesp.br/portal#!/noticia/35273/modelo-matematico-preve-areas-de-risco-de-hantavirose-no-brasil/

PodCast Unesp – Doutoranda da Unesp colabora em pesquisa inédita sobre hantavírus em morcegos da América:

https://podcast.unesp.br/8135/doutoranda-da-unesp-colabora-em-pesquisa-inedita-sobre-hantavirus-em-morcegos-da-america

Ensino e Pesquisa

Unesp Ciência – Relato de anticorpos para hantavírus em morcego nas Américas: http://unan.unesp.br/destaques/19123/Relato-de-anticorpos-para-hantavirus-em-morcego-nas-Americas

Diário do Rio Claro – Compromisso Dos Ecólogos Com O Meio Ambiente: http://diariodorioclaro.com.br/2015/11/03/o-compromisso-dos-ecologos-com-o-meio-ambiente-65097/

Revista Pesquisa FAPESP – Possíveis reservatórios do hantavírus: https://revistapesquisa.fapesp.br/2015/09/29/possiveis-reservatorios-do-hantavirus/