MIRIAM LUCIA LAGES PERILLI

WE, PREDATORS: HUMANS, APEX PREDATORS AND PREYS IN THE ATLANTIC FOREST TROPHIC CASCADES

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ecologia, para a obtenção do título de *Doctor Scientiae*.

VIÇOSA
MINAS GERAIS - BRASIL
2016

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T
P444w
2016

Perilli, Míriam Lucia Lages, 1981-
We, predators: humans, apex predators and their preys in the Atlantic Forest trophic cascades / Míriam Lucia Lages Perilli. – Viçosa, MG, 2016.
1 tese eletrônica (xiii, 94 f.): il.

Inclui anexos.
Orientador: Ricardo Ribeiro de Castro Solar.
Tese (doutorado) - Universidade Federal de Viçosa, Departamento de Biologia Geral, 2016.
Inclui bibliografia.
DOI: https://doi.org/10.47328/ufvbbt.2021.184
Modo de acesso: World Wide Web.

1. Mamíferos - Mata. 2. Ecossistemas - Modelos estatísticos. 3. Níveis tróficos. I. Solar, Ricardo Ribeiro de Castro. II. Universidade Federal de Viçosa. Departamento de Biologia Geral. Programa de Pós-Graduação em Ecologia. III. Título.

CDD 22. ed. 599.0981

Bibliotecário(a) responsável: Renata de Fátima Alves CRB6/2578

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APROVADA: 15 de dezembro de 2016.

Milton Cezar Ribeiro

Adriano Paglia

Adriano Pereira Paglia

Laury Cullen Junior

Flávio Henrique Guimarães Rodrigues

Ricardo Ribeiro de Castro Solar

Ricardo Ribeiro de Castro Solar
(Orientador)

A minha mãe e meu pai, que impulsionaram o caminhar
À minhas irmãs, companheiras de caminhada
Ao Fernando, que compartilha o agora, a vida e os sonhos
e
Ao Ian, que faz do caminho leve e alegre e me inspira a continuar

AGRADECIMENTOS

Escrever os agradecimentos dessa tese é uma tarefa difícil e repleta de emoção. Foram quatro anos intensos, que incluíram muitas etapas e personagens. Já aviso que vai ser um texto longo!

Tudo começou em 2012, quando entrei no doutorado para estudar a população de onças-pintadas do Parque Estadual do Rio Doce - PERD, MG. Comecei a ir à campo para conhecer a região e auxiliar nas capturas de jaguatiricas do projeto da pesquisadora Cynthia Widmer de Azevedo. Foi uma experiência de campo fantástica participar das campanhas da Cynthia. Aprendi muito! O cuidado dela com os animais, a seriedade protocolar e a capacidade técnica me impressionaram muito. Cyn, gostaria de agradecer por todos os seus ensinamentos em campo e por toda nossa história de amizade e carinho que nasceu ali. Após auxiliar a Cynthia nas campanhas, iniciei juntamente com o Dr. Fernando Azevedo as visitas às propriedades rurais com ataques por onças. Durante essa etapa pude aprender muito com o Fernando. Obrigada Fernando, todo o aprendizado e foi muito enriquecedor para mim. Agradeço ainda à equipe de funcionários do PERD, especialmente ao diretor Vinícius de Assis Moreira pelo apoio ao projeto e aos funcionários Cimar, Cláudio, Alexandra e Tião.

Infelizmente, começamos a ter problemas com a verba e um grande corte no orçamento começou a inviabilizar os planos iniciais. Somado a isso, um acidente em janeiro de 2014 com uma cirurgia na coluna impossibilitou meu retorno para campo. Durante esse período, gostaria de agradecer imensamente ao apoio e carinho da Gwen e do Timothy Kittel. Gwen e Tim, many thanks for all your support during our stay and after my surgery in Colorado! Your presence and warmth were very important to my recover.

Depois de, com muito pesar, optar por não estudar mais a população de onças do Rio Doce. Sem recurso, sem bolsa, sem projeto e sem conseguir vislumbrar uma boa perspectiva, decidi não dar continuidade ao doutorado. Nesse momento preciso agradecer à Prof. Flávia Maria da Silva Carmo. Ela foi a grande responsável por eu dar prosseguimento. Flávia, obrigada pelo apoio, carinho e exemplo de que é possível ser mulher/pesquisadora/mãe! Se não fosse por você provavelmente eu não estaria apresentando essa tese. Agradeço também ao Prof. Carlos Sperber que exaltou minha capacidade e também me incentivou a continuar.

Em 2015 o Dr. Ricardo Solar assumiu oficialmente a minha orientação e comecei um novo projeto de doutorado. Ricardo, muito obrigada por me acolher como orientada sem me conhecer! Obrigada pela paciência, cuidado e seriedade com que me orientou. Suas contribuições e ensinamentos foram e são extremamente valiosas para minha formação como pesquisadora. Agradeço também ao Prof. Dr. Milton Ribeiro, colaborador e mentor muito presente no último ano. Miltinho, obrigada pelo carinho e encorajamento sempre. Agradeço também à Keila pelas conversas e carinho e aos meninos (Camilo e Nicolas) por alegrarem nossos encontros.

Agradeço também ao professor Dr. Otso Ovaskainen e a Dra. Nerea Abrego, colaboradores neste estudo. Nerea and Otso, thanks for borrowing to me your mathematical knowledge!

À pesquisadora Dra. Sandra Cavalcanti. San, obrigada pelas conversas e conselhos ao longo de tantos anos (13 desde que fui sua estagiária!). Por todo o aprendizado nos tempos do Pantanal e por seu exemplo de pesquisadora. Sua tese de doutorado e o tempo que passei trabalhando com você ainda são uma inspiração para mim! Obrigada também por concordar que eu usasse os dados que coletamos em Paranapiacaba.

Durante todo o doutorado, e antes dele, conversei e pedi conselhos, acadêmicos ou não, ao querido amigo Alexandre Martensen. Tank, obrigada pela paciência e por seu apoio em todas as etapas. Você é uma pessoa - e cientista - admirável. Agradeço também pela ajuda em campo, por nos levar em pontos que pareciam impossíveis e pelas cachacinhas nos dias gelados de campo! Por nos apresentar para as pessoas que seriam fundamentais no trabalho e por nos receber sempre tão bem na sua casa. Pelo auxílio em campo e hospitalidade também agradeço a Kika!

À amiga Erica Maggiorinni, companheira de campo, de atolamentos, de aventuras na Mata Atlântica quase desconhecida. Obrigada pela parceria Erica!

Agradeço a Viviane Brito pelo auxilio com a tabulação dos dados. Obrigada Vivi!

Agradeço também a todos que auxiliaram durante as coletas em campo. Essas foram as pessoas, especialmente o Matias, o Emmanuel, o Sr. Cid e o Nenê Caipira que me apresentaram uma Mata Atlântica até então para mim desconhecida. O sertão da Mata Atlântica, onde eu tive um vislumbre e me transportei para o que imagino ser algo próximo do que deveria ser essa floresta na época do descobrimento. Além de escutar causos de onças, aves, árvores e rios. Foi inesquecível! Obrigada. Estendo os agradecimentos aos demais companheiros das atividades de campo Sr. Zé Vieira, Sr. Paulinho, Sr. Pedro, Isaias e Jairo. Agradeço também ao Sr. Antônio e a Dona Maria pela hospitalidade e pelos cafezinhos.

Agradeço pelas valiosas contribuições durante a minha banca de doutorado ao Dr. Fabiano Rodrigues de Mello, ao Dr. Milton Cezar Ribeiro, ao Dr. Lucas Paolucci e à Dra. Flávia Maria da Silva Carmo.

À Fernanda Cavalcanti, parceira nessa empreitada! E que empreitada! Estradas, hotéis, doces de leite, burocracias e pizzas em fatias com cerveja em Viçosa. Saudades dos nossos perrengues! Obrigada pela parceria Fer! Tenho um carinho e admiração enormes por você!

Aos amigos, Dr. Rogério Cunha de Paula, Dr. Ronaldo Morato e Dr. Frederico Gemésio que se prontificaram a ceder dados e me apoiaram quando optei por mudar de projeto de doutorado. A Dra. Kátia Ferraz pelo apoio e conselhos. Ao Dr. Mauro Galetti pelas sugestões e ideias.

Aos meus amigos queridos, sempre presentes, especialmente Alessandra Bertassoni, Elisa Vianna, Felipe Fernandes, Fernanda Lira, Karina Felipe, Luciana Zuccherato, Lais Vitral, Ligia Faria Netto, Ligia Rodrigues, Maria Helena Calixto, Priscilla Teixeira e Talita. Aproveito para pedir desculpas pela minha ausência nos últimos tempos!

A querida Rosilene pelo carinho e atenção com o Ian (e conosco). Obrigada Rose, você foi fundamental para a conclusão desse trabalho!

Desde que entrei para a escola até a conclusão dessa tese se passaram 29 anos de estudo e vida acadêmica. Os principais responsáveis por isso, que fomentaram e permitiram que eu seguisse meus sonhos e construísse uma carreira acadêmica, foram os meus pais. Mãe e pai, chega a ser difícil escrever essas palavras sem um nó na garganta. Obrigada, obrigada, obrigada! Por me criarem com tanta presença e amor, por serem meu esteio! Por me incentivarem a desenvolver minhas potencialidades, por me cercarem de cultura e espírito crítico, por acreditarem no meu potencial e por me darem os melhores presentes: minhas irmãs. Mãe, obrigada pela paciência e me desculpe por tirar seu sono e sossego tantas e tantas vezes enfurnada no mato. Obrigada também pelos conselhos, pelo exemplo de sensibilidade e de mulher forte e corajosa! Pai, obrigada pelo apoio em todos os momentos e pelos conselhos sempre tão sensatos. Você é meu exemplo de caráter e justiça!

Rê e Lú, minhas irmãs tão amadas. Vocês são minhas companheiras de vida! Melhores amigas, melhores conselheiras e maiores incentivadoras. Seja para seguir carreira de cientista, seja para abrir uma padaria rs. Obrigada por estarem sempre de ouvidos a postos e braços abertos!

As minhas tias queridas, que também fazem parte da minha história e que sempre foram tão presentes e amorosas. Tia Reré, obrigada pelo incentivo, por todas as conversas, farofas e livros! Tenho um carinho especial por todos eles. Tia Vivi, obrigada pelo carinho. Por ser sempre acolhedora, por se preocupar com todos nós e por não permitir que a vida corrida nos distancie.

Aos queridos tio Paulo, tia Rosa e primos Thomaz e Paulinho.

Ao meu querido cunhado Felipe, sempre

Às queridas Léa, Cintia e Cyrlei e aos meninos Lucas, Gabriel e Ivo tão queridos e importantes para o Fernando e para nossa família.

Aos meus avós, que infelizmente já não estão aqui, mas que também fazem parte da minha história e do meu passado, e que deixaram um legado. Ao meu avô Thomaz agradeço pelo cuidado, carinho e pelos ensinamentos. Foi com ele que escrevi as primeiras letras e que descobri o mundo por um globo terrestre. A minha avó Maria, exemplo de generosidade e simplicidade. Com quem tinha um afeto muito especial. Sinto muito a falta de vocês.

Durante o período doutorado eu e o Fernando no re-encontramos, namoramos, casamos e tivemos um filho! Tudo em quatro anos. Fer, faltam palavras para agradecer sua paciência, dedicação e amor. Obrigada por compartilhar essa jornada comigo. Por ser meu companheiro, melhor amigo, conselheiro e colaborador cientifico! Obrigada por dividir sonhos, sorrisos e lágrimas, por dividir a vida. Seu brilho nos olhos e curiosidade sempre me movem. Sua presença me traz segurança e serenidade. Sua dedicação como pai, seu carinho e cuidado com o Ian me comovem e encantam. Te amo tanto e cada dia mais. Ainda temos muitas aventuras pela frente! Obrigada meu amor.

Desse amor todo aí de cima nasceu o Ian, melhor presente que a vida me deu! Com ele nasceu o amor mais inexplicável, o maior medo e a alegria mais verdadeira. O encanto de vê-lo descobrindo o mundo é uma inspiração incrível! Obrigada filho por cada gargalhada e por todos os melhores abraços! Mesmo sem entender a loucura desses últimos meses, sua presença fez com que tudo ficasse mais fácil e que sua mãe se tornasse mais valente. Mamãe já pode voltar a te levar mais pra passear, a te mostrar o céu com o papai e te ajudar a voar. Te amo “pipitico”.

Infelizmente, imagino que tenha esquecido algumas pessoas. Se for o caso, me desculpem e se sintam imensamente agradecidas.

Agradeço ao Instituto Pró-Carnívoros pela administração do projeto “Iniciativa Corredor da Onça-Pintada na Mata Atlântica”, à Panthera pelos equipamentos e financiamento e ao CENAP/ICMBio pelo apoio. Agradeço também pelas bolsas recebidas do Programa Hidroex-UNESCO e da CAPES.

Espero com essa tese contribuir de alguma forma para a conservação da comunidade de grandes mamíferos e da Mata Atlântica. Que possamos investir mais em ciências, políticas públicas e em restauração. Criar a possibilidade para que a vida e os processos sigam seu percurso e nos surpreendam.

“Throughout our history as a species we have tolerated the dangerous, problematic presence of big predators, finding roles for them within our emotional universe. But now our own numerousness, our puissance, and our solipsism have brought us to a point where tolerance is unnecessary and danger of that sort is unacceptable. The foreseeable outcome is that in the year of 2150, when human population peaks at around eleven billion, alpha predators will have ceased to exist - except behind chain-link fencing, high-strength glass, and steel bars. After that time, as memory recedes and the zoo populations become ever more genetically attenuated, ever more conveniently docile, ever more distantly derivative from the real thing, people will find it hard to conceive that those animals were once proud, dangerous, unpredictable, widespread, and kingly, prowling free among the same forests, rivers, estuaries, and oceans used by humanity. Adults, except a few recalcitrant souls, will take their absence for granted. Children will be startled and excited to learn, if anyone tells them, that once there were lions ate large in the very world.”

*(*David Quammen)

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RESUMO

PERILLI, Miriam Lucia Lages. D.Sc., Universidade Federal de Viçosa, dezembro de 2016. **Humanos, Predadores de Topo e suas Presas nas Cascatas Tróficas da Floresta Atlântica.** Orientador: Ricardo Ribeiro de Castro Solar.

Florestas tropicais são os ecossistemas mais biodiversos do planeta e, no entanto, se encontram severamente ameaçadas por impactos antrópicos. Entre os principais impactos, destacam-se a perda de habitats e a fragmentação e degradação das áreas remanescentes (e.g. caça, extração de madeira, queimadas). Quando grandes vertebrados conseguem persistir nesses ambientes, tanto o habitat remanescente como a reorganização intraespecífica podem influenciar a distribuição e a abundância das espécies. No entanto, é difícil separar os efeitos dentro das comunidades daquele causados por seres humanos, como a maior parte dos trabalhos faz. Por isso, além da modificação dos habitats é preciso considerar o impacto direto da caça furtiva nessas florestas tropicais. Nesse contexto, na presente tese abordamos a distribuição espaço-temporal dos mamíferos de médio e grande porte em um dos maiores remanescentes de Floresta Atlântica Brasileira e propusemos a inserção dos humanos como uma espécie com impacto desproporcional na cadeia alimentar. No Capítulo I descrevemos a dinâmica espaço-temporal da comunidade de mamíferos de médio e grande, registradas por meio de armadilhas-fotográficas, utilizando um modelo de distribuição agrupada de espécies. Neste capítulo conseguimos observar que os mamíferos terrestres de médio e grande porte apresentaram respostas variadas às condições ambientais, bem como padrões de co-ocorrência que podem indicar compartilhamento de nichos ambientais e de interações intraguilda. No Capítulo II propusemos um modelo conceitual com quatro cenários, incluindo o papel dos predadores de topo e dos seres humanos na cadeia alimentar. Nele concluímos que a caça furtiva apresenta grande impacto nas cadeias alimentares e não deve ser tratada como uma ameaça “invisível”.

ABSTRACT

PERILLI, Miriam Lucia Lages, D.Sc., Universidade Federal de Viçosa, December, 2016. **We, Predators: Humans, Apex Predators and their Preys in the Atlantic Forest Trophic Cascades**. Adviser: Ricardo Ribeiro de Castro Solar.

Tropical forests represent Earth's richest biodiversity ecosystems and yet are severely threatened by anthropogenic effects. Humans major trends affecting tropical forests are habitat loss, fragmentation, and degradation of remaining forest. When large vertebrate species are able to persist in fragmented landscapes, the remaining habitat and the reorganization of species biotic interactions may influence their distribution and abundance. Yet, it is difficult to separate those effects from the direct impact of humans. Therefore, in addition to habitat modification we must also account for the direct impact of vertebrate harvest by humans in Neotropical forests. In the following chapters, we observed the current picture of medium and large mammals' distribution in one the core forest remnants and proposed to incorporate humans as a “hyperkeystone” species in the Atlantic forest food webs. In Chapter I, we described the spatio-temporal dynamics of meso and large mammals, using a joint-species distribution model to the data recorded by camera-traps. We observed that the medium and large terrestrial mammal community varied in their responses to environmental conditions and showed patterns of co-occurrences that may indicate shared environmental niches or intra-guild interactions across time and space. In Chapter II, we proposed a conceptual model with four likely scenarios for the role of apex predators and human beings in natural interaction webs. We concluded that poaching has outsized impacts on the food webs and must not be considered an “invisible” threat. Thus, from the ecological and conservationist perspective, we must account for our own species not as external separate entity, but as an active part of the ecosystems that have direct impacts on trophic interactions.

SUMÁRIO

GENERAL INTRODUCTION

Tropical forests are Earth's richest biodiversity ecosystems and yet are severely threatened by anthropogenic effects (Barlow et al. 2016). Humans major trends affecting tropical forests are conversion to nonforest, degradation of remaining forest via hunting, selective logging, fire, edge effect and regeneration of secondary forest (Lewis et al. 2015). In this scenario of intense habitat loss, fragmentation and disturbance, it is essential to understand biodiversity responses (Fahrig 2003; Betts et al. 2014; Haddad et al. 2015).

A well-known consequence of habitat fragmentation is the edge effect in fragment borders. More fragmented landscapes contain more edge and this can increase the probability of an individual leaving for the matrix, and increase human wildlife contact and conflict (Wang et al. 2015; Fahrig 2003). In the Atlantic Forest, only 7.7% of the total forest area remnants is located farther than one kilometer from any edge, and 12 km is the maximum distance from any nonforested area (Ribeiro et al. 2009). The result is a severely fragmented landscape where a significant portion of the habitat in under severe edge effect. The responses to forest edge associated with large mammals is usually related to (1) an increase in exposure to threats and conflicts with humans in fragment borders, especially for large carnivores (Woodroffe 1998; O'Brien et al. 2003; Balme et al. 2010; Fahrig 2003); (2) changes in herbivores foraging patterns due abiotic environment responses to microclimate modification that affected seedling recruitment and tree diversity (Asquith & Mejía-Chang 2005; Norris et al. 2008).

Another consequence of habitat modification is species loss. Besides the impacts on foraging resources availability and refuge, one major impact of human-induced changes to tropical forests is hunting and megafauna extinctions (Lewis et al.

2015). The loss of large vertebrate species can be critical for the maintenance of the community's integrity (Redford 1992; Terborgh et al. 2001; Galetti & Dirzo 2013). Large carnivores loss, for example, may cause severe consequence for the ecosystems, and their ecological importance is apparent, as even a few individuals can exert strong top-down control on prey populations (Roemer et al. 2009; Ryall & Fahrig 2006; Terborgh et al. 2001). Species with these features occupy the elevated position of "apex predators" on the trophic ladder, and their role as ecosystem regulators is now firmly embedded in ecological theory (Estes et al. 2011; Ripple et al. 2014; Wallach et al. 2015). Top-down ecological consequences of apex predators removal and trophic cascades have been described on marine (e.g. Pinnegar et al. 2000; Baum & Worm 2009; Estes et al. 2011) and terrestrial ecosystems (e.g. da Fonseca & Robinson 1990; Miller et al. 2001; Terborgh et al. 2001). Large carnivores may also have direct influence on the intermediary predators and consequently throughout the community structure through the effect known as mesopredator release - proliferation of intermediate predators that reduce or eliminate smaller vertebrate species (Crooks & Soulé 1999; da Fonseca & Robinson 1990; Ritchie & Johnson 2009).

However, it is difficult to separate the effects of carnivores from those of humans and evidences of trophic regulation must be viewed with caution as anthropogenic modifications have already altered most of tropical systems (Miller et al. 2001). Humans can directly affect the trophic regulation by harvesting preys (acting like an apex predator or a hyperseystone species) (Darimont et al. 2015; Worm 2015; Worm & Paine 2016) or indirectly by creating a landscape of fear (Brown et al. 1999; Laundre et al. 2010), although those effects usually are not incorporated in trophic ecology studies. The role humans play in trophic cascades could be reached by studying ecosystems in which both humans and apex predators have coexisted for extended periods (Dorresteijn et al. 2015), as in the case of the Atlantic Forest. Investigating how humans alter trophic regulation is mandatory given the extent and speed of global anthropogenic environmental change (Dorresteijn et al. 2015).

The direct impact of vertebrate harvest by humans in Neotropical forests have been investigated in Amazonia (e.g. Peres 2001; Bodmer & Lozano 2001; Jerozolimski & Peres 2003; Peres & Palacios 2007; Endo et al. 2010; Levi et al. 2011), an in a smaller scale in the Atlantic Forest (e.g. Cullen et al. 2000; Cullen et al. 2001; Canale et al. 2012; da Silva et al. 2016). There is evidence that poaching causes changes on mammal assemblages structure and on biomass and abundances of large vertebrates in Neotropical forests (Cullen et al. 2000; Jerozolimski & Peres 2003; Endo et al. 2010). Indeed, in the Atlantic Forest poach seems to be the main factor emptying forest fragments in short-term (Cullen et al. 2000), and supposedly accelerate large bodies species local extinctions (Canale et al. 2012).

The lack of information on species responses to habitat and to biotic relationships, including here the different actors of the food web and responsible for important ecosystem services, can create a false sense of preserved system only by the presence of the species. Nevertheless, most studies investigating species occurrence and abundance explore the relation of species presence only with environmental variables, and do not consider species interactions that may affect observed patterns (Araújo & Luoto 2007). In 2011, we conducted a large camera-trap sampling in one the largest Atlantic Forest remnants to investigate jaguar populational status. From that dataset, we were able to gather a picture of medium and large mammals spatio-temporal dynamics, that we describe in Chapter I. In Chapter II, grounded on the concept of human beings as an “hyperkeystone” species, we constructed an opinion piece where we propose a conceptual model that incorporate the impact of poaching in Atlantic Forest trophic webs.

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CHAPTER I: FORMATTED ACCORDING *JOURNAL OF ANIMAL ECOLOGY* SUBMISSION INSTRUCTIONS

PATTERNS OF SPATIO-TEMPORAL CO-OCCURRENCE OF MESO AND LARGE MAMMALS IN THE CORE OF THE BRAZILIAN ATLANTIC FOREST

Miriam Lucia Lages Perilli[1,2*], Fernando Lima[3,4], Nerea Abrego[5], Otso Ovaskainen[5,6], Milton Ribeiro[4], Alexandre Camargo Martensen[7], Sandra Maria Cintra Cavalcanti[2], Ricardo Ribeiro de Castro Solar[1,8]

[1] Programa de Pós-graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa - UFV, Viçosa, Minas Gerais, Brazil;

[2] Instituto para Conservação dos Carnívoros Neotropicais - Pró-Carnívoros, Atibaia, São Paulo, Brazil;

[3] IPÊ - Instituto de Pesquisas Ecológicas, Nazaré Paulista, São Paulo, Brazil;

[4] Programa de Pós-graduação em Ecologia e Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista – UNESP, Rio Claro, São Paulo, Brazil;

[5] Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway;

[6] Department of Biosciences, University of Helsinki, Helsinki, Finland;

[7] Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada;

[8] Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais - UFMG, Belo Horizonte, Minas Gerais, Brazil.

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

SUMMARY

1. In a scenario of ongoing habitat loss, fragmentation, and deterioration, it is essential to understand how the native biota responds in order to design evidence-based conservation plans as well as predict the resilience of native communities.

2. In the Brazilian Atlantic Forest there is a low density of predators and a depleted prey assemble, which might lead to a spatial-temporal reorganization of species and their interactions.

3. The spatio-temporal dynamics of mammals can be a consequence of competition due trophic overlap, an answer to predator-prey race or as the result of shared resources and habitat.

4. Here we describe the spatio-temporal dynamics of meso and large mammals, within the core of the remaining Brazilian Atlantic Forest, using a joint-species distribution model to the data recorded by camera-traps.

5. We observed that the medium and large terrestrial mammal community varied in their responses to environmental conditions and showed patterns of co-occurrences that may indicate shared environmental niches or intra-guild interactions across time and space.

6. Most of the species were negatively associated with domestic dog and poachers. This is a remarkably important information as we must incorporate this “invisible” threats in conservation policies. In the Atlantic Forest scenario, we believe that the steps forward for the ecosystem conservation must account not only for restauration but also for habitat integral protection.

Key-words: species interaction, camera-traps, joint-species distribution model, predators, preys, domestic dog impact, hunting impact.

INTRODUCTION

Despite representing the richest biodiversity ecosystems on Earth, tropical forests are at the forefront of conservation concerns, as they have been severely threatened by anthropogenic effects (Slik et al. 2015; Barlow et al. 2016). Among the most important anthropogenic threats for the native tropical biota, deforestation and degradation of remaining forests via intensive hunting, selective logging and man-made fire worth highlighting (Gibson et al. 2011; Lewis et al. 2015). In this scenario of ongoing habitat loss, fragmentation and deterioration, it is essential to understand how the native biota responds to these changes in order to design evidence-based conservation plans as well as predict the resilience of native communities (Fahrig 2003; Betts et al. 2014; Haddad et al. 2015).

The Atlantic Forest is among the most threatened tropical forests, and draws a high conservation concern due its strong concentration of endemic and small-ranged species (Jenkins et al. 2015). In this biome, almost 93% of the total remaining forest area is located up to 1km from any forest edge. Most striking, 12km is the maximum distance from remnants to any nonforested area (Ribeiro et al. 2009). Therefore, the spatial configuration of the remnant Atlantic Forest is in a severely fragmented landscape, where a significant portion of the forest area consists is located near to edges or is embedded in nonforested matrix. In this context, native large mammal communities are highly influenced by the amount of forests edges, since edges increase the exposure of mammals to humans and thus increase the probability of conflicts, especially in the case of large carnivores (Woodroffe 1998; O'Brien et al. 2003; Balme et al. 2010; Wang et al. 2015; Fahrig 2003). Further, the microclimatic modifications in edge habitats affect seedling recruitment and tree diversity, and consequently the foraging patterns of herbivores (Asquith & Mejía-Chang 2005; Norris et al. 2008).

A major consequence of habitat loss and deterioration is the loss of sensitive species (i.e. defaunation), among which large vertebrate loss are particularly critical for the maintenance of ecosystem functioning (Redford 1992; Terborgh et al. 2001; Galetti & Dirzo 2013). Among of the myriad of defaunation causes, hunting activities can be considered the main direct cause in the remaining forest fragments of the

Atlantic Forest (Cullen et al. 2000; Canale et al. 2012; Galetti et al. 2016). After decades of poaching, animal populations have declined at multiple trophic levels. Yet, there is a lack of knowledge of how these declines are perceived at the community level, and especially about how declines of certain species influence other species. Thus, information on interspecific interactions, focusing on species located at different trophic levels, can provide a more predictive perspective for conservation. For instance, the jaguar (*Panthera onca*, the Atlantic Forest apex predator) has been drastically extirpated and is now present in only 2.8% of the remaining habitat, with no subpopulations larger than 85 individuals (Paviolo et al. 2016). In fact, anthropogenic activities are exposing jaguars to a high risk of extirpation, eliminating an apex predator from an entire tropical biome for the first time (Galetti et al. 2013). Others trophic levels are under the same threats, including large seed predators, such as peccaries, deers and tapirs, that are also facing population declines, which might have drastic consequences for seed predation and eventual dispersal in this biome (Azevedo & Conforti 2008; Altrichter et al. 2012; Galetti, Bovendorp, et al. 2015). Furthermore, in addition to its role as seed predators, peccaries and deers are important prey for jaguars as well (Emmons 1987; Aranda 2002; Azevedo 2008). Thus, in the Atlantic Forest we have a low density of predators and a depleted prey assemble, which might lead to a spatial-temporal reorganization of species and their interactions (i.e. competition and predation).

Theoretically, interspecific competition is enhanced when species from same trophic levels overlap their use of a limited resource (Hairston et al. 1960). But for large vertebrates, it is a challenge to empirically record such interactions, especially when focusing on entire communities (Ritchie et al. 2009).

The spatio-temporal dynamics of mammals can also be associated with the predator-prey race. Preys develop evolutionary strategies to avoid predators (Brown et al. 1999). The fear of predation cause preys to be more vigilant and to select safer habitats and time periods that potentially reduce their vulnerability to predation – a so called “landscape of fear” (Brown et al. 1999; Laundre et al. 2010). Nevertheless, species may co-occur if they simply share their habitat requirements. Likewise, species may purely have divergent habitat requirements and appear to be negatively related (Sebastián-González et al. 2010)

In this paper we describe the spatio-temporal dynamics of meso and large mammals within the core of the remaining Brazilian Atlantic Forest. Our main aim is to understand the patterns of species co-occurrences that may indicate shared environmental preferences or intra-guild interactions across time and space. To assess these patterns, we first controlled major environmental variables that are prone to influence species detectability and spatial-temporal distribution at the study site. We also considered the characteristics of the location in which each camera-trap station was installed, as it may impact species detectability, as well as we checked for the influence of domestic dogs and poachers presence on the large mammals community.

We hypothesize that some pairs of species within trophic guilds, and with very similar niches requirements to have negative co-occurrence patterns as a result of competitive interactions. At the same time, we expect some heterospecific attraction due similar habitat requirements. For this, we fitted a joint-species distribution model to mammal occurrence data recorded by camera-traps.

METHODS

STUDY AREA AND SAMPLING DESIGN

Mammal's occurrences were recorded from June to October of 2011 along one the largest continuous forest remain of the Brazilian Atlantic Forest, located in the

Serra do Mar bioregion (Fig. 1). The study area extended from the region of Alto Paranapiacaba (AP) in the North to Vale do Ribeira (VR) in the South, and covered approximately 800 km^2. During the period of the study the AP region was comprised by several private ranches, with different activities (e.g. ecotourism, mining, forestry). The VR portion was located inside one large private palm farm. Due to the large geographic extension, the survey was carried out simultaneously by two field teams, one in the North and other in the South. The sampling consisted of 39 camera-trap station composed of two paired camera traps, operating 24 hours/day. The sampling locations were selected in order to maximize the chances of mammal records (roads and game trails). The mentioned roads were used for surveillance and presented only sporadic vehicle traffic. All the records were inserted in a relational database (Camera Base - Copyright 2012 Mathias Tobler) structured in Microsoft Access DBMS. For the analysis, we established 60 minutes as the minimum interval for independence among mammal presence detections.

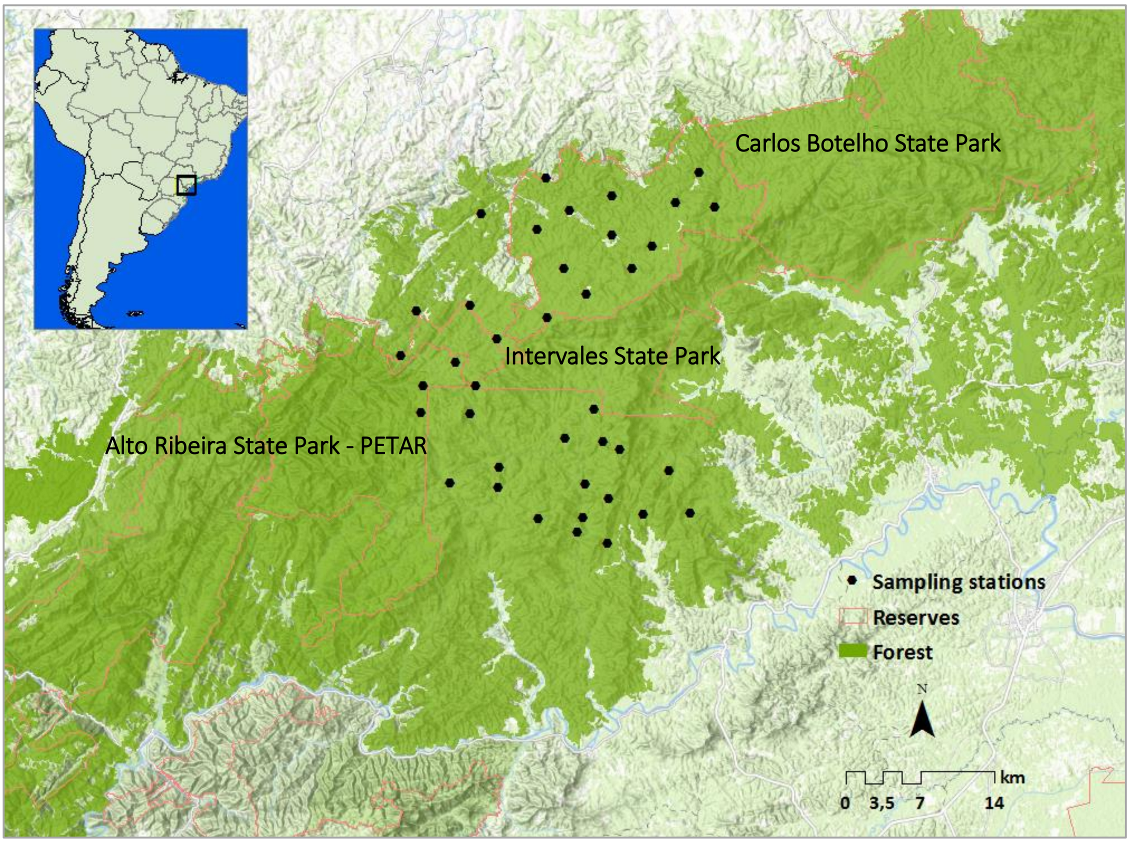

Fig. 1. Study area with spatial distribution of camera-trap stations. Sources: Esri, HERE, DeLorme, increment P Corp., NPS, NRCan, Ordnance Survey, © OpenStreetMap contributors, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

ENVIRONMENTAL VARIABLES

We selected as environmental co-variables "altitude", "distance to the edge", "distance to water" and the camera-trap station location "on the road" or "off the road", meaning the stations on game trails. Altitude was calculated from a Digital Elevation Model (DEM) (SMA-SP, 2016). The "distance to the edge" was calculate as the Euclidian distance from each sampling point to the nearest forest boundary. The forest vector layer used was from the "Atlas of the Atlantic Forest Remains" from 2013-2014, SOS Mata Atlântica (http://mapas.sosma.org.br/dados/). The water courses layer was based on the drainage network extracted from the DEM. All the Geographic Information System (GIS) proceedings were executed on ArcMap 10.4.1.

STATISTICAL ANALYSES

We fitted a spatio-temporally explicit joint species distribution model to the data (Warton et al 2015), which involved species-specific traits and measured environmental covariates. We modelled the presence-absence of mammals in each 60 min interval of each camera-trap station using a probit regression. To account for the spatio-temporal structure of the data, we included the spatial location of the camera-trap stations as a spatially explicit random effect, and days as a temporally explicit random effect. We included the station-day pair as a random effect aimed at identifying co-occurrences among the species. For fitting the random effects we used the method described in Ovaskainen et al 2016a, 2016b. We included as continuous environmental covariates the altitude, distance to the nearest forest edge, distance to the nearest water source and if the camera-trap station was located on the road or off the road (on animal trail). To model the hourly temporal dynamics of mammals, we also included as predictors the periodic functions $(\cos\left(2 * \pi * \frac{hour}{24}\right)$ and $\sin(2 * \pi * \frac{hour}{24}))$. All continuous covariates were normalized to mean zero and standard deviation one prior to analyses. As species-specific traits, we included a classification of the species into the five trophic categories: large carnivores, large herbivores, meso carnivores, meso herbivores, and omnivores. The influence of traits in determining species' responses was modelled as in Ovaskainen et al. (2016b). We fitted the model to the data with Bayesian inference, using the posterior sampling scheme of Ovaskainen et al. (2016a). We assessed how accurately the model predicted species occurrences at the levels of days, camera-trap stations, and station-day pairs by computing the squared correlations between the predicted and true numbers of occurrences. To assess how much of the variation in species occurrences was explained by traits, measured environmental covariates and random effects, we used the variation partitioning procedure described in Ovaskainen et al (unpub).

We used the parameterized model to infer the residual positive and negative species-to-species associations (i.e. variation remaining after accounting for the environmental variation) at the levels of days, camera-trap stations and station-day pairs, by applying the method described in Ovaskainen et al (2016a).

RESULTS

SPATIAL AND TEMPORAL STRUCTURE OF MAMMAL COMMUNITIES

Altogether we recorded 951 occurrences of 22 medium and large-sized mammals (>2kg) over 3473 camera-trap stations/days (Table 1). The mean altitude of sampled area was 617m (94 - 876m). The mean station distance from the forest edge was 3200m (120 - 9000m), and from water courses 356m (5 - 1260m).

Table 1. Medium and large mammals recorded during the camera trapping survey in Paranapiacaba region in 2011, São Paulo state, Brazil. We excluded repeated species records within 60 minutes' interval.

Species	Common	N.records	Trophic guild	Status (IUCN)
Cabassous tatouay	great naked-tail armadillo	01	myrmecophaga	Least Concern
Cerdocyon thous	crab-eating fox	10	omnivore/insectivore	Least Concern
Cuniculus paca	spotted paca	38	meso herbivore	Least Concern
Dasyprocta azarae	agouti	07	meso herbivore	Data Deficient
Dasypus novemcinctus	nine-banded armadillo	12	omnivore/insectivore	Least Concern
Eira barbara	tayra	27	meso carnivore	Least Concern
Leopardus pardalis	ocelot	54	meso carnivore	Least Concern
Leopardus guttulus	oncilla	26	meso carnivore	Vulnerable
Leopardus wiedii	margay	23	meso carnivore	Near Threatened
Mazama bororo	small red-brocked deer	45	large herbivore	Vulnerable
Mazama gouazoubira	deer	15	large herbivore	Least Concern
Panthera onca	jaguar	40	large carnivore	Near Threatened
Procyon cancrivorus	crab-eating raccoon	29	omnivore/frugivore	Least Concern

Puma concolor	puma	90	large carnivore	Least Concern
Puma yagouaroundi	jaguarundi	05	large carnivore	Least Concern
Sapajus nigritus	black capuchin	01	meso herbivore	Near Threatened
Speothos venaticus	bush dog	01	meso carnivore	Near Threatened
Tapirus terrestris	tapir	388	large herbivore	Vulnerable
Canis familiaris	domestic dog	43	Meso carnivore	-
Homo sapiens	Poacher	17	Large carnivore	-
Bos taurus	Cattle	01	Large herbivore	-

Averaged over the species, the models explained 29% of the variation in species occurrences at the daily level (Fig. 2a). Pooling the data over the days, the model explained 67% of the variation among the stations (Fig. 2b). Conversely, pooling the data over the stations, the model explained 38% of the variation among the days (Fig. 2c).

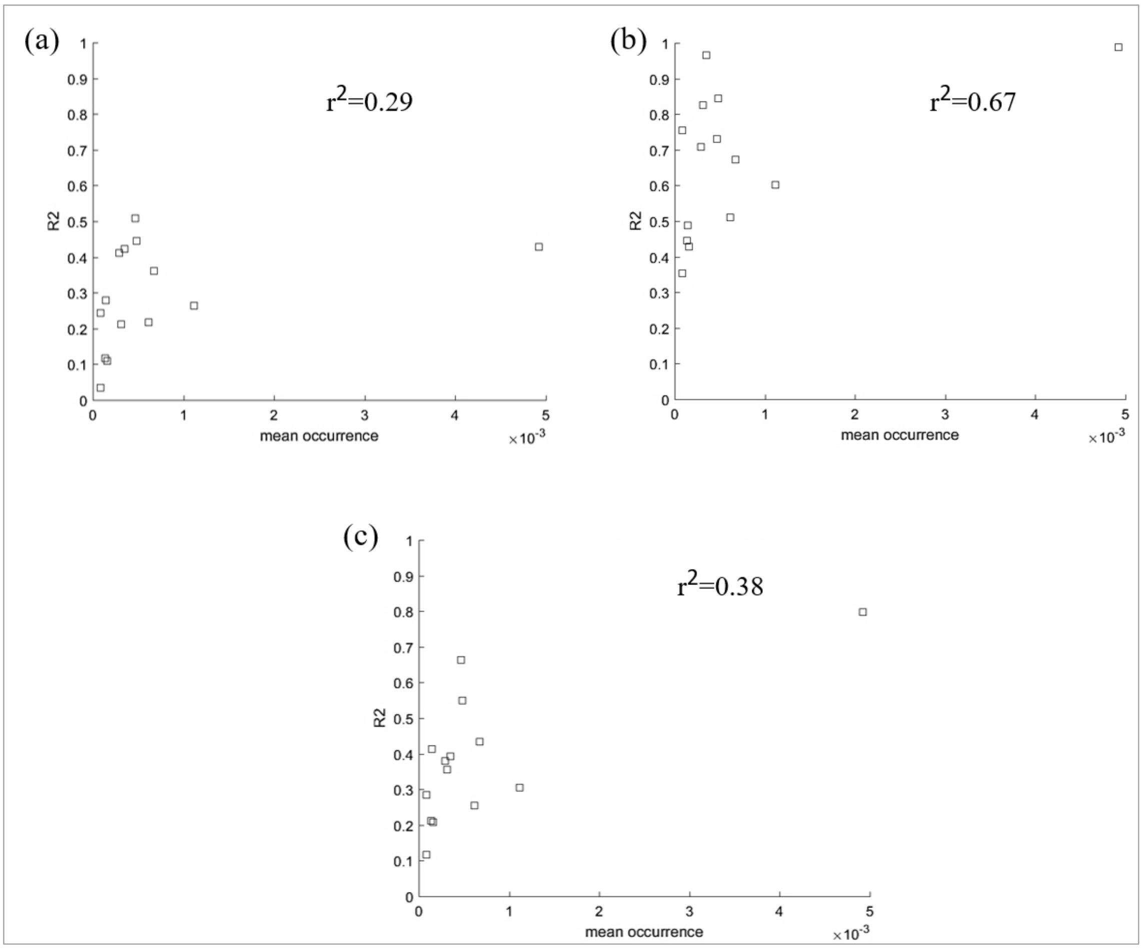

Fig. 2. Squared correlations between the predicted and true numbers of species occurrences at the levels of days (a), camera-trap stations (b), and station-day pairs (c).

The fixed effects (i.e. responses of large mammals occurrences to the measured environmental covariates) contributed with 74% of the explained variation, and thus the random effects accounted for the remaining 26% (Fig. 3). The most important predictor (26% of explained variation) was whether the camera-trap was located on a road or not, whereas the second most important predictor was the periodic variation in species occurrence related to the time of the day (14%). Among the remaining covariates, the higher variance was attributed to the presence of dogs (12%), followed by proximity to water (7%), altitude (6%), and the presence of poachers (5%). The trait classification explained 58% of the species responses to the measured covariates, meaning that the species responses to the covariates were more similar within the trait categories than between them. Among the random effects, station (11%) and station-day combination (10%) explained a similar amount of variation, whereas the effect of day (5%) was smaller.

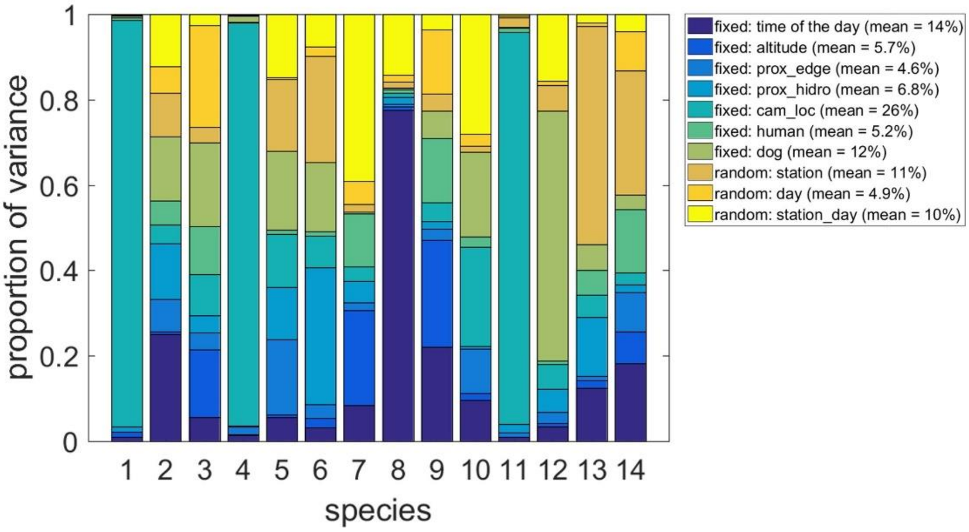

Fig. 3. The relative proportions of variation in species occurrence attributed to the fixed effects and to the random effects at the different spatio-temporal scales.

Species varied in their responses to the environmental conditions (Fig. 4). Some species occurred on locations at higher altitudes (*Cerdocyon thous, Leopardus wiedii, Tapirus terrestris*) and others on locations at lower altitudes (*Dasyprocta azarae, Mazama gouazoubira*) (Fig. 4a). Five species (*Leopardus guttulus, Panthera onca, Procyon cancrivorus, Puma concolor and Tapirus terrestris*) were more often found in locations far away from edges and three (*Cuniculus paca, Dasypus novemcinctus, Leopardus pardalis*) in locations near edges (Fig. 4b). Four species were more commonly observed in locations far from water sources (*Leopardus guttulus, Procyon cancrivorus, Puma concolor, Puma yagouaroundi*) and four in locations near water sources (*Cerdocyon thous, Cuniculus paca, Leopardus pardalis, Leopardus wiedii*) (Fig. 4d).

Whether the camera-trap station was on a road or not had a major influence on the occurrences of many species: *Leopardus pardalis, Leopardus wiedii, Mazama gouazoubira, Panthera onca* and *Puma concolor* were more commonly observed at cameras located at a road, whereas *Cerdocyon thous, Cuniculus paca, Dasypus novemcinctus, Leopardus guttulus, Mazama bororo, Procyon cancrivorus* and *Puma yagouaroundi* were more commonly observed at cameras located on game trails (Fig. 4c). Except for *Mazama bororo*, the presence of domestic dogs decreased the probability of detection for all species, though not all of these gained a strong statistical support (Fig. 4e). The presence of humans decreased the probability of observing all the other species, the result gaining strong statistical support for 8 out of the 14 species (Fig. 4f).

The activity patterns of most species peaked either during the night hours (Fig. 5), while for a few species they peaked in the day (*Dasyprocta azarae, Eira barbara,* *Puma concolor, Puma yagouaroundi*) or in the evening (*Mazama bororo, Panthera onca*).

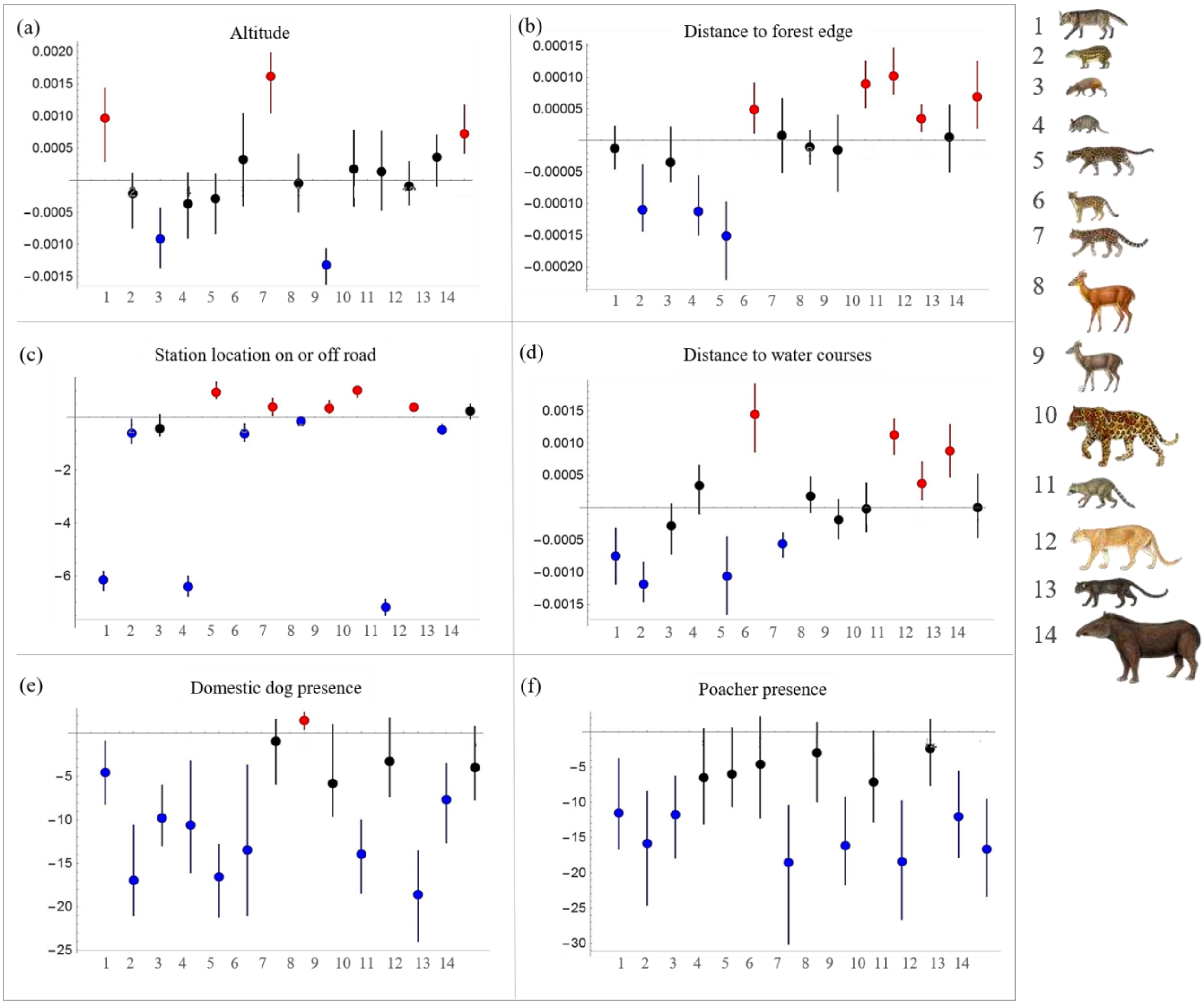

Fig. 4. 95% credible intervals for the parameters measuring the influence of measured covariates in explaining the occurrences of mammal species. The vertical axes comprise the normalized covariates. Marked with blue those results for which the covariates negatively influenced the occurrences of the species and with red the results for which the covariates positively influenced the occurrences of the species. In black the results where the co-variates did not show strong statistical support. *1. Cerdocyon thous, 2. Cuniculus paca, 3. Dasyprocta azarae, 4. Dasypus novemcinctus, 5. Leopardus pardalis, 6. Leopardus guttulus, 7. Leopardus wiedii, 8. Mazama bororo, 9. Mazama gouazoubira, 10. Panthera onca, 11. Procyon cancrivorus, 12. Puma concolor, 13. Puma yagouaroundi, 14. Tapirus terrestris.*

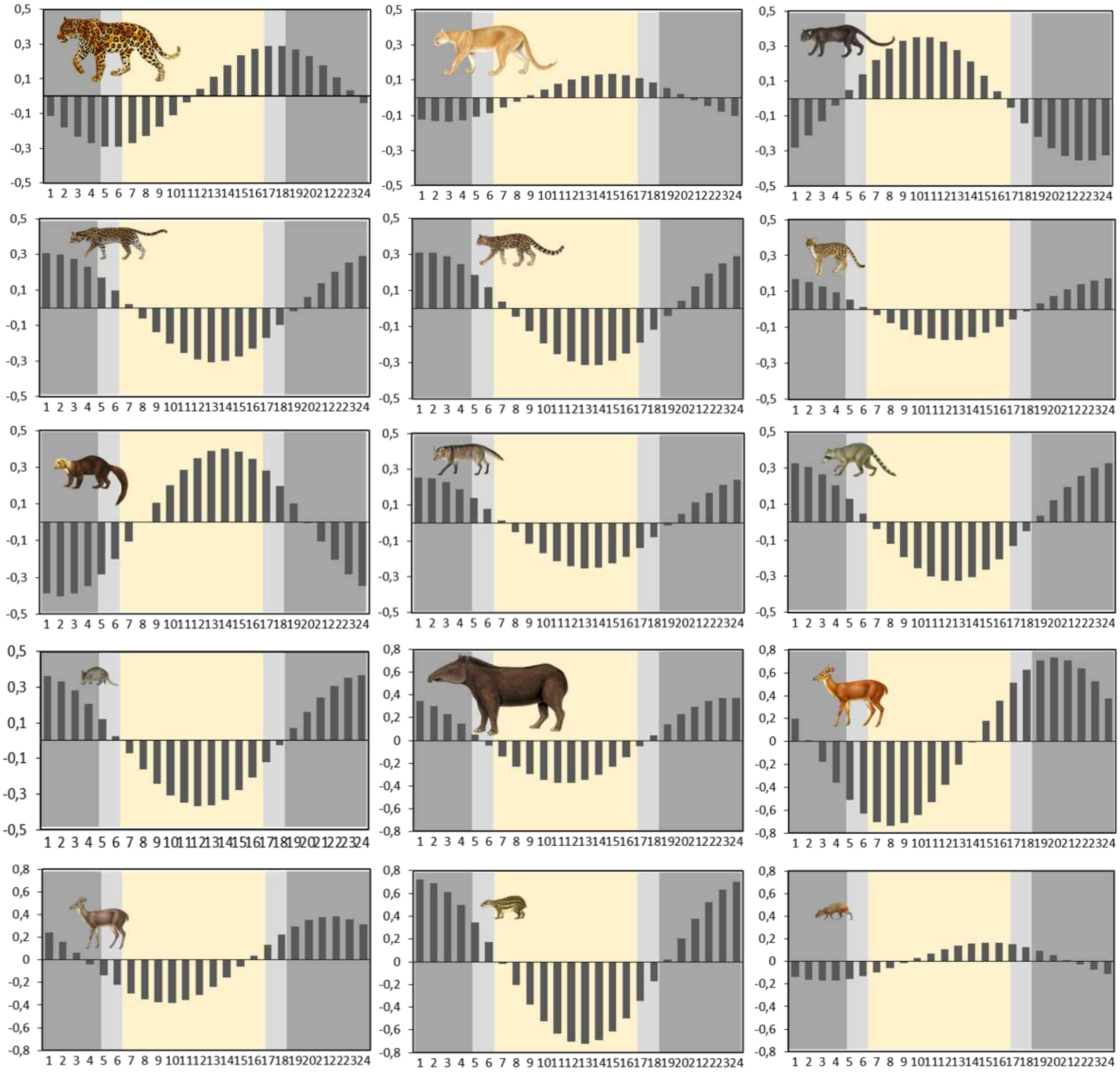

Fig. 5. Mammal activity patterns during the day hours (1-24h). Positive values indicate that the animals are active, and negative that they are not. In order from top to botton, left to righ: *Panthera onca, Puma concolor, P. yagouaroundi, Leopardus pardalis*, *L. wiedii*, *L. guttulus, Eira barbara*, *Cerdocyon thous*, *Procyon cancrivorus*, *Dasypus novemcinctus*, *Tapirus terrestris, Mazama bororo, M. gouazoubira, Cuniculus paca* and *Dasyprocta azarae.* Dark grey representing nigh, light grey crepuscular and tan day.

SPATIO-TEMPORAL CO-OCCURRENCE PATTERNS OF MAMMALS

While the random effects of station and day are likely to present the influences of missing environmental covariates, the random effect of station-day may contain signals of species interactions. The species-to-species associations at this level were predominantly positive (Fig. 6), meaning that if some species was observed in a given day in a given station, also the other species were generally more likely to be seen. Especially strong positive associations were seen between *Cuniculus paca, Leopardus wiedii, Mazama bororo, Panthera onca, Procyon cancrivorus, Puma concolor* and *Tapirus terrestris.*

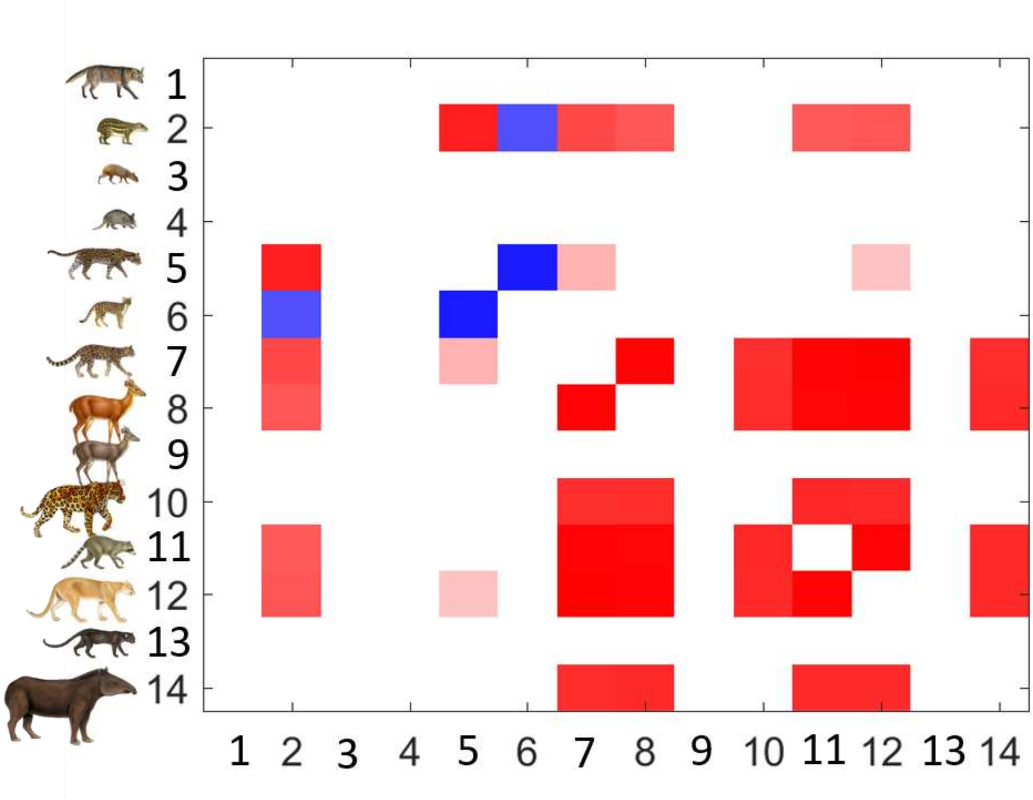

Fig. 6. Matrix station-day. Mammal species-to-species associations at the levels camera-trap stations-day with at least 95% posterior probability. Species pairs showing a positive association are indicated by red, species pairs showing a negative association are indicated by blue and the remaining cases are shown by white. 1. *Cerdocyon thous,* 2. *Cuniculus paca,* 3. *Dasyprocta azarae,* 4. *Dasypus novemcinctus,* 5. *Leopardus pardalis,* 6. *L. guttulus,* 7. *L. wiedii,* 8. *Mazama bororo,* 9. *M. gouazoubira,* 10. *Panthera onca,* 11. *Procyon cancrivorus,* 12. *Puma concolor,* 13. *P. yagouaroundi,* 14. *Tapirus terrestris.*

DISCUSSION

In this study, we observed that the medium and large terrestrial mammal community varied in their responses to environmental conditions and showed patterns of co-occurrences that may indicate shared environmental niches or intra-guild interactions across time and space. Our hypothesis was that the presence of one species in a specific day and location would affect the presence of other species, especially within trophic guilds. In a daily scale we were able to identify species co-occurrence responses, and once we pull together the species-to-species association in a spatio-temporal perspective we detected several positive associations that can be related to habitat quality and heterospecific association. We highlight that we must be careful about inferring species interactions since they may result from differences in habitat preferences among species or from spurious correlations with other factors.

Some species of the large mammals assemble were further recorded near or far forest edges. The species that were found near habitat edge, specially *L. pardalis*, could be avoiding the presence of larger competitors, as *P. onca* and *P.concolor*, that were more commonly observed far away from edges. Also, *L. pardalis* may be benefiting from an expected increase in small prey abundances near the ecotone. Large mammals responses to edge effect was also noticed for elephants in Sumatra (Kinnaird et al. 2003) and for sambar and muntjac deers in Borneo (Brodie et al. 2015). In Amazon, no evidence was found to suggest a direct response of large mammals to edges (Norris et al. 2008). As already stablished for other groups, as small mammals and birds (e.g. Metzger et al. 2009; Stevens & Husband 1998; Pires et al. 2004), our results demonstrate that edge effect can also affect certain large mammals.

The location of the camera-trap station was an important predictor, as expected. Apart from *M. gouazoubira*, the species positively associated with roads were all predators (*L. pardalis, L. wiedii, P. onca, P. yagouaroundi*). Similarly, most of the species negatively associated with roads can be considered under a predator pressure (i.e. *C. paca, D. azarae, D. novemcinctus, P. cancrivorus*), agreeing with the "landscape of fear" hypothesis. By avoiding predation-prone open spaces, such as roads, the species may be alleviating its risk of predation. The non-lethal effect of predators on prey can be more important than predation itself, and prey and predators can respond behaviorally to each-other in very sophisticated ways (Brown et al. 1999). *C. paca* association with water courses can also be related to an anti-predator strategy, since water bodies can be used as an escape path (Goulart et al. 2009). Two species of cats were negatively associated with roads, *P. concolor* and *L. guttulus*. Both species may select smaller game trails as to avoid encounters with the larger intraguild competitors, respectively *P. onca.* and *L. pardalis.* Indeed, one way of inferring interspecific competition is to measure whether species avoid places and time periods in which species from the same trophic level and similar ecological behavior are present (Steinmetz et al. 2013). We did not found a negative co-occurrence pattern among large carnivores or between large carnivores and meso carnivores. Among the meso carnivores we observed species spatio-temporal avoidance between *L. pardalis* and *L.guttulus*. The closer morphological characteristics and size ratios of the existing smaller felids assemblage suggests some differential habitat use for coexistence (Kiltie 1984; Donadio & Buskirk 2006). *L. guttulus* was negatively related to forest edge and avoided roads, what can be a strategy for segregation from *L. pardalis* (positively associated with forest edge). Another way of intraguild segregation is the temporal one.

Di Bitetti et al. (2010) found that this may be the case for *L.guttulus* and *L. pardalis*. In their study site, also in the Atlantic Forest, *L.guttulus* were active any time of the day, with a peak of activity in the morning, different from *L. pardalis* that were predominantly nocturnal (Di Bitetti et al. 2010). However, in our study all the three smaller spotted cats were nocturnal, what reinforce that they may segregate in space. Apart from the spotted cats, the other meso felid, *P. yagouaroundi* showed an activity period completely opposed, being strictly diurnal.

Neotropical large herbivores seems to play non-redundant role in the Neotropical forest and there are no records of interference competition between then. Large herbivore competition was described with smaller native species (Galetti, Bovendorp, et al. 2015) and with large exotic ones, as cattle and boar (Galetti, Camargo, et al. 2015; Desbiez et al. 2009). In our study, we found a positive association between the large herbivores *T. terrestris* and *M. bororo*, which may indicate a shared habitat.

Some of the species that had shown strong positive association, as *L. wieddi*, *M. bororo, P. onca* and *T. terrestris,* are known to be sensitive species and to have high habitat requirements, and all of them are classified under threatened status (IUNC 2016). Therefore, their association may be a proxy for habitat quality.

Conflicting with habitat quality, the presence of dogs and poachers decreased the probability of observing most of the species. Other studies also shown the occurrence and impact of domestic dogs and poachers on Atlantic Forest (e.g. Galetti & Sazima 2006; Srbek-Araujo & Chiarello 2008; Paschoal et al. 2016; Torres & Prado 2010; Cullen et al. 2000; Canale et al. 2012; da Silva et al. 2016). Dogs were recorded in 18 of the 39 camera-trap stations and poachers along 13 camera-trap stations, value that may be underestimated as poachers usually divert from passing in front of or even destroy the camera-traps when they see then. This information about domestic dogs and poacher are remarkably important as we must incorporate this “invisible” threats in ecological studies and in conservation policies.

Per geographic distribution, abundance, and group behavior, we expected to record peccaries (*Tayassu pecari* and *Pecari tajacu*) and coatis (*Nasua nasua*). There were few records of collared-peccary (*P. tajacu*) near the study site in the state reserve Parque Estadual Carlos Botelho (PECB) (Brocardo et al. 2012; Silveira et al. 2010). As for white-lipped peccary (*T. pecari*), after several evidences that the species could be locally extinct, recently a small group (2-4 individuals) was recorded also in PECB (Beisiegel et al. 2014). White-lipped peccary is considered very sensitive to human threats, such as poaching, livestock-born epizootics and habitat destruction, being very prone to sudden extinctions (Taber et al. 2016; Cullen et al. 2000; Altrichter et al. 2012; Beisiegel et al. 2014). For example, in a time spam of only three decades, healthy populations of the species were considered locally extinct from large Atlantic Forest remnants: the Iguaçu National Park at Parana State, Turvo State Park in Rio Grande do Sul State and from Morro do Diabo State Park in São Paulo state (Beisiegel et al. 2014). Regarding poaching only, in our study, besides the records on cameras, we also observed several points of poachers shelters and baits for wildlife while installing the cameras. Thus, the potential recovery of the white-lipped peccary population in the Paranapiacaba forest urges for management actions in order minimize poaching.

The lack of information on large mammals responses to habitat and to biotic relationships, including here the different actors of the food web and responsible for important ecosystem services, can create a false sense of preserved system only by the presence of the forest. Indeed, the spatial and temporal patterns of large mammals distribution may have consequences for species persistence and influences on plant recruitment and habitat regeneration (e.g. Tabarelli & Peres 2002). In our study, we were able to demonstrated that there are spatial-temporal patterns of large mammals occurrence. Our sampling design and amount of data allowed us to improve our inference power by adding temporal variables, and our findings should be integrate in conservation initiatives of delimiting remaining suitable areas for single or multi-specie.

ACKNOWLEDGEMENTS

This study was part of the project "Atlantic Forest Jaguar Initiative" funded by Panthera in partnership with Pró-Carnívoros Institute (IPC) and support of CENAP/ICMBio. M.L.L.P received grants from IPC, Hidroex-Unesco and CAPES. We would like to thank the landowners that allowed our work in their properties. We express our gratitude to all the field assistants.

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CHAPTER II: FORMATTED ACCORDING TO *TRENDS IN ECOLOGY AND EVOLUTION* SUBMISSION INSTRUCTIONS

INCORPORATING HUMANS IN TERRESTRIAL TROPHIC WEBS: INSIGHTS FROM THE ATLANTIC FOREST

Miriam Lucia Lages Perilli[1,2], Fernando Lima[3,4], Milton Cezar Ribeiro[4], Laury Cullen Junior[3], Ricardo Ribeiro de Castro Solar[1,5]

[1] Programa de Pós-graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa - UFV, Viçosa, Minas Gerais, Brazil;

[2] Instituto para Conservação dos Carnívoros Neotropicais - Pró-Carnívoros, Atibaia, São Paulo, Brazil;

[3] IPÊ - Instituto de Pesquisas Ecológicas, Nazaré Paulista, São Paulo, Brazil;

[4] Programa de Pós-graduação em Ecologia e Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista – UNESP, Rio Claro, São Paulo, Brazil;

[5] Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais - UFMG, Belo Horizonte, Minas Gerais, Brazil.

Keywords: Hyperkeystone species, apex predators, trophic cascades, poaching

Abstract (100 - 120 words)

Humans major threats on tropical forests are habitat loss, fragmentation, and degradation of remaining forest. When large vertebrate species are able to persist in fragmented landscapes, the remaining habitat and the reorganization of species biotic interactions may influence their distribution and abundance. Yet, it is difficult to separate those effects from the direct impact of humans, and we must account for the direct impact of vertebrate harvest by humans in Neotropical forests. Here we proposed to incorporate humans as a “hyperkeystone” species in the Atlantic forest food webs, based on four possible scenarios for the role of apex predators and human beings in natural interaction webs. We concluded that poaching has outsized impacts on the food webs.

“Humans have the widest distribution of any terrestrial mammal species, inhabiting every continent on earth (although there are no permanent settlements on Antarctica). A small group of humans has been introduced to space, where they inhabit the International Space Station.” Global Mammal Assessment Team. 2008

Background knowledge and conceptualization

In a recent article in *Trends in Ecology and Evolution* journal, B. Worm and R. T. Paine (WP) proposed an innovative approach recognizing humans as playing an outstanding role in the interaction web, which they defined as “hyperkeystone” species [1]. The novelty of the approach is that it focusses on our role as a specie, not just as agents of environmental disturbance. This concept reflects that humans disproportionally jiggle food webs by altering traditional keystone species position [1]. However, they left open, among other questions, what exact trophic position humans occupy and what processes – bottom-up or top-down – are in fact humans affecting other species. Including humans in trophic ecology has indeed gained attention in the scientific community [2–4]

In the Neotropical region, poaching impact on biodiversity have been investigated and discussed for almost 4 decades and ecological collapses caused by trophic cascades were describe in this short timeframe (e.g. [5–9]). Therefore, investigating the role played by humans in altering trophic regulation is mandatory given the scenario of global anthropogenic change [10]. Indeed, due the severity of species loss and populational declines, we are living amid the so called “Anthropocene defaunation” [11], or the sixth mass extinction.

Originally, the food web concept was about species interactions throughout trophic links, their direction and strength of trophic relationships. The latter ultimately depends on the functional role played by a specie within a given food web, and whether the presence or absence of that species would influence the occurrence or abundance of others [12]. If the role a species play in a system is responsible for such unique interactions in a food web dynamics, despite its density it is considered a “keystone” species [13]. Their removal potentially create a cascading effect downward trophic levels disrupting the system stability [12,13]. In this sense, apex predators are an example of such species, as their eradication precipitate ecological chain reactions that leads to ecosystem degradation and even other species loss [14–16]. This trophic dynamics is known as “top-down” regulation, in opposite to trophic webs where the primary producers regulate the upper levels abundances (i.e. “bottom-up”) [17].

To mammals the consequences of apex predators loss are diverse. It can be an increase in the intensity of herbivory, due trophic release of their prey, leading to harsh consequences for plant recruitment in tropical ecosystems [15,16,18]. They may also have direct influence on the intermediary predators and consequently throughout the community. This late phenomenon named “mesopredator release” – a proliferation of intermediate predators that reduce or even eliminate smaller vertebrate species [19,20]. Such top-down consequences of predator loss have been described both marine (e.g. [21–23]) and terrestrial ecosystems (e.g. [14,18,19]). Nevertheless the keystone specie concept is not restricted to predators, herbivores also fits the concept as some species play functional roles such as seed predation and dispersal with consequences for forest structure and dynamics [8,24–26]. Consequently, defaunation has ecological implications and consequences that are way beyond concern for the species themselves [11].

Until recently, most discussions about food webs mentioned that human activities could influence trophic relations, however they often treat our species as a separate entity, not as an active part of the ecosystems and as a specie itself. Only recently, some publications started to address the inclusion of human beings as an additional link among other species in trophic ecology [2,4,27].

Differently from the temperate forests, tropical forests are much more complex, which makes challenging the establishment of trophic interactions strength and the identity of keystone species. With the high diversity of species, the links between trophic levels are more multifaceted, and different pathways can lead to ecosystem stability. In the specific case of the Atlantic Forest (AF) biome in South America, the jaguar (*Panthera onca*) is the apex predator, which have been extirpated from the most portions of the biome and is now present in only 2.8% of the already low remaining habitat [28]. It is also noteworthy that the large herbivores that share the jaguar habitat, including large seed predators, such as peccaries (*Tayassu pecari* and *Pecari tajacu*), deers (*Mazama* spp.) and tapirs (*Tapirus terrestris*) are under the same threats and also facing severe population declines [29–33]. Apart from their role as seed predators, peccaries and deers are among the main prey species for jaguars as well [34–36]. Thus, it seems that in AF humans have been the main responsible for shaping the ecosystems, not only through habitat modifications, but also interacting directly with other species as a competitor and as a predator by poaching both apex predators and their prey [26,37–39].

Poaching in Brazil is completely illegal – with occasional exceptions in order to control invasive species such as wild boars. Yet still a common practice all over the country. The illegality of it, associated with a severe gun control policy, make this a very secretive activity and formal statistics about its impact on biodiversity is generally raised through indirect methods. Another challenge in measuring this variable and incorporating human role in tropical food webs, is the inherent noise generated by differences in social-economic realities, cultures and local habits from region to region. Nevertheless, we strongly believe that we need a start point, an initial model that can be tested and evaluated in future studies. For that, we propose a conceptual model including the impact of poaching in trophic webs, within different conservation scenarios, with and without the absence of the Neotropical apex predator: the jaguar.

Conceptual model

We built a trophic web model based on the jaguar and its primary prey species in the Atlantic Forest [40–43], and on the knowledge of humans' preferential prey [37,44–46]. We then add the potential cascading effects and new interactions resulting from changes in the apex predator presence/absence. As we are not accounting for patch size or shape, we assumed a threshold of forest remnants for our conceptual model based on literature. Therefore, our conceptual model is based on forest remnants larger than 2000 ha, a size were it is still possible to find a functional assemble of large mammals [39].

Box 1: Assumptions

1.There is marked variation in large mammal's occurrence and abundance along the Atlantic Forest, that is not equivalent to the original species occurrence, with some local species loss (defaunation);

2.The Atlantic Forest apex predator was extirpated from more than 90% of its original distribution;

3.Poaching is still a common practice, and even an intense one, in some sites along the Atlantic Forest. Experts included poaching of both jaguar and its prey as one the main threats for the specie.

We included four scenarios in our trophic web model (Figure 1). The first scenario represents what we would expect to find in pristine habitat with the main prey base available and being regulated by the jaguar (Figure 1A). In this scenario we included species that were recorded jaguar feeding habits studies in the Atlantic Forest, and use the proportion of their occurrence in jaguar diet as a proxy of the strength of the interactions [36,40,42]. This is a rare scenario to be found in the Atlantic Forest, theoretically being found only inside large Reserves of Integral Protection (IP). However, poaching is a very pervasive activity and present within possibly 10 to 20 km from villages, roads and navigable rivers [9]. In fact, in the Brazilian AF, 12 km is the maximum distance between any remaining forests from non-forested areas [47]. With that said, it is very likely that poaching activities are present all over the distribution of AF, including reserves. Yet, one could expect to find scenario 1A in areas dominated by hilly terrains and difficult to access. Even in this situation, a recent sample employing camera traps in a large core area of the Atlantic Forest, with steep terrain, poachers where recorded in 13 of our 39 stations (Chapter 1 of this thesis).

The second scenario includes humans as poachers (Figure 1B). As described above, we are assuming the concept of humans as hyperkeystone species, influencing the food web dynamics by altering species abundances of both the apex predator (jaguars) and of the other connected species (i.e. jaguar prey). Often, the poaching on jaguars are due retaliations for damage caused by predation on livestock. In this scenario (Figure 1B) we expect to find low abundances of the game species that are also jaguar prey: peccaries, spotted paca (*Cuniculus paca*), armadillos (Dasypodidae, mainly *Dasypus novencinctus*) and deers (Mazama sp.). Despite tapirs (*Tapirus terrestris*) been recorded in the AF jaguar diet [40], it cannot be considered a very common prey for jaguar. Even so, we keep it in the model due its importance in the system [38,48,49]. Besides, the tapir low reproductive rate (one cub per cycle) and a long gestational period, a few individuals withdrawn from the population can have a dreadful effect for the species demography [50].

The third scenario is what we understand as being the most realistic picture of the larger portions of the AF, in which functional jaguar populations are not found [28], but there is still intense human harvesting of large and medium mammalian species (Figure 1C). The reason we think this is the most common scenario of the AF lies on the fact that from all available suitable habitat for jaguars, 74% of them have no records of the species [28]. Although in the absence of the apex predator it would be expected a trophic release of preys [14,23,51], human species role as a hyperkeystone may be overshadowing this phenomenon. In this case, one would expect to find a reduction in ungulates abundance as they are among the preferential game species.

The fourth and last scenario is one that there is neither the apex predator nor humans. In this situation competition and bottom-up trophic regulation becomes responsible for regulating prey population densities (Figure 1D). This scenario may occur in areas where poaching is not severe, or near large forestry and agricultural landscapes, where there is intensive private surveillance, but no jaguars.

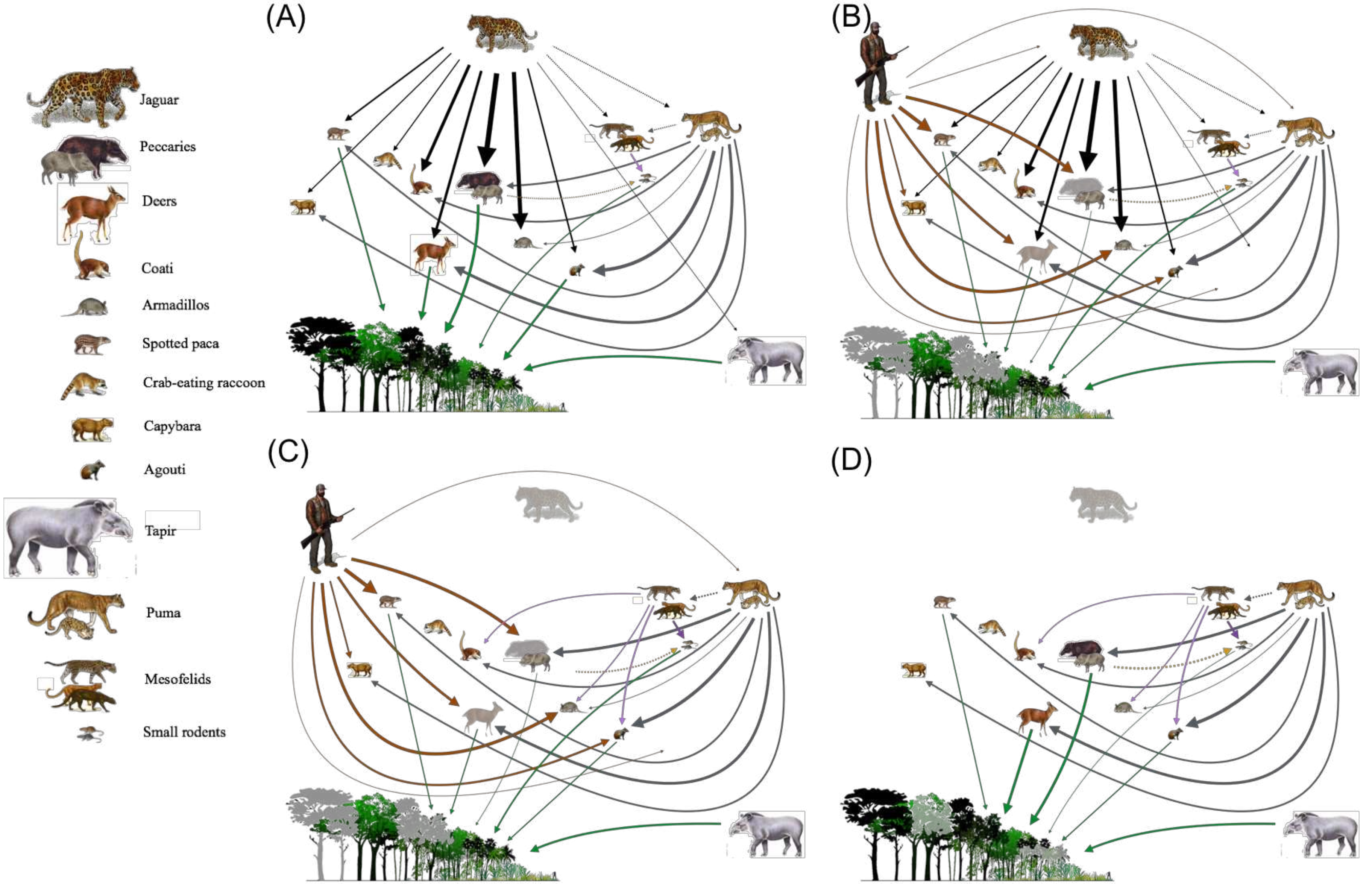

Figure 1. Food webs and humans as hyperkeystone species in the Atlantic Forest. Arrows indicate direct, consumptive effect (solid line) or non-consumptive effects (dashed line). The line size indicates stronger or weaker interaction based on the information available on species diet and correlations.

Conservation implications and future directions

In this paper, we propose a conceptual model with four likely scenarios for the role of both apex predators and humans in natural interaction webs. The next steps are to confront our conceptual model with existing databases gathered from studies with camera traps and from literature data. Explanatory variables can incorporate top-down regulation, represented by the apex predator (jaguar) presence and poaching intensity.

In all the jaguar populations and sites studied, experts included poaching of both jaguar and its prey as a main threat for the species, even in protected areas [28]. Therefore, we believe that from the proposed conceptual scenarios, 1B and 1C would be more realistic. This means that humans are present all over the AF and are likely to be present surrounding most of the tropical forests in the world [10], with outsized impacts on food webs, acting as a hyperkeystone species. That said, a priority policy for conservation in the Anthropocene is to stablish funding support and study groups and policies prioritizing poaching quantification, strategies for poaching reduction, habitat restoration and apex predator's populations reestablishment.

Box 2. How can we integrate insights from the study of individual interaction chains in global models?

Supportive to WP suggestions, we believe that food webs conceptual baselines should be built, and predictions generated to help mapping the ecological consequences of anthropogenic changes. One of the "Outstanding Questions" raised by WP was how can we integrate insights from the study of individual interaction chains in global models.

Mostly apex predator's populations are threatened and with populations locally extinct in some degree. For example, all the tropical forest large Pantherinae cats are under some global risk of extinction [52–55] . Likewise, poaching is issue in mostly remaining tropical forests [56,57]. Therefore, we extrapolated our AF conceptual forest to a global tropical food web model (Figure 2).

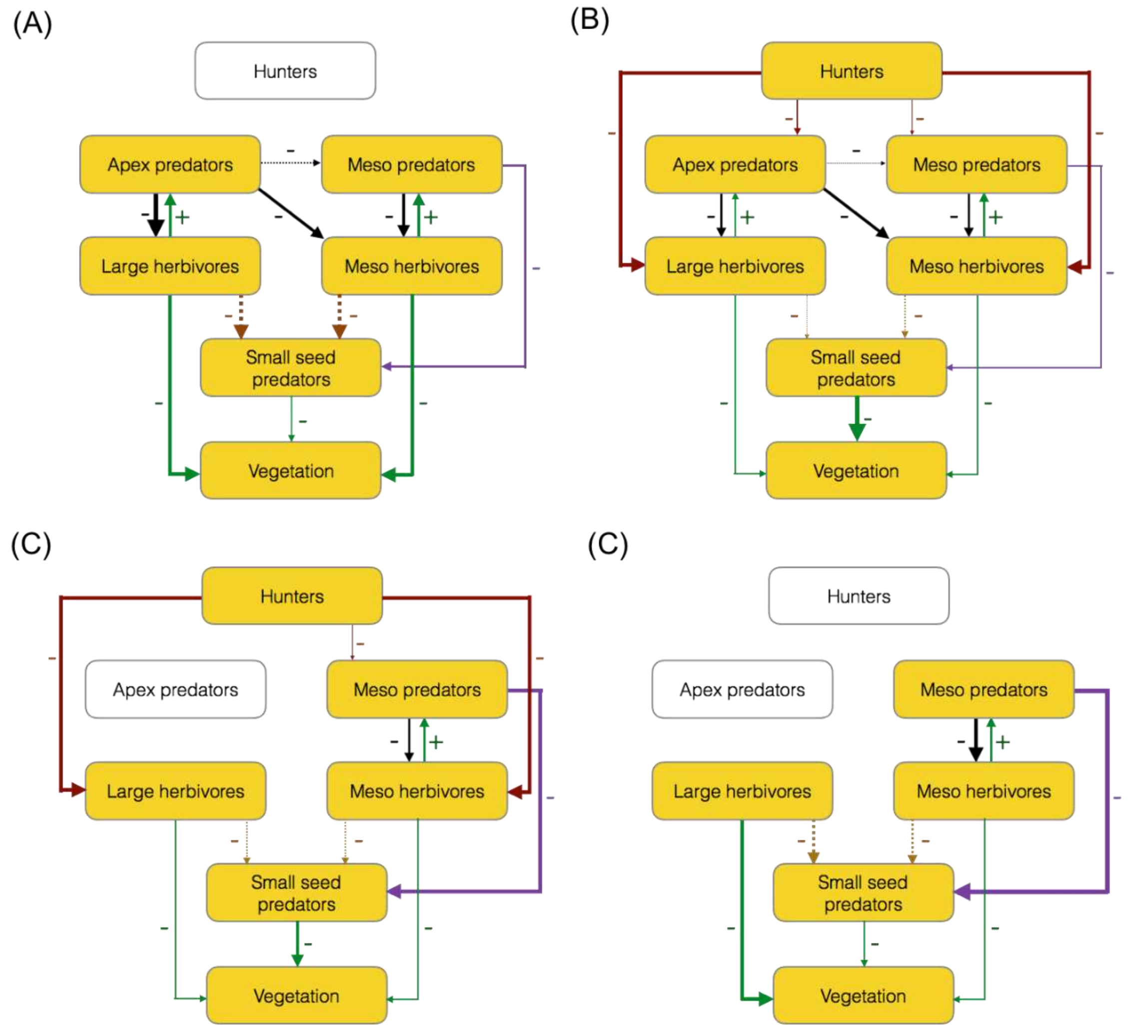

Figure 2. Global model illustrating a tropical forest food web that incorporate human hunting impacts.

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GENERAL CONCLUSION

Our study provided evidences that large mammals occurrence and distribution patterns in one the largest Atlantic Forest remnants is a result of an intricate network of ecological interactions among species. At first glance, one could argue that this inference sounds quite obvious. Even so, quantitative evidence that brings light over these processes in tropical forests, here and worldwide, are rare and still a valuable source of information to ecologists. Our sampling design and amount of data allowed us to step towards the spatial approach and improve our inference power by adding temporal variables. Indeed, strong interactions hidden under the strict spatial analysis were revealed when reevaluated over time. We were able to find out how the spatio-temporal co-occurrence patterns of medium and large mammals have profound implications in the way we conduct community studies. Ultimately, our findings should also be incorporated in conservation initiatives, as many efforts are focused in detecting and delimiting remaining suitable areas for single or multi-species. We have seen an exponential increase in mammal studies in the last decades thanks to the development of camera-traps technology associated with a relative reduction in costs and accessibility. Nevertheless, this availability was not followed by rigorous sampling design and posterior data analysis, and many times unrelated to ecological questions. As a result, we are currently facing an unprecedented amount of anecdotal records, that may provide some interesting natural history and fill important species distribution gaps. Even so, we are still just scratching the surface of the real potential of these data in provide answers to ecological questions and conservation initiatives in a biome and continental scale. We advocate the use of this large amount of camera-trap data in investigating large mammal’s interactions applying both spatial and temporal scales as a tool to subside habitat conservation and restoration.

Our study also showed the negative associations of human actions (e.g. domestic dogs and poachers) to large mammals’ assemblage. In fact, in the second chapter we discussed how this activity is so deeply incorporated in natural systems that we proposed a distinct approach: to incorporate it as part of the system, not as an outside “disturbance”. The novelty here is that we incorporated humans as species, and playing a predator role, not as an agent of habitat transformation. To date, apart from indigenous communities, only a few trophic cascades studies have explicitly included humans as part of the system, adding human activities as variables. Within this perspective, our study aims to stimulate the challenge of including humans in investigations not as an invisible variable or unmeasurable threat and unrelated with the anthropological view of the noble savage. Through that we hope to stimulate the development of objective tools and long term studies measuring poaching pressure and linked trophic cascades along tropical forests.

Finally, our study concludes that in the Atlantic Forest we have mainly the combination of apex predators and humans suppressing lower trophic levels causing top-down effects. We, humans, certainly fit in the hyperkeystone specie concept in most of the remaining tropical forests, as we have a disproportional effect on the lower trophic levels – apex predators included. However, as important as it is to incorporate this concept in trophic ecology is to recognize that our role as hyperkeystone specie is unsustainable in long term. Without realistic hunting management and policies based on sound science and objective information we will continue to modify biological and evolutionary processes globally.

APPENDIX 1

Pictures

Access to the study site in the Paranapiacaba region

Access to the sampling points to install de camera-traps and a record of palm heart extration

Camera-trap stations installation

SCIENTIFIC REPORTS

OPEN

Received: 16 May 2016
Accepted: 25 October 2016
Published: 16 November 2016

A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America

Agustin Paviolo[1,2], Carlos De Angelo[1,2], Katia M. P. M. B. Ferraz[3,4], Ronaldo G. Morato[4,5], Julia Martinez Pardo[1,2], Ana C. Srbek-Araujo[6,7], Beatriz de Mello Beisiegel[8], Fernando Lima[9,10], Denis Sana[4,11], Marina Xavier da Silva[12], Myriam C. Velázquez[13], Laury Cullen[9], Peter Crawshaw Jr[5], María Luisa S. P. Jorge[14], Pedro M. Galetti[15], Mario S. Di Bitetti[1,2,16], Rogerio Cunha de Paula[4,5], Eduardo Eizirik[4,17], T. Mitchell Aide[18], Paula Cruz[1,2], Miriam L. L. Perilli[4,19], Andiara S. M. C. Souza[15], Verónica Quiroga[1,2], Eduardo Nakano[20], Fredy Ramírez Pinto[13], Sixto Fernández[13], Sebastian Costa[2,21], Edsel A. Moraes Jr[22] & Fernando Azevedo[4,23]

The jaguar is the top predator of the Atlantic Forest (AF), which is a highly threatened biodiversity hotspot that occurs in Brazil, Paraguay and Argentina. By combining data sets from 14 research groups across the region, we determine the population status of the jaguar and propose a spatial prioritization for conservation actions. About 85% of the jaguar's habitat in the AF has been lost and only 7% remains in good condition. Jaguars persist in around 2.8% of the region, and live in very low densities in most of the areas. The population of jaguars in the AF is probably lower than 300 individuals scattered in small sub-populations. We identified seven Jaguar Conservation Units (JCUs) and seven potential JCUs, and only three of these areas may have $\geq$50 individuals. A connectivity analysis shows that most of the JCUs are isolated. Habitat loss and fragmentation were the major causes for jaguar decline, but human induced mortality is the main threat for the remaining population. We classified areas according to their contribution to jaguar conservation and we recommend management actions for each of them. The methodology in this study could be used for conservation planning of other carnivore species.

[1]Instituto de Biología Subtropical, CONICET-Universidad Nacional de Misiones (UNaM), Bertoni 85, (N3370AIA) Puerto Iguazú, Misiones, Argentina. [2]Asociación Civil Centro de Investigaciones del Bosque Atlántico, Bertoni 85, (N3370AIA) Puerto Iguazú, Misiones, Argentina. [3]Departamento de Ciências Florestais, ESALQ, Universidade de São Paulo, Piracicaba, SP, Brazil. [4]Instituto Pró-Carnívoros Atibaia, Av. Horácio Neto, 1030 12954–010, Atibaia, SP, Brazil. [5]Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros CENAP/ICMBio, Av. Hisaichi Takebayashi, 8600 12946–051, Atibaia, SP, Brazil. [6]Programa de Pós-graduação em Ecologia de Ecossistemas, Universidade Vila Velha (UVV), Vila Velha, ES, Brazil. [7]Instituto SerraDiCal de Pesquisa e Conservação, Belo Horizonte, MG, Brazil. [8]Floresta Nacional de Capão Bonito/ICMBio, Capão Bonito, SP, Brazil. [9]IPÊ - Instituto de Pesquisas Ecológicas, Nazaré Paulista, SP, Brazil. [10]Programa de Pós-graduação em Ecologia e Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista – UNESP, Rio Claro, SP, Brazil. [11]PPG Ecologia- UFRGS, Porto Alegre, RS, Brazil. [12]Projeto Carnívoros do Iguaçu, Parque Nacional do Iguaçu/ICMBio, Rodovia BR 469 Km 22,5, Foz do Iguaçu, PR, Brazil. [13]Fundación Moisés Bertoni, Asunción, Paraguay. [14]Vanderbilt University, Nashville, TN, United States. [15]Departamento de Genética e Evolução, Universidade Federal de São Carlos, São Carlos, SP, Brazil. [16]Facultad de Ciencias Forestales, Universidad Nacional de Misiones (UNaM), Misiones, Argentina. [17]PUCRS, Faculdade de Biociências, Porto Alegre, RS, Brazil. [18]Department of Biology, University of Puerto Rico, San Juan, Puerto Rico. [19]Programa de Pós-graduação em Ecologia, Universidade Federal de Viçosa, MG, Brazil. [20]Instituto de Pesquisas Cananéia, Cananéia, SP, Brazil. [21]Instituto nacional de Medicina Tropical, Puerto Iguazú, Argentina. [22]Biotrópicos – Instituto de Pesquisa, MG, Brazil. [23]Departamento de Ciências Naturais - Universidade Federal de São João del Rei. São João Del Rei, MG, Brazil. Correspondence and requests for materials should be addressed to A.P. (email: paviolo4@gmail.com)

Apex predators, particularly large carnivores, are key components of ecosystems as they help maintain biodiversity and ecological processes via multiple food web pathways[1,2]. These species require large areas of habitat with a stable prey base for their long-term survival, and they are particularly susceptible to population declines in human modified landscapes[3]. Human persecution, global habitat loss and fragmentation have exposed most species of large carnivores to extinction risk worldwide[2]. However, the impact of these threats varies across regions and species[2]. While some populations of large carnivores in North America and Europe are recovering as forested areas increase, along with protective legislation and greater human tolerance[4,5], most large tropical carnivore populations are still declining[2,6].

Tropical forests sustain most of the global terrestrial biodiversity, but they have suffered high rates of deforestation and defaunation of large vertebrates[7,8]. Even though, the loss of top predators in these forests can have direct effects on the diversity and function of these biologically diverse ecosystems[7,2]. The conservation of top predators often is a challenge that requires large efforts to evaluate population status through extensive areas, and coordinated international efforts to develop conservation planning strategies[2,6].

The Atlantic Forest (AF) of South America is one of the Earth's Biodiversity Hotspots with high levels of diversity and endemism[9].The AF extends through more than 1.7 million km^2 across Brazil, Argentina and Paraguay, and during the last centuries, it has undergone an intense landscape transformation. Today less than 12% of the original forest cover still exists[10]. Due to the high levels of diversity and the extreme loss of forest cover, the region is among the eight "hottest hotspot" of the world[9] and is considered a top priority area by most of the largest international NGOs (e.g. Word Wildlife Fund, Conservation International). Most of the remaining AF has lost its largest mammals, including its top predator, the jaguar (*Panthera onca*; refs 11 and 12). If this trend continues, the AF will be the first tropical forest ecoregion to lose its top predator[13].

The jaguar is the top predator of the Neotropical region, currently occurring from southern United States to northern Argentina. It has disappeared from about 54% of its original range, due to habitat loss, depletion of the prey base and human persecution[14]. Although it is listed as near threatened by the IUCN[6], it has become locally extinct or critically endangered in some areas, including the AF, which is currently the southern distribution limit of the species[14–16].

Historically, the jaguar occurred throughout the AF[14,16], but its' current distribution has been greatly reduced. Although many research teams have evaluated the population status of the jaguar in different regions or countries within the AF[15–21], no study has evaluated its' status across the entire ecoregion. During the last 10 years, governments, scientists and NGOs developed conservation plans for the Argentinean AF[22] and the Brazilian AF[23], but there is still no international conservation strategy for the entire region. Saving the jaguar population in the AF requires a better understanding of its status throughout the entire region, as well as international planning and cooperation for conservation[24]. This article addresses this limitation by combining data sets from 14 jaguar research projects from across the AF to: (i) evaluate current jaguar habitat availability, (ii) estimate the area of occupancy and population size, (iii) identify potential connectivity cost among subpopulations, (iv) identify the main threats to jaguar conservation in the region, (v) propose integrated actions for long-term conservation, and (vi) use our study as a model to assist conservation efforts of jaguars and other large carnivores in other regions facing similar conservation problems.

Results

Habitat suitability for jaguars and areas of occupancy.

Of the original 1.7 million km^2 of the AF, 15.1% was classified as habitat currently suitable for jaguars, but only 0.7% (9,017 km^2) occurred in areas classified as highly suitable (Fig. 1). The remainder of suitable habitat was classified as medium suitability (6%; 81,473 km^2), or marginal suitability (8.4%; 114,860 km^2). Jaguar habitat loss varied among countries: Brazil lost 87% of its' original AF suitable habitat, Paraguay 64% and Argentina 39%. Of the total remaining jaguar suitable habitat in the AF, 27% is fragmented into 12,608 patches smaller than 100 km^2, 43% into 305 fragments of between 100 km^2 and 1,000 km^2, and 29% into 35 patches larger than 1,000 km^2.

The habitat suitability model for jaguar that we developed for these estimations was highly significant ($p < 0.001$, area under the receiver operating characteristic: $AUC = 0.82 \pm 0.05$) and presented low omission error (~22%). The post-hoc validation using the independent recent presence-only records confirmed that the model was highly accurate, with only 5.1% omission error. According to our model, jaguar habitat in the AF was mainly determined by high forest cover and marshlands (53.1%), intermediate elevation (19.4%) and low human accessibility (17.3%).

Jaguar presence was confirmed in only a few areas of the AF (Fig. 2). In the coastal region of Brazil, the species is apparently extinct in the southern and northern extremes, with populations currently confined to the states of São Paulo, Rio de Janeiro and Espírito Santo. In the interior portion of the AF, the species occurs in the state of Minas Gerais and along the Paraná River basin, in habitat fragments in Argentina, Paraguay and Brazil (Fig. 2). We estimated that the area of jaguar occupancy (AJO) in the AF covers only 35,441 km^2. If we include as AJO the areas with jaguar records nearby (closer than 1.7 km), the AJO increases to 37,825 km^2. Thus, the jaguar is occupying only 2.8% of the AF and 18.4% of the current jaguar suitable habitat. In addition, 16,420 km^2 of jaguar habitat (1.2% of the AF and 8% of the total current jaguar suitable habitat) were very close to AJOs and are areas of potential jaguar occupancy (APJO, Fig. 2). In 151,105 km^2 (73.6%) of available jaguar habitat in the AF we do not have jaguar records, most probably representing areas without jaguars (Fig. 2).

The AJOs were mainly the largest patches of remaining habitat. Jaguars appear to have disappeared from 96% of the habitat fragments with less than 100 km^2, 86% of the habitat fragments between 100 km^2 and 1,000 km^2, and 40% of the habitat fragments larger than 1,000 km^2.

Jaguar density and population size.

Jaguars were not detected in eight of the 30 camera-trap surveys conducted in the AF (Table 1). These surveys without jaguar records were conducted in the AJO of the Serra do

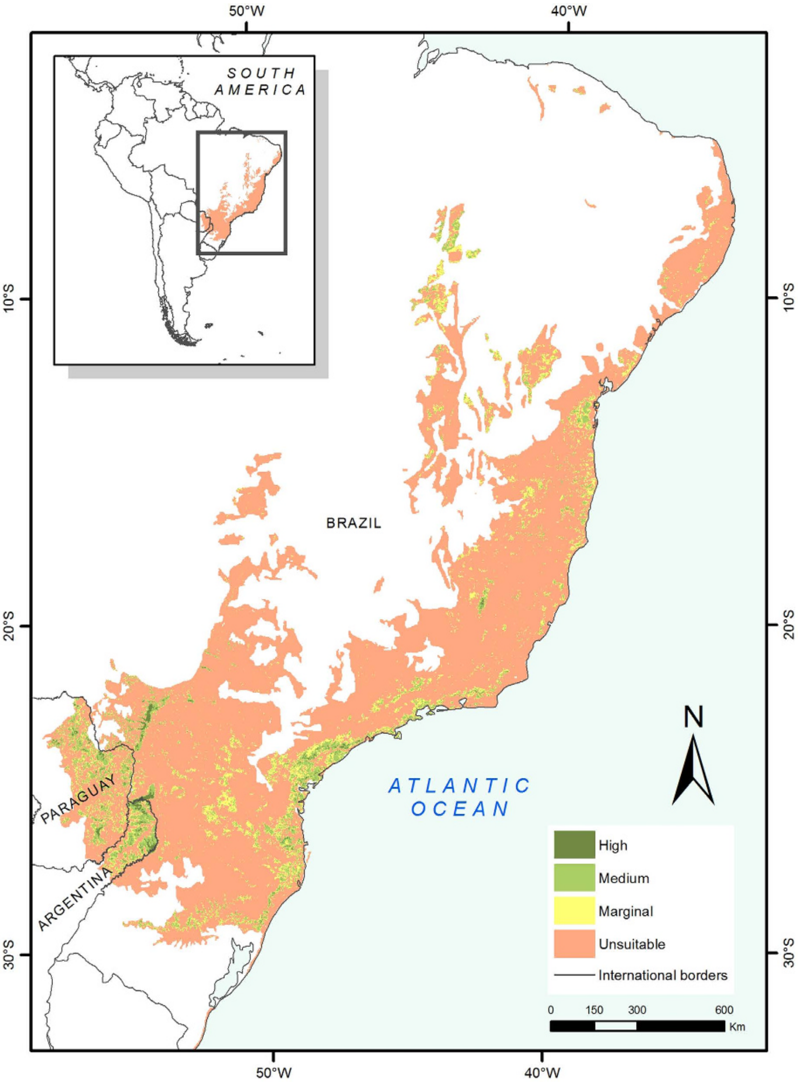

Figure 1. Habitat suitability for jaguars in the Atlantic Forest. The colored area inside the left corner inset details the location of the study area in South America. The map was created with ArcGis 10.3 (www.arcgis.com).

Mar, Serra do Mar do Norte and Serra dos Órgãos (Supplementary Fig. S1 and Table S1). In 13 other surveys, the number of individuals recorded was insufficient to apply spatially explicit capture-recapture population models (SECR) to estimate jaguar density (Table 1). We estimated densities based on data from nine surveys from six areas. In these surveys, we recorded between eight and 42 individuals and estimated densities between 0.66 and 2.42 jaguars/100 km^2 (Table 1). The highest density estimates were obtained in the Linhares-Sooretama region and in the Morro do Diabo State Park, and the lowest were from a forest block including the Intervales State Park and Alto Ribeira State Touristic Park (Table 1, see also Supplementary Fig. S1).

The estimated number of jaguars for each region varied according to density estimates and the size of habitat fragments that were surveyed (Table 2). The largest subpopulations occurred in the Green Corridor, the Upper Parana-Paranapanema and the Serra do Mar region (Table 2). Smaller subpopulations, were located in the Mbaracayú and Linhares-Sooretama regions (Table 2).

Priority areas for jaguar conservation. We identified seven areas with presence of males and females that were categorized as Jaguar Conservation Units (JCU) and five Potential Jaguar Conservation Units (PJCU; no detection of both sexes). Three JCUs contained, or probably contained 50 individuals or more and were categorized as JCU Type I (JCUs with higher probability of long-term population persistence): the Green Corridor, the Upper Parana-Paranapanema, and the Serra do Mar regions (Table 2, Fig. 3). These three JCU were all larger than 5,000 km^2. While the population of the Serra do Mar JCU was probably smaller than 50 individuals, we classified it as a Type I JCU because the habitat availability of the area is large enough to maintain a larger population (Table 2). These three JCUs together constitute more than 60% of the current priority areas for jaguar conservation in the AF (Table 2).

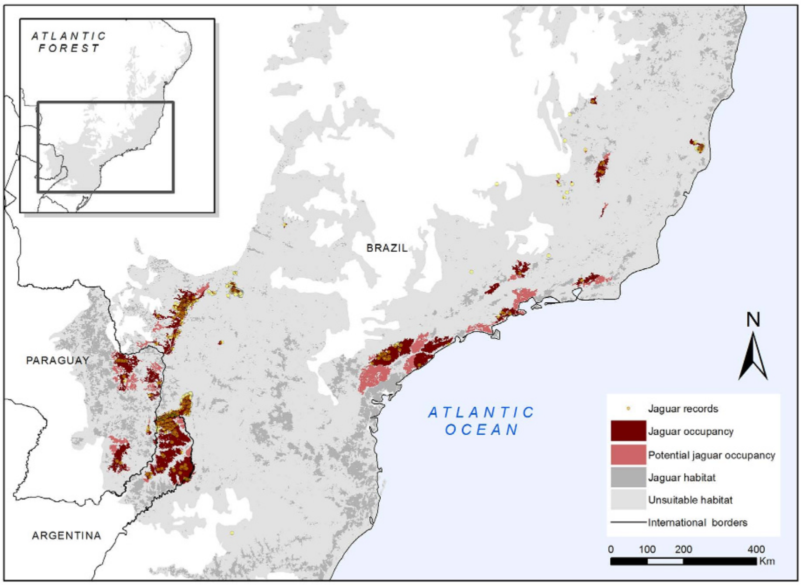

Figure 2. Jaguar records obtained along the AF and the areas of jaguar occupancy (AJO), the areas of potential jaguar occupancy (APJO) and the distribution of available jaguar habitat in the Atlantic Forest. The map was created with ArcGis 10.3 (www.arcgis.com).

The other four JCU are smaller and probably contain less than 50 individuals each consequently were classified as JCU Type II. These JCUs varied in terms of size, density and habitat conditions (Table 2). The largest is Mbaracayú, in eastern Paraguay, which encompasses 4,086 km^2 of jaguar habitat. The other three vary between 503 km^2 and 3,915 km^2 and are located in Minas Gerais State and the coastal region of Brazil (Fig. 3). These Type II JCUs cover 18% of the priority areas for jaguar conservation in the AF (Table 2).

We identified five PJCUs in western Paraguay and the Brazilian coast (Fig. 3). The size of the PJCUs varied between 539 km^2 and 2,941 km^2, and together they constitute 16% of the priority area for jaguar conservation in the AF (Table 2). Despite the presence of jaguars in these PJCUs, jaguar records were scarce and densities are apparently very low (Table 1). Small fragments with jaguar presence were spread across different areas of the AF and constitute a very small fraction of the jaguar habitat (Table 2). Records in these areas are occasional and probably of nonresident individuals.

Several areas where jaguar were not detected could be important for jaguar conservation in the future because they are large areas with good quality jaguar habitat. Two of these areas are located near the Green Corridor JCU and the Serra do Mar JCU, and if they were connected they could expand the size of these existing JCUs (Fig. 4). We also identified potential core areas that may sustain jaguar's subpopulations in the future, and are potential areas for reintroduction programs. These areas are located in the northern part of the AF (Bahia and Piauí states of Brazil), along the coast of Paraná and Santa Catarina states (Brazil), and in western Paraguay (Fig. 4). These areas varied between 232 and 1,072 km^2 and together cover 12,218 km^2 of potential core areas.

Potential connectivity among the Jaguar Conservation Units.

The relative cost (i.e., costs for a jaguar attempting to move between two JCUs) or potential connectivity among the JCUs was highly variable. The Linhares-Sooretama and Rio Doce JCUs showed the highest connectivity cost and isolation of all the JCUs (Supplementary Table S2). Other JCUs and PJCUs could be grouped into two main regions: the Upper Paraná Atlantic Forest-JCUs, in the West, and the Coastal Atlantic Forest-JCUs, in the East (Supplementary Table S2). Connectivity between these two regions appears to have excessively high cost to allow jaguar movements (Supplementary Table S2). Furthermore, the Upper Paraná Atlantic Forest-JCUs showed higher cost distance values, suggesting more isolation, whereas the Coastal Atlantic Forest-JCUs present lower values and thus higher potential of connectivity (Supplementary Table S2).

Jaguar threats.

The relative importance of threats varied among the different JCUs (Table 2). Ranked in order of importance, the threats included poaching, scarcity of prey, small population size, site isolation, human retaliation due to cattle predation, habitat loss, and road kills.

Discussion

The population status of the jaguar in the AF is critical. Habitat loss and fragmentation have had a tremendous impact, and the species is locally extinct in most of the region. The few remaining subpopulations are small, scattered, highly isolated, and associated with relatively large forest remnants. This dramatic situation is similar to that faced by endangered large carnivore species in other regions of the World[2].

Considering that a couple of centuries ago the species inhabited all the AF[14,16], we found that approximately 85% of the jaguar habitat has been lost, and less than 7% of the region has medium to highly suitable habitat. Clearly, habitat loss has been the major driver of jaguar population decline in the AF, as was previously described

Survey	Stations	Trap days	Jaguar records/100 camera trap days	Individuals	Density (95% CI) jaguars/100 km^2
Morombí PR I	5	918	0.11	1 (1 u)	NE
Morombí PR II	10	930	0.75	4 (1 m, 3 u)	NE
Mbaracayú	25	1844	2.87	8 (3 f, 2 m, 3 u)	1.29* (1.29 to 2.8)
Urugua-í	53	2611	0.11	1 (m)	NE
PN Iguazú	46	2942	0.58	6 (3 f, 2 m, 1 u)	NE
Yabotí	60	2676	0.15	1 (m)	NE
Iguazú-San Jorge	49	2287	1.92	13 (6 f, 4 m, 1 u, 2c)	1.2 (0.56 to 1.89)
Iguazú-Urugua-í	47	2327	2.15	16 (8 f, 8 m)	0.89 (0.58 to 1.24)
PN do Iguaçu I	36	3240	0.21	3 (2 h,1 u)	NE
Green Corridor I	80	5038	1.47	21 (10 f, 7 m, 2 u, 2c)	0.91 (0.61 to 1.22)
PN do Iguaçu II	34	3060	0.75	4 (2 h, 2 m)	NE
Green Corridor II	122	5297	3.51	42 (18 f, 12 m, 1 u, 10c)	1.07 (0.8 to 1.33)
Morro do Diabo	36	1440	5.41	10 (6 f, 4 m)	2.39 (2.31 to 2.57)
Ivinhema	13	1495	2.07	12 (8 f, 3 m, 1 u)	1.66 (0.76 to 2.55)
Vale NR I	30	3032	2.74	8 (4 f, 3 m, 1 u)	2.42 (2.01 to 3.26)
Vale NR II	10	3468	0.09	3 (3 f)	NE
Vale NR III	10	3034	0.07	2 (1 m, 1 u)	NE
Vale NR IV	8	1033	3.1	4 (1 f, 3 m)	NE
Vale NR V	30	1440	1.67	2 (2 m)	NE
Carlos Botelho	16	2170	0.23	4 (1 f, 3 u)	NE
Intervales	14	1497	1.94	4 (2 f, 2 m)	NE
Intervales-PETAR	24	2712	1.25	8 (3 f, 3 m, 2 u)	0.66 (0.29 to 1.17)
Juréia-Itatins	21	2483	0	0	NE
Ilha do Cardoso	8	744	0	0	NE
Serra da Bocaina	26	3054	0	0	NE
Santa Virginia	26	2512	0	0	NE
Serra dos Órgãos I	18	1354	0	0	NE
Serra dos Órgãos II	20	6624	0	0	NE
Serra dos Órgãos III	44	4597	0	0	NE
Serra dos Órgãos IV	48	4788	0	0	NE

Table 1. Information of the camera-trap surveys in the Atlantic Forest including number of stations, effort in camera-trap days, rate of records of jaguars, number of individuals recorded (age and sex), density estimate and its 95% confident interval (95%CI). Abbreviations: (u) adult jaguar of undetermined sex, (m) adult male, (f) adult female, (c) cub and (NE) not estimated due to scarcity of records. *Estimated with CAPTURE + information of the home range size of three individuals monitored with GPS collars in this area. The number of stations, the effort, the jaguar record rate and the number of individuals correspond to values of the total sampling effort developed in every survey. The density estimation and its 95% CI correspond to values obtained during the portion of the survey that was used to estimate these parameters.

for regions within the AF[11,12,16,25]. Our model shows that loss of forest cover and marshlands, and increases in human accessibility had a negative effect on jaguar habitat suitability in the AF. These changes were related to demographic and economic processes that affected Brazil, Paraguay and Argentina at different times and different degrees[26]. Most of the jaguar habitat in the Brazilian AF was probably lost between 1900 and 1980 due to the development of cities and large-scale agriculture[10]. In Paraguay, the loss of jaguar habitat mostly occurred during the last 30 years with the expansion of large-scale agriculture[27]. In Argentina, there has been less deforestation and degradation, and a larger proportion of the original habitat remains[26].

We estimate that less than 27% of the suitable jaguar habitat of the AF contains jaguars. Although the species occurs in some relatively small and medium-size fragments, jaguars are mainly present in fragments larger than 1,000 km^2. Habitat fragmentation can produce a large impact on the persistence of carnivores[3,28,29]. Only large areas of suitable habitat can sustain jaguar populations that are resilient to stochastic events[29]. According to our results, more than 70% of the habitat in the AF is fragmented into small remnants that cannot sustain more than 10 individuals at current densities. Jaguar subpopulations in these small fragments have a high probability of becoming extinct in a short period of time[29,30], and have already been shown to lose genetic diversity at a very high rate[31]. Therefore, it is probable that habitat loss and fragmentation were, in an interaction with poaching and scarcity of prey, the main causes of local jaguar extinctions and large areas of empty suitable habitat.

The absence of records and the low rate of jaguar pictures in many camera-trap surveys of the AF suggest that several remnant subpopulations occur at very low densities. This is worrying given that most of these surveys were conducted in large forest areas of good jaguar habitat (e.g. protected areas), suggesting that population decline and local extinction are not only occurring in small fragments because habitat loss and fragmentation,

Name	Type	Total area (km^2)	AJO (km^2)	APJO (km^2)	% AJO surveyed with camera-traps	Population in surveyed areas	Main threats to jaguar population	Main management recommendation
Green Corridor	JCU Type I	14535	13430	1105	62%	52 (38–64)	Jaguar poaching, Kill of jaguars for conflicts with cattle, Road kills	Reduce all sources of jaguar mortality and poaching of prey. Maintain the connectivity between their two main habitat blocks. Evaluate connectivity with Itaipu and San Rafael PJCUs. Monitor jaguar population.
Upper Parana-Paranapanema	JCU Type I	6724	5343	1380	49%	47 (26–67)	Kill of jaguars for conflicts with cattle, Jaguar poaching, Small and isolated area	Reduce all sources of jaguar mortality and the conflict with livestock owners. Improve connectivity of their three main habitat blocks. Evaluate connectivity with Mbaracayu JCU, Itaipu PJCU and the Pantanal. Monitor jaguar population.
Serra do Mar	JCU Type I	13547	7315	6232	32%	14 (6–24)	Scarcity of prey, Jaguar poaching, Habitat conversion	Reduce all sources of jaguar mortality. Stop poaching of prey and palm harvest. Maintain connectivity among its main habitat blocks. Confirm jaguar presence in the APJO areas and monitor jaguar population. Improve the connectivity with the Serra do Mar Norte JCU.
Mbaracayu	JCU Type II	4086	2643	1443	48%	12 (8–18)	Jaguar poaching, Small and isolated area, Scarcity of preys	Reduce all sources of jaguar mortality and poaching of prey. Reduce habitat loss and maintain connectivity among its main habitat blocks. Evaluate connectivity with Upper Parana-Paranapanema JCU, Itaipu PJCU and the Pantanal. Monitor jaguar population.
Linhares-Sooretama	JCU Type II	503	503	0	79%	10 (9–14)	Small and isolated area, Scarcity of prey, Road kills	Reduce all sources of jaguar mortality and poaching of prey. Evaluate the supplementation of individuals. Monitor jaguar population with emphasis in the genetic diversity.
Rio Doce	JCU Type II	1407	1113	294	0	NA	Small and isolated area, Kill of jaguars for conflicts with cattle, Scarcity of preys	Reduce all sources jaguar mortality and the conflict with livestock owners. Evaluate jaguar population including genetic diversity. Evaluate the supplementation of individuals. Evaluate potential connectivity with Cerrado jaguar population.

Continued

Name	Type	Total area (km^2)	AJO (km^2)	APJO (km^2)	% AJO surveyed with camera-traps	Population in surveyed areas	Main threats to jaguar population	Main management recommendation
Serra do Mar Norte	JCU Type II	3915	1006	2908	3%	NA	Scarcity of prey, Jaguar poaching, Habitat conversion	Reduce all sources jaguar mortality and poaching of prey. Improve habitat connectivity with Serra de Mar JCU and neighbor PJCU. Evaluate jaguar populations including genetic diversity. Evaluate the supplementation of individuals.
San Rafael	PJCU	2941	1958	983	0	NA	Unknown	Evaluate the status of the population. If a jaguar population exists, reduce all sources jaguar mortality. Evaluate its main threats and habitat connectivity with Green Corridor and Mbaracayu JCUs.
Itaipu	PJCU	2258	1460	798	0	NA	Unknown	Evaluate the status of the population. If a jaguar population exists, reduce all sources jaguar mortality. Evaluate its main threats and habitat connectivity with Green Corridor, Upper Parana-Paranapanema and Mbaracayu JCUs
Serra dos Órgãos	PJCU	1578	827	751	47%	NA	Unknown	Evaluate the status of the population. If a jaguar population exists, reduce all sources jaguar mortality, and evaluate its main threats. Evaluate habitat connectivity with Serra do Mar Norte JCUs
Itatiaia	PJCU	1336	1000	336	0	NA	Unknown	Evaluate the status of the population. If a jaguar population exists, reduce all sources jaguar mortality, and evaluate its main threats. Evaluate habitat connectivity with Serra do Mar Norte JCU and Campos do Jordao PJCU
Campos do Jordão	PJCU	539	536	3	0	NA	Unknown	Evaluate the status of the population. If a jaguar population exists, reduce all sources jaguar mortality, and evaluate its main threats. Evaluate habitat connectivity with Serra do Mar Norte JCU and Itatiaia PJCU

Continued

Name	Type	Total area (km²)	AJO (km²)	APJO (km²)	% AJO surveyed with camera-traps	Population in surveyed areas	Main threats to jaguar population	Main management recommendation
Small fragments	Small fragment	877	690	187	0	NA	Very small areas	Areas too small to maintain jaguar populations. Reduce jaguar mortality threats. Evaluate connectivity with a JCU. Studies related with jaguar movements in human dominated matrix are recommended
Total		54,245	37,825	16,420	41%	135 (87 to 187)		

Table 2. Information of the priority areas for jaguar conservation in the Atlantic Forest including name, type, total area, area of jaguar occupancy (AJO), area of potential jaguar occupancy (APJO), percentage of the AJO that was surveyed with camera traps, population estimate of this surveys using population models, main threats to jaguars and management recommendation for jaguar conservation.

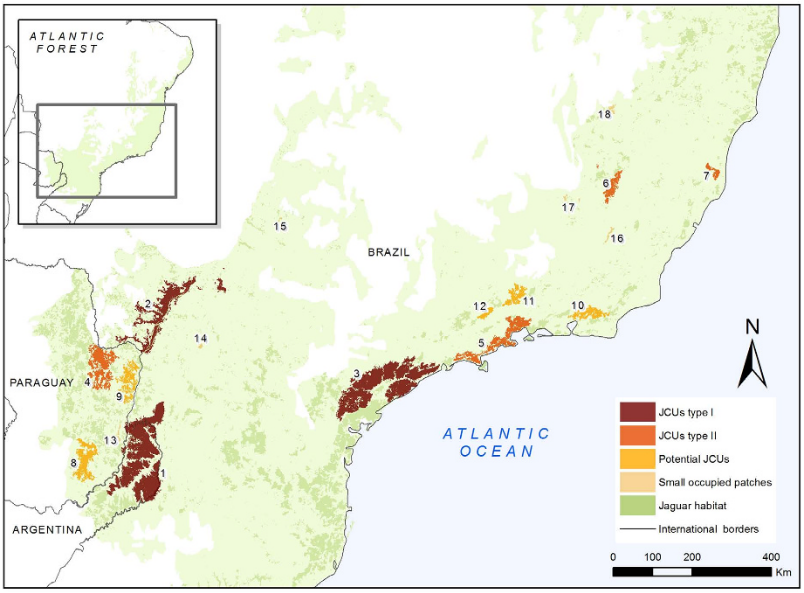

Figure 3. Distribution of the Jaguar Conservation Units (JCU), the Potential Jaguar Conservation Units (PJCU) and the small fragments with jaguar presence. References: (1) Green Corridor, (2) Upper Parana-Paranapanema, (3) Serra do Mar, (4) Mbaracayú, (5) Serra do Mar Norte, (6) Rio Doce, (7) Linhares-Sooretama, (8) San Rafael, (9) Itaipú, (10) Serra dos Órgãos, (11) Itatiaia, (12) Campos do Jordao, (13) East Paraguay, (14) Das Perobas Reserve, (15) Rio Tiete-West SP, (16) PE Serra do Brigadeiro, (17) Mantiqueira and (18) Espinhaço. The map was created with ArcGis 10.3 (www.arcgis.com).

but also in larger and more connected habitat fragments. The few areas where we recorded several individuals and could estimate densities, in general, were well-managed protected areas with relatively low poaching pressure[20,21].

Poaching can reduce jaguar densities in the AF even in areas of good habitat quality[20]. Illegal hunting is widespread in the AF and is responsible for the frequent poaching of jaguars[20,32] and the depletion of their prey base[33–36]. Jaguar killing in the AF is frequent, mainly by poachers that consider the species a trophy or by cattle ranchers that eliminate individuals as retaliation for livestock losses[20,32,37]. Large home range requirements of carnivores often expose them to the edges of protected areas, where they are in contact with human activities and are susceptible to high levels of human-induced mortality[3]. This "edge effect" could drive important changes in abundance inside the protected areas and increase the effect of habitat fragmentation[3,38,39]. Jaguar roadkill is also a threat in the AF, where the protected areas are adjacent to or crossed by roads or highways[40]. Road-killed jaguars have been recorded in protected areas of the AF, and thus, roads emerge as an additional threat for the species[40].

The jaguar population of the AF is small and severely fragmented into a few subpopulations that we defined as Jaguar Conservation Units. As we have not completely surveyed any of the JCU, we do not have the exact population size of them. Considering that most of the camera-traps surveys were conducted in areas with high habitat quality within protected areas[20,21], it is highly probable that the density in the other areas are much lower. The low rate of jaguar records (track, feces, sightings, etc.) found in these areas in our and other studies[15,41] support this hypothesis. Considering this and the extent of the AJO, it is probably that all the JCUs Type II have less than 25

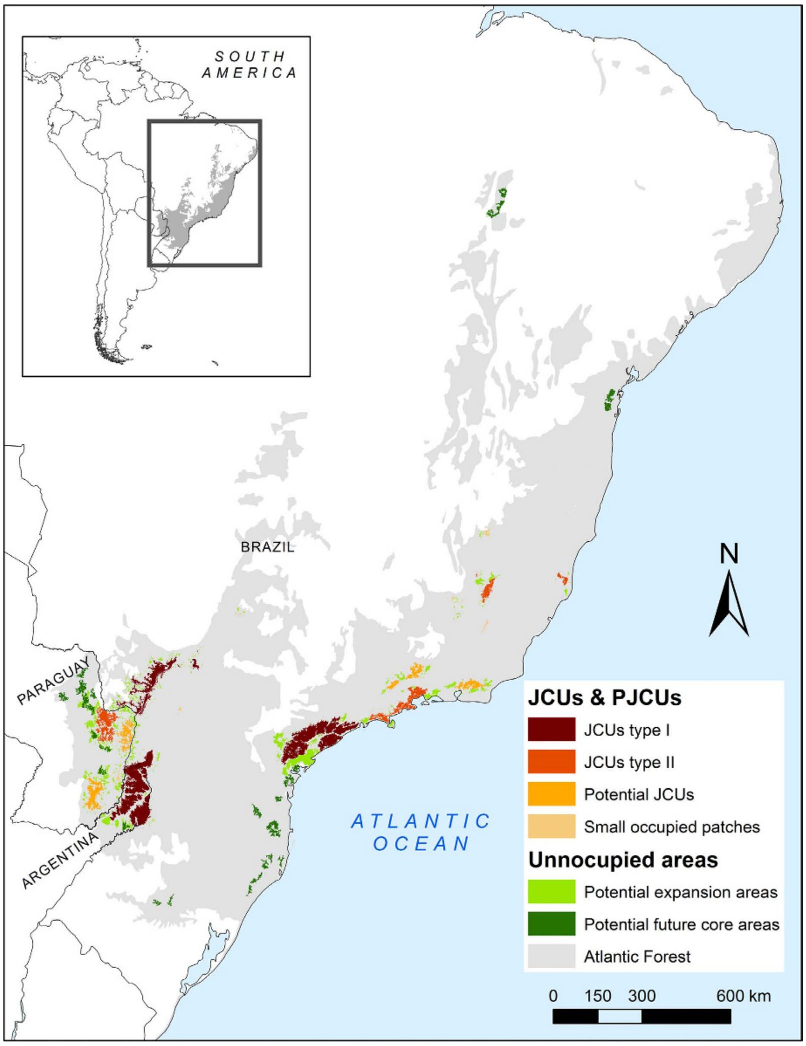

Figure 4. Other important areas for jaguar conservation in the Atlantic Forest. Potential core areas may be considered as potential areas to reintroduce the species to create new subpopulations. Potential expansion areas may be considered to enlarge JCU, PJCU and Potential core areas. The map was created with ArcGis 10.3 (www.arcgis.com).

animals each, that none of the JCU Type I have more than 85 individuals, and that the total population of the AF is roughly estimated to be in the range of between 150 and 300 individuals (Table 2, Fig. 5).

Previous population viability analysis of jaguars estimate that populations with 50 individuals may persist in the medium-long term (100 years) if mortality is low[30,42], while populations with fewer than 25 individuals have low probabilities of surviving for 100 years[30,42]. However, if the carrying capacity of a population is relatively high (e.g. large protected habitat with high prey populations), the chances of surviving increase considerably[30,42]. If we consider our highest density estimates as the potential carrying capacity for the AF, most of the JCUs are far below their carrying capacity. These subpopulations have the potential to increase in size and viability if protection is enforced and their numbers and those of their prey are allowed to increase. Currently, their small population size and isolation from other fragments have already resulted in loss of genetic diversity and likely decreased evolutionary potential[31,43], implying that additional measures (*e.g.* restoration of connectivity to other areas or supplementation of individuals) will be needed for long-term persistence (Table 2, Fig. 6).

In contrast to other large carnivores with higher reproductive potential (e.g. leopards, pumas, tigers), jaguar populations cannot support even intermediate levels of harvest, and they decline rapidly when mortality is high[42,29]. In this scenario, reducing jaguar mortality appears to be the most important action to conserve jaguars in AF (Table 2, Fig. 6). Poaching must be reduced by increasing support for law enforcement, but also by developing high-impact education and communication campaigns[20], as well as by implementing sustainable alternatives of living for communities neighboring protected areas. Reducing illegal hunting will not only reduce jaguar killing, but it will also increase its' prey base and the carrying capacity of forest fragments. In addition, the loss of jaguars in retaliation to predation on livestock must be reduced through proactive policies from governmental agencies. For the smallest populations, periodic arrivals or supplementation of individuals could increase the probability of persistence[30], and this must be considered as a viable alternative if we want these populations to persist in the long term (Table 2, Fig. 6).

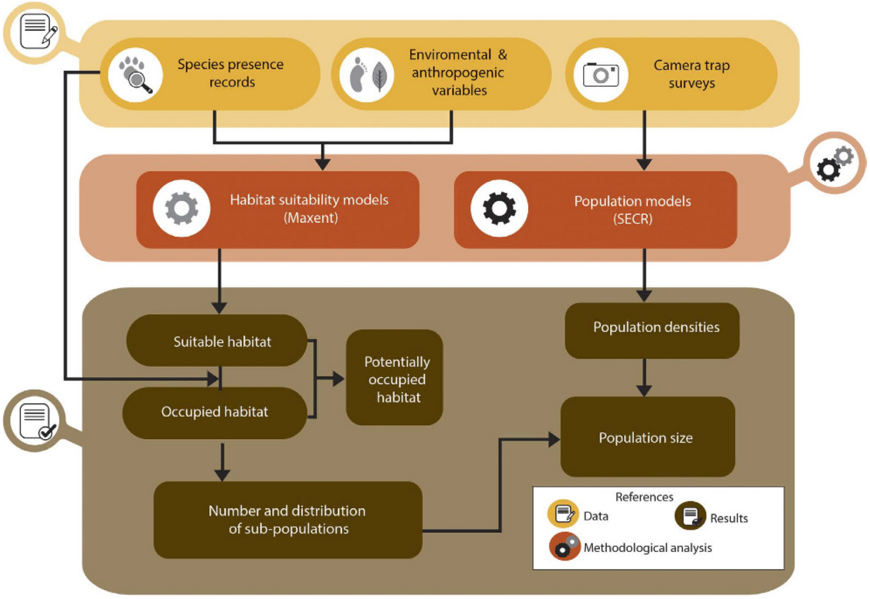

Figure 5. Methodology used to estimate the distribution and size of the subpopulations and the population size of jaguars in the Atlantic Forest. The same methodology could be used to evaluate the populations status of other carnivore species. The authors created this figure.

Enhancing landscape connectivity is a key strategy of modern biodiversity conservation worldwide[44]. Our results show that the potential connectivity between JCUs is highly variable. The high cost and long distances between the JCUs in the Upper Parana Atlantic Forest will be a challenge for creating successful corridors. In this region, the role of the Itaipu PJCU is crucial, acting as a potential stepping-stone between the Green Corridor, the Upper Parana-Paranapanema and Mbaracayú JCUs (Fig. 3 and Supplementary Table S2). These last two JCUs could also play a very important role as a connection between the Atlantic Forest and Pantanal jaguar populations[44]. The Coastal Atlantic Forest JCUs show higher potential for connection. Hence, it will be more effective to promote corridors as a management policy in this area. In contrast, the high cost distance value of Rio Doce and Linhares-Sooretama JCUs suggests that they are highly isolated from the rest of the JCUs and that the chances of arrival of jaguars via natural dispersal will be extremely low. Furthermore, it seems quite difficult to implement natural functional corridors between the Upper Parana Atlantic Forest JCUs and Coastal Atlantic Forest JCUs since the cost-distance value is very high. In this scenario, we will need to develop an active management strategy including carefully planned and monitored translocation or supplementation of individuals to reinforce some jaguar populations and maintain their genetic diversity (Table 2 and ref. 43).

This study is the results of a collaborative effort among scientist of different countries to save the top predator of the AF. By joining sparse data and using different analytical techniques, we evaluated the size and distribution of AF´s jaguar subpopulations (Fig. 5). Using a combination of new and previous[14,45] approaches, we defined the priority areas to conserve the species and proposed spatially explicit conservation actions (Fig. 6). This step-by-step process was an efficient way to transform basic information into management recommendations, and could be applied to jaguar populations in other regions, or other species of large carnivores.

Our work can be considered as the first step to understand the general population status of jaguars in the whole AF and guide priority conservation actions. However, this effort must be continued to improve our knowledge, cover existing information gaps and refine the conservation strategies. In the near future, population surveys in the AF should focus on exploring areas where jaguar presence was not confirmed (APJO and large high quality habitat patches identified by our model), regularly monitoring jaguar population size of the JCUs (including the evaluation of unsurveyed areas of the JCU) and its genetic diversity. In addition, it is crucial to understand how the jaguars move in this fragmented landscape, evaluating the feasibility and effectiveness of the establishment of corridors and techniques for supplementation or translocation of individuals (Table 2). Finally, it is also necessary to evaluate the best ways to reduce the human induced mortality of jaguars by analyzing alternatives to solve jaguar-cattle rancher conflicts, and to reduce poaching and the impact of roads.

The extinction of jaguars in the AF could have important consequences[13]. In the absence of jaguars, it is expected that populations of other species and many processes will change with unpredictable consequences for the ecosystem[1,2]. To protect and increase the jaguar populations and the natural areas that they depend on, constitute an enormous challenge for the next decades, but there are reasons for hope. Our population estimates for the Green Corridor (Table 1) suggest that this subpopulation is increasing after a marked decline in the 1990's[20], probably as a result of efforts of governmental institutions and NGOs in combating poaching and other threats. The survivorship of small and presumably isolated subpopulations in the Morro do Diabo and Linhares-Sooretama areas during the last decades also brings hope, in spite of their documented loss of genetic diversity[31,40]. Finally, the increasing collaboration among institutions of Brazil, Paraguay and Argentina to coordinate and develop transnational actions to study, monitor and conserve the species is also an asset.

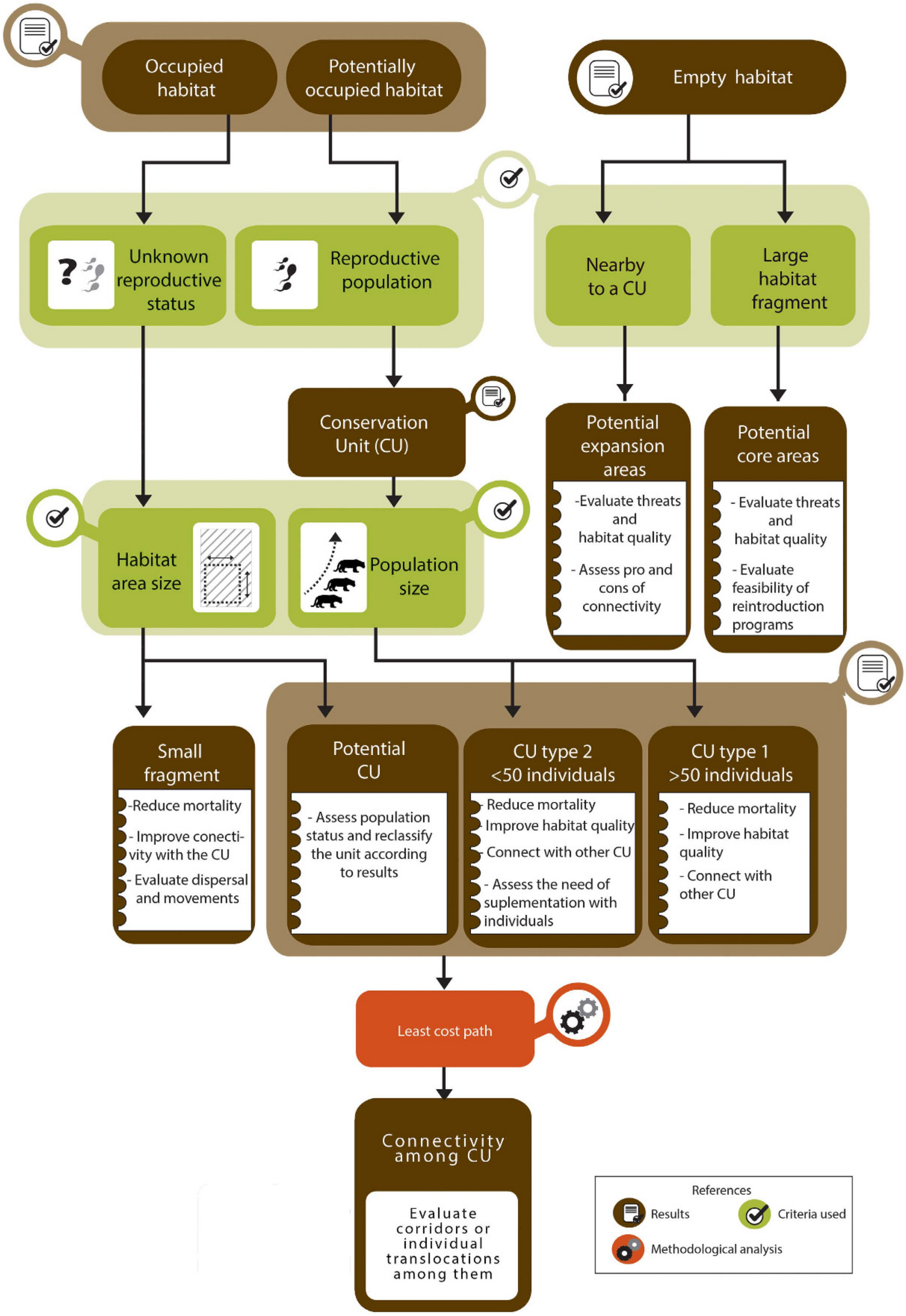

Figure 6. Methodology used to define the important areas for conservation of the species and management recommendations for each area. The same methodology could be used for conservation planning of other carnivore species. The authors created this figure.

During the last decades, a large amount of scientific evidence demonstrated the importance of large carnivores as key parts of ecosystems[1,2]. However, the survival of these species is still a challenge, especially in tropical ecosystems. Following the creation of the Large Carnivore Initiative for Europe Specialist Group for the IUCN, Ripple *et al.*[2] proposed the creation of a Global Large Carnivore Initiative to maintain and restore, in coexistence with people, viable populations of large carnivores as an integral part of ecosystems and landscapes. We agree with this vision, and propose to put special attention and effort in the most threatened regions and ecosystems of the World. In this context, special attention must be given to the continued challenge of conserving the jaguar population of the Atlantic Forest.

Methods

Habitat suitability for jaguars. To evaluate the size and location of the remaining suitable areas for jaguars in the AF, we developed a species distribution model. We gathered 2,179 jaguar presence points (Fig. 2) collected in the region between 2003 and 2014 by 14 teams researchers and its collaborators involving more than 300 hundred people. Jaguar records correspond to camera-trap pictures, locations of collared individuals, poached or road-killed animals, sightings and jaguar confirmed tracks and feces obtained in systematic and non-systematic surveys (Supplementary material Methods S1). To reduce the spatial correlation among records from this dataset (e.g. many records corresponding to the same individual), we divided the study area in cells of the size of a female jaguar potential home range in the AF (144 km^2), the smallest range of an individual of the species in region[11], and randomly selected only one presence point from each cell[11,16,46]. The resulting 72 presence records that remained were partitioned randomly into training (70%) and testing (30%) datasets for cross-validation with replacement ($n = 10$).

We selected six non-correlated (Pearson's $r < 0.70$) environmental and anthropogenic variables as predictors, from an initial set of 18 variables (Supplementary Table S3) that explained jaguar distribution in previous studies performed in the region[11,12,16,25]. The final variables were: human accessibility cost, % of natural habitats (native forest cover and marshlands), % of pastures, human population density, distance to rivers, and elevation. Because the characteristics of the species and the methodologies used in our surveys prevented obtaining locations of true absences, we chose the Maxent algorithm (Maxent 3.3.3 k) for running species distribution models[47,48]. As model parameters, we used a convergence threshold of 10−5 with 500 iterations, 10,000 background points, auto features, random seed, analysis of variable importance and response curves[48].

The logistic output resulted in an average model with values ranging from 0 (unsuitable) to 1 (suitable)[47]. We set the 'maximum test sensitivity plus specificity' (0.364) as a decision threshold rule[49] making the distinction between suitable ($\geq$0.364) and unsuitable ($\leq$0.364) areas. Then, we reclassified the final model in four classes with equal intervals, but adjusting the first value 0.250 to the threshold of 0.364. Final models resulted in: unsuitable (0 to 0.364), and the suitable habitat divided in marginal (0.364 to 0.5), medium (0.5 to 0.75) and highly suitable (0.75 to 1) areas for jaguars.

We evaluated the final model by the area under the receiver operating characteristic curve (AUC) value, a threshold-independent measure of overall model performance (mean ± standard deviation; ref. 50). The AUC ranges from 0 to 1, assuming that $AUC \geq 0.75$ is a high score[51]. We also evaluated omission errors and model significance by binomial probability associated to the threshold used[52]. Finally, after the conclusion of the modeling analysis, we gathered new records from the field ($n = 107$, Supplementary material Methods S1), which we decide to use as an independent dataset to further test the model's predictive ability for jaguar occurrence in the AF.

Estimation of areas of jaguar occupancy. To identify the fragments of habitat with jaguar occupancy along the AF (as used by the IUCN to assess species status), suitable habitat areas obtained in the final model were converted to polygons, splitting the resulting habitat fragments by main and secondary roads. We overlaid all the jaguar occurrence points onto suitable habitat remnants, selecting those with confirmed jaguar presence. As some occurrence points were located outside the suitable habitat fragments, we calculated the median distance from these points to the closest habitat fragment (1.7 km). This value can be interpreted as the distance that jaguars usually reach when they move outside the suitable habitat. Therefore, to be conservative, we only considered as area of jaguar occupancy (AJO) every fragment of continuous suitable habitat containing jaguar records and those that had a jaguar record closer than 1.7 km (Fig. 5). Additionally, we considered as areas of potential jaguar occupancy (APJO) those fragments without jaguar records inside or near them, but that were closer than 1.7 km to an occupied fragment of suitable habitat (Fig. 5).

Estimation of jaguar abundance, density and population size. To estimate relative abundance and density, we compiled jaguar records from 30 camera-trap surveys conducted between 2003 and 2014 (Table 1, see also Supplementary Fig. S1 and Table S1). Most of the surveys were specifically designed to evaluate jaguar abundance and were performed by our own teams, but we also included information from surveys conducted by other collaborators (17% of the surveys). The surveys covered portions of most of the largest fragments of remaining jaguar habitat in the AF, including areas with different levels of human activity and legal protection (Supplementary Fig. S1 and Table S1).

The surveys varied widely in terms of effort, distance among cameras-trap stations and area covered, and jointly they accumulated more than 80,000 camera-trap days from more than 900 different stations located in jaguar suitable habitat (Table 1, Supplementary Table S1). In general, camera-traps were deployed in pairs, facing each other along roads, trails or inside the forest, trying to cover places regularly used by jaguars. We used photographs to identify individual jaguars through their unique spotting pattern, and the sex and age by the presence or absence of scrotum and corporal build. For density estimation we only used data of perceived adult animals. Surveys with relatively few jaguar records (<6 individuals) were only used to estimate jaguar photographic rate and to confirm the presence of females in the area.

We estimated jaguar densities through spatially explicit capture-recapture population models (SECR) that combine capture-recapture records with their geographic location[53,54]. These models have been used previously to estimate jaguar density[55–57], and simulations studies show that they generate the less biased density estimations in a wide range of conditions in relation to different sizes of areas covered by cameras and jaguar home range sizes[57]. To apply the SECR models, we used the Bayesian approach and Markov chain Monte Carlo simulations through the R package SPACECAP 1.1.0[54,58,59]. A detailed description of the procedures and parameters employed to estimate density is provided in Supplementary material Methods S2.

The lack of records of jaguar individuals at different stations in the Mbaracayu survey precluded the use of SECR models in this area. We thus estimated its jaguar density using non-spatial capture-recapture models in combination with information of the estimated home range size of the animals[20,60] and using the jackknife estimator of abundance in the program CAPTURE2[61]. The effectively sampled area was estimated by applying to every camera-trap station a buffer equal to the radius of the mean home range of three animals monitored by GPS collars in this area (5.8 km; Ramirez *et al.*, unpublished results). The resultant polygons around each camera were merged into one polygon that was considered the sampled area[20,55].

To obtain the population size, in areas where we obtained density estimates with camera traps and population models, we used the NSuper parameter obtained in SECR analysis as the number of animals present in the surveyed area (Fig. 5). We also used 95% confidence interval limits as the minimum and maximum number of individuals living in each area.

Identifying priority areas for jaguar conservation. We identified priority areas for jaguar conservation, defined as Jaguar Conservation Units, as those containing a jaguar population and suitable habitat. This approach was originally proposed by Sanderson *et al.*[14], and has been used widely to update and redefine the JCUs originally proposed (e.g., refs 11,45, 62 and 63). In our work, we defined JCUs as those habitat units with confirmed presence of females and males as a proxy for existing reproductive populations (Table 1 and Fig. 6). We classified these JCUs into two categories, according to the known number of adult individuals present: Type I JCUs were areas with an estimated population size of $\geq$50 adults and Type II JCUs were areas with $<$50 adults (Fig. 6 and ref. 14).

To identify habitat units that can potentially constitute JCUs, we focused on the areas of jaguar occupancy and potential occupancy, and grouped them into those that were less than 15 km from a fragment with jaguar presence. This distance is the radius of the largest home range estimated for jaguar in the AF (Morato *et al.* unpublished results), and could be considered as a distance that is not usually traveled by resident jaguar individuals outside suitable habitat. One exception in this grouping procedure was Morro do Diabo State Park (Brazil) that was included in the Upper Parana-Paranapanema JCU. This fragment was more than 15 km apart from the other fragments of this Unit, but historical and political issues determine the feasibility of the development of a common conservation strategy and management actions with the rest of this JCU.

In this contribution, we also classified other habitat units into different categories according to their importance for jaguar conservation (Fig. 6). Habitat units occupied by jaguars but without the confirmation of males and females were classified according to their potential of becoming a JCU. Areas that had habitat in good condition (medium to high suitability) larger than the habitat in good condition of the smallest JCU (230 km^2 in Linhares-Sooretama JCU) were categorized as 'Potential Jaguar Conservation Units' (PJCU, 42). Areas with confirmed jaguar presence but harboring less than 230 km^2 of habitat in good condition were classified as 'small fragments with jaguar presence' (Fig. 6).

Areas of suitable habitat but without jaguar records, were categorized considering their proximity to an occupied area of the JCU or PJCU and the size of the habitat fragment. A fragment of suitable habitat at $<$15 km of a JCU or PJCU was categorized as potential expansion area of these units. Isolated fragments of continuous habitat in good condition (medium or high suitability) larger than 230 km^2 were categorized as potential future core areas (Fig. 6).

Evaluating the potential connectivity among JCUs. To determine the potential connectivity of jaguar populations among all the JCUs and PJCUs, we used a least-cost functional connectivity model[44,64]. We created a resistance to movement surface, which was calculated as an inverse function of our habitat suitability model[65]. This approach assumes that habitat quality has a direct relationship with facility to movement[65,66]. To determine the least cost path we used the Linkage Mapper 0.9[67]. This software uses core habitat areas (JCUs and PJCUs) and raster resistance surfaces to identify and map least-cost linkages between adjacent core areas. Linkage Mapper calculates accumulated costs as it moves away from a core area, and takes into account the distance and direction to create a single composite cost-distance grid.

Evaluation of threats to jaguars in the JCUs. To identify and rank the main threats to jaguars in every JCU, we developed a questionnaire with a list of the known pressures on jaguars in the AF, and asked for potential additional ones. The questionnaire was responded by 9 experts that are conducting research in the different JCUs. This approach has been used before to identify the threats to jaguars on a continental scale[14]. We asked experts to rank potential threats to jaguars, and requested information about recent cases of jaguar mortality induced by humans in the region as a way to corroborate the ranking of threats for every JCU.

Finally, according to the obtained results on population estimates, isolation of every area and jaguar threats, we propose management actions to mitigate the most important threats to jaguars and improve the chances of the species population growth (Table 2 and Fig. 6).

Data availability

The datasets used in the analysis and the shape files obtained during the current study (habitat suitability model, shape files of the AJO, APJO and important areas for jaguar conservation) will be available in a public repository.

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Acknowledgements

We thank all the people that provided jaguar records and information of camera-traps surveys. We also thank the field assistants of our teams that collaborate during the field activities and Silvia Benito for their help with the design of the figures. A.P., C.D.A., J.M.P., M.D.B., P.C., V.Q. and S.C. thank to CONICET, Fundacion Vida Silvestre Argentina, WWF, Rufford Small Grant Foundation, WCS, Lincoln Park Zoo, SCGIS and ESRI for financial support and the Ministry of Ecology of Misiones Province and National Park Administration of Argentina for logistic support. K.M.P.M.B.F. thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2014/09300-0) and *Fundação* Grupo *Boticário* de Proteção à Natureza for financial support. KMPMBF and PMGJ thanks and Universidade Vila Velha (UVV 21/2015) and Fundação de Amparo à Pesquisa do Espírito Santo (FAPES 0607/2015) CNPq for the productivity fellowship. ACSA thanks the financial support from Vale S.A./Instituto Ambiental Vale. F.L., D.S., L.C., M.P. thanks to Fundo Brasileiro para a Biodiversidade - Tropical Forest Conservation Act agreement (FUNBio/TFCA), Liz Claiborne and Art Ortenberg Foundation, Companhia Energética de São Paulo - CESP, The Mohamed bin Zayed Species Conservation Fund, Panthera Small Grants Program, Oregon Zoo Future for Wildlife Program and Wildlife Direct Inc. for financial support. BMB thanks FAPESP (2008/03099-0).

Author Contributions

A.P. did the general coordination of the study; A.P., C.D.A., K.M.P.M.B.F., R.M., M.X.S., R.C.P., B.M.B., P.M.G.J., A.S., F.L., M.V., V.Q., P.C., S.C. and J.M.P. participated in the discussion workshops for the elaboration of the study; A.P., C.D.A., M.D.B., A.C.S.A., B.M.B., F.L., D.S., M.X.S., M.V., L.C., P.C., E.N., F.R.P. and S.F. provided camera traps data; C.D.A., K.M.P.M.B.F. and M.L.J. did the habitat suitability analysis; A.P. and V.Q. did the density estimation analysis; A.P., B.M.B., M.X.S., D.S., F.L., L.C., M.P., M.V., A.C.S.A., and E.N. evaluated the main threats in the JCU; A.P., C.D.A with the participation of all the authors made the identification of priority areas for conservation and the management recommendations for jaguar conservation. J.M.P., C.D.A. and A.P. did the connectivity analysis. A.P., C.D.A., K.M.P.M.B.F., R.M., P.C., J.M.P. wrote the main manuscript. A.P., C.D.A., K.M.P.M.B.F., R.M., J.M.P., A.C.S.A., B.M.B., F.L., D.S., M.X.S., M.V., L.C., P.C., M.L.J., P.G., T.M.A., P.C., M.P., A.S.M.C.S., V.Q., E.N., F.R.P., S.F., S.C., E.A.M. and F.A. reviewed and approved the manuscript.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Paviolo, A. *et al.* A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America. *Sci. Rep.* **6**, 37147; doi: 10.1038/srep37147 (2016).

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RESEARCH ARTICLE

Can Scat Analysis Describe the Feeding Habits of Big Cats? A Case Study with Jaguars (*Panthera onca*) in Southern Pantanal, Brazil

Miriam L. L. Perilli[1,2,3]*, **Fernando Lima**[4,5], **Flávio H. G. Rodrigues**[3,6], **Sandra M. C. Cavalcanti**[3]

1 Programa de Pós-graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa - UFV, Viçosa, Minas Gerais, Brazil, **2** Programa de Pós-graduação em Ecologia e Conservação, Universidade Federal do Mato Grosso do Sul - UFMS, Campo Grande, Mato Grosso do Sul, Brazil, **3** Instituto para Conservação dos Carnívoros Neotropicais - Pró-Carnívoros, Atibaia, São Paulo, Brazil, **4** IPÊ - Instituto de Pesquisas Ecológicas, Nazaré Paulista, São Paulo, Brazil, **5** Programa de Pós-graduação em Ecologia e Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista – UNESP, Rio Claro, São Paulo, Brazil, **6** Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais - UFMG, Belo Horizonte, Minas Gerais, Brazil

* miriamperilli@gmail.com

Citation: Perilli MLL, Lima F, Rodrigues FHG, Cavalcanti SMC (2016) Can Scat Analysis Describe the Feeding Habits of Big Cats? A Case Study with Jaguars (*Panthera onca*) in Southern Pantanal, Brazil. PLoS ONE 11(3): e0151814. doi:10.1371/journal.pone.0151814

Editor: Mathew S. Crowther, University of Sydney, AUSTRALIA

Received: September 29, 2015

Accepted: February 27, 2016

Published: March 22, 2016

Data Availability Statement: All relevant data are within the paper.

Funding: Scat analysis funding was provided by Fundação Grupo Boticário de Proteção à Natureza (Boticário Group Foundation). Funding for jaguar monitoring was provided by the Wildlife Conservation Society (WCS). Sociedade Civil Mamirauá (SCM) and Fundação Brasileira para o Desenvolvimento Sustentável (FBDS - Brazilian Foundation for Sustainable Development) provided administrative and logistical support at the research station. MLLP received scholarship from Coordenação de

Abstract

Large cats feeding habits have been studied through two main methods: scat analysis and the carcasses of prey killed by monitored animals. From November 2001 to April 2004, we studied jaguar predation patterns using GPS telemetry location clusters on a cattle ranch in southern Pantanal. During this period, we recorded 431 carcasses of animals preyed upon by monitored jaguars. Concurrently, we collected 125 jaguar scats opportunistically. We compared the frequencies of prey found through each method. We also compared the prey communities using Bray-Curtis similarity coefficient. These comparisons allowed us to evaluate the use of scat analysis as a means to describe jaguar feeding habits. Both approaches identified prey communities with high similarity (Bray-Curtis coefficient > 70). According to either method, jaguars consume three main prey: cattle (*Bos taurus*), caiman (*Caiman yacare*) and peccaries (*Tayassu pecari* and *Pecari tajacu*). The two methods did not differ in the frequency of the three main prey over dry and wet seasons or years sampled. Our results show that scat analysis is effective and capable of describing jaguar feeding habits.

Introduction

The ecological importance of large mammalian carnivores such as the jaguar (*Panthera onca*) is easily recognized, as even a few individuals can exert strong top-down control on prey populations and smaller predators [1–3]. These 'apex predators' occupy an elevated position on the

Aperfeiçoamento de Pessoal de Nível Superior (CAPES). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

trophic ladder, and their role as ecosystem regulators is now firmly embedded in ecological theory [4–6]. The jaguar is the largest of the Neotropical cats and is considered Near Threatened by the IUCN [7], with a decreasing population trend. Habitat degradation, consequent loss of natural prey, and hunting pressure has led to a reduction in range and historical occurrence of the jaguar [8]. Because of these threats, jaguar populations are either restricted to remote areas with low human densities or forced to coexistence with man and livestock [9,10]. This coexistence increases the possibility of these carnivores preying on livestock instead of their natural prey [10–12]

The Pantanal in Brazil is a vast flood plain that shelters abundant wildlife and is considered essential for the long-term conservation of jaguars, as it holds the highest abundance of the species[8,13]. The region is characterized by large-scale private cattle ranches, and the extensive management of the cattle brings the herds into direct contact with jaguars, which eventually prey upon them [13–15]. Predation on livestock is considered the biggest source of conflict between jaguars and ranchers and is often used as a justification for jaguar poaching [9,12,15,16]. Studies on jaguar feeding habits are important not only to increase our knowledge on the foraging patterns of the species but also to provide subsidies to develop mitigation measures for livestock depredation.

The first studies on the feeding habits of jaguars emerged in the late 1970s and the 1980s in the Pantanal [13,17,18], Belize [19] and Peru [20]. We now know that the species feeds on a wide variety of prey, ranging from small rodents to large mammals such as the marsh-deer (*Blastocerus dichotomus*) and tapir (*Tapirus terrestris*). Much of the information currently available about jaguar diet originates from scats [14,19–38]. As a noninvasive method, scat analysis is an important tool for studying cryptic animals, which are difficult to observe and capture.

Another method of studying jaguar feeding habits is through the detection of kills by individuals monitored with telemetry [13–15]. With advances in global positioning system (GPS) telemetry technology for wildlife studies, it became possible to build more detailed databases on the feeding habits of large cats by detecting clusters of locations [15,39–41]. This method consists of investigating locations that have consecutive GPS records in close proximity to each other, indicating that the animal spent a considerable amount of time in a specific site [39]. These technologies are relatively recent and, despite generating high quality data, involve high costs and direct manipulation of individuals (*i.e.* physical constrain and anesthesia). A potential flaw in this method is that small and medium-sized species are often completely consumed or their remains can be carried out by scavengers, reducing the probability of detection and creating a bias for larger prey [42].

Here, we compare the results of two methods of jaguar feeding ecology investigation: the direct method of GPS telemetry location clusters with results from the indirect method of scat analysis. Our main objective was to evaluate each method, and we hypothesize that the scat analysis—cheaper and less invasive—is efficient in describing the feeding habits of jaguars. Our investigations were particularly focused on assessing whether the prey communities detected by each method are quantitatively similar and whether both methods show the same pattern of occurrence for the main prey in the jaguar diet.

Methods

Study area

The study was conducted at a private, 460 km^2 cattle ranch (approximately 6,000 head of cattle) in southern Pantanal (19°57'S, 56°25'W). The area is characterized by a mosaic of natural vegetation comprised mainly by grassland, cerrado woodland (cerradão), cerrado (bush savanna), marshes, semideciduous forest, gallery forest, and floating vegetation [43]. A hot and wet season extends from October to March, when the region's rivers flood a large portion of the area. A warm and dry season extends from April to September.

GPS location clusters

GPS location clusters were obtained from radio collars. Jaguars were captured with the aid of trained hounds and immobilized with tiletamine hydrochloride and zolazepam hydrochloride (Telazol® 6–10mg/kg). The sedative was administered intramuscularly using a dart fired from a CO2 pistol or a rifle. Upon darting the animal, the hounds were removed from the immediate area for safety [44]. We examined each jaguar for body condition, sex, age and weight, and then fitted them with a GPS collar (Simplex, Televilt International, Sweden). After handling we released them at the site of capture, monitoring from distance until they were able to leave the site on their on.

Capture and handling protocols were approved by the Brazilian Institute of Environment and Natural Resources (permit B-23-9114). All procedures were accompanied by an experienced veterinary. All efforts were made to minimize distress to both dogs and jaguars, and no animals or wildlife were harmed in the course of the study.

The GPS collars were scheduled to obtain seven locations/night in 2002 (fixes every 2 h between 1800 and 0600 h) and 12 locations/day from the end of 2002 to 2004 (fixes every 2 h through 24-h period). With the aid of an aircraft, these data were retrieved remotely by a radio receiver (RX-900; Televilt International) at 21-day intervals, and were plotted on a map of the study area (1:100,000) using ArcView (Environmental Systems Research Institute, Inc., Redlands, California). We classified all clusters of consecutive locations within a 100-m radius as a potential kill site [39]. Inserting the coordinates of one or more locations of those clusters into a portable GPS unit, the research team then explored the area for prey remains over a maximum distance of 100 m in diameter. Additional information on the methods described above can be found in [15].

Scats collection, handling and prey identification

We collected scat samples opportunistically during fieldwork. We selected only the samples collected during the period when the jaguars wore the GPS collars (November 2001 –April 2004). We distinguished jaguar scats from those of puma (*Puma concolor*) based on their general appearance (only the ones with a diameter > 4 cm) as well as their association with nearby footprints and the exact locations of monitored jaguars. We are aware of the importance of genetic markers for confirming the predators identity (e.g. [35,45]). However, by the time we collected the scats samples, the field of molecular analysis of scats was in its early days and our samples were not properly stored for this kind of procedure. As a security measure, we choose to discard samples we could not rely that were from jaguars.

Collected samples were dehydrated in a screen box exposed to the sun and stored in paper bags. In the laboratory, we put the samples in two layers of pantyhose handmade bags and washed them in a semi-automatic washing machine (Atlanta, Newmaq®) for two or three cycles.

To test for hair contamination between samples washed together, we performed an experimental trial. We used scats that we discarded either due to lack of information or because they belonged to other species. For the experimental trial, we washed between two and six samples together with some "fake samples" made of cotton and small stones to simulate the weight of real scat samples. We validated our procedure after noting that no hair entered the fake samples.

Food items found in scats were identified taxonomically through the examination of hair, hair microstructure patterns [46], teeth, claws, nails, osteoderms, scales and feathers. We considered each prey found in a scat sample as an independent capture or one individual. In order to minimize pseudo-replication, subsequent samples collected in close proximity on the same day and containing the same prey species were discarded (personal observation, [27]). We described the components present in the scats in terms of relative frequency of occurrence (number of times a prey species was found relative to total prey).

Data analysis

To compare the frequency of occurrence of food items (prey) to the prey communities found by the two methods, we used the Bray-Curtis similarity index [47–49]. This index is indicated to reflect accurate quantitative similarity between communities [50]. The Bray-Curtis similarity coefficient, *S*, between the two prey communities identified by two different methods is defined as

$$S = 100\left(1 - \frac{\sum |y_{i1} - y_{i2}|}{\sum_i y_{i1} + \sum_i y_{i2}}\right)$$

Where y_{i1} is the amount *i* of one species of prey in GPS clusters and y_{i2} is the amount *i* of one species of prey in scat analysis. Equivalent frequencies of prey between methods represent a similarity coefficient of 1.

The Pantanal natural climatic variation is known to determine ecological patterns and strongly affect terrestrial organisms [51]. For this reason, we opted to separate the data into two datasets: rainy season (October–March) and dry season (April–September).

Our hypothesis that scats analysis is able to provide a valid description of jaguar feeding habits when compared with GPS location clusters were tested by chi-square tests of independence [52]. We also examined the over time variation on the proportion of species found both in kills from GPS clusters and in scat samples. All the analyses were implemented with the Package MASS [53] on R [54].

Results

Ten jaguars were captured and monitored with GPS collars (5 adult males, 1 subadult male, and 4 adult females) [15]. We found a total of 431 kill at GPS location clusters and, concurrently, we identified 153 prey items in 125 jaguar scat samples. The species found through both methods are presented in Table 1.

The similarity of the total prey occurrence between the two methods was high ($S = 77.34\%$). The three main prey detected by both methods were cattle (*Bos taurus*), caiman (*Caiman yacare*) and peccaries (*Tayassu pecari* and *Pecari tajacu*) (Table 1). Together, these species accounted for more than 70% of the jaguar diet according to both methods and in both seasons (Table 2). For that reason, we chose to use the data for these 3 main prey only to compare the efficiency of each method.

We found no difference in the frequency of the main prey detected between both methods during the dry season ($\chi^2_2 = 2.83$, $P = 0.24$) or during the wet season ($\chi^2_2 = 0.69$, $P = 0.70$) (Fig 1). The GPS method was able to detect a variation in prey composition as an influence of season (climatic influence of dry season x wet season) ($\chi^2_2 = 10.14$, $P = 0.006$), and so did the scat analysis $\chi^2_2 = 6.54$, $P = 0.03$) (Fig 1). Both methods were able to record a peak in livestock predation during the year of 2002, followed by a reduction in livestock consumption and an

Table 1. Jaguar prey species identified through two main methods, kills found at GPS location clusters of 10 radio-collared jaguars, and prey remains found in 125 scats. November 2001 to April 2004, southern Pantanal, Brazil.

		Kills		Scats	
		n = 431		n = 153	
Prey species		**Total**	**%**	**Total**	**%**
Cattle	*Bos taurus*	135	31.32	55	35.95
Caiman	*Caiman yacare*	107	24.83	24	15.69
Peccaries*	*Tayassu pecari/Pecari tajacu*	93	21.58	30	19.61
Feral hog	*Sus scrofa*	17	3.94	1	0.65
Marsh deer	*Blastocerus dichotomus*	16	3.71	1	0.65
Giant anteater	*Myrmecophaga tridactyla*	13	3.02	2	1.31
Capybara	*Hydrochoerus hydrochaeris*	9	2.09	5	3.27
Lesser anteater	*Tamandua tetradactyla*	7	1.62	7	4.58
Armadillos*	*Dasypus novemcinctus/Euphractus sexcinctus*	6	1.39	1	0.65
Deer*	*Mazamasp./Ozotoceros bezoarticus*	6	1.39	6	3.92
Coati	*Nasua nasua*	5	1.16	5	3.27
Maned wolf	*Chrysocyon brachyurus*	3	0.70	-	-
Crab-eating fox	*Cerdocyon thous*	3	0.70	-	-
Raccoon	*Procyon cancrivorus*	3	0.70	3	1.96
Tapir	*Tapirus terrestris*	2	0.46	-	-
Capuchin monkey	*Sapajus libidinosus*	-	-	1	0.65
Felid	ni	-	-	1	0.65
Agouti	*Dasyprocta azarae*	-	-	1	0.65
Tapeti	*Sylvilagus brasiliensis*	-	-	1	0.65
Gray four-eyed opossum	*Philander opossum*	-	-	1	0.65
Small rodent	ni	-	-	1	-
Jabiru stork	*Jabiru mycteria*	1	0.23	0	-
Boat-billed heron	*Cochlearius cochlearius*	1	0.23	0	-
Great egret	*Ardea alba*	1	0.23	0	-
Bird	ni	0	0	5	3.27
Red-footed tortoise	*Chelonoidis carbonaria*	1	0.23	0	-
Anaconda	*Eunectes* sp.	1	0.23	0	-
Caiman lizard	*Dracaena paraguayensis*	1	0.23	0	-
Lizard	ni	0	0	1	0.65
Crab	ni	-	-	1	
		431		153	

*More than one species combined.

ni = unidentified species.

doi:10.1371/journal.pone.0151814.t001

increase in peccary predation in 2003 (Fig 2). The year of 2002 was the driest (550 mm of rainfall) and the year of 2003 was the wettest (1,700 mm of rainfall) of 8 consecutive years (1997–2004) on the study site. The GPS method detected a reduction from 49% of cattle in jaguar kills in 2001 to 20% in 2002 ($\chi^2_1 = 20.48$, $P < 0.001$), and scats analysis detected a reduction of 59% to 39% ($\chi^2_1 = 3.93$, $P = 0.04$). On the other hand, the proportion of peccaries in jaguar kills increased from 9% in 2002 to 31% in to 2003 ($\chi^2_1 = 24.82$, $P < 0.001$), and from 2% to 31% in jaguar scats ($\chi^2_1 = 11.26$, $P < 0.001$). Similarly to the GPS method, scat analysis did not find a difference in caiman occurrence between seasons ($\chi^2_2 = 2.66$, $P = 0.10$) (Fig 1) or years (Fig 2).

Table 2. Frequency of occurrence (FO) and relative frequency of occurrence (%O) of kills found on jaguars GPS location clusters, and prey remains found in 125 jaguar scats, during dry and wet seasons from 2001 to 2004, Southern Pantanal, Brazil.

	Kills					Scats			
	Dry season		Wet season			Dry season		Wet season	
	n = 260		n = 171			n = 114		n = 39	
Prey	**FO**	**% O**	**FO**	**% O**	**Prey**	**FO**	**% O**	**FO**	**% O**
Cattle	93	35.77	42	24.56	Cattle	48	42.11	7	17.95
Caiman	54	20.77	53	30.99	Peccary	20	17.54	10	25.64
Peccary	49	18.85	44	25.73	Caiman	16	14.04	8	20.51
Marsh deer	10	3.85	6	3.51	Coati	5	4.39	0	0.00
Tapir	2	0.77	-	-	Lesser anteater	4	3.51	3	7.69
Feral hog	9	3.46	8	4.68	Capybara	3	2.63	2	5.13
Giant anteater	9	3.46	4	2.34	Deer	3	2.63	3	7.69
Capybara	8	3.08	1	0.58	Raccon	3	2.63	-	-
Brocket deer	4	1.54	2	1.17	Giant anteater	2	1.75	-	-
Maned wolf	3	1.15	-	-	Bird	2	1.75	3	7.69
Lesser anteater	5	1.92	2	1.17	Small mammals	2	1.75	-	-
Coati	4	1.54	1	0.58	Marsh deer	1	0.88	-	-
Red-footed tortoise	1	0.38	-	-	Feral hog	1	0.88	-	-
Crab-eating fox	2	0.77	1	0.58	Armadillo	1	0.88	-	-
Raccon	2	0.77	1	0.58	Felid ni	1	0.88	-	-
Armadillo	2	0.77	4	2.34	Lizard ni	1	0.88	-	-
Anaconda	1	0.38	-	-	Crab	1	0.88	-	-
Bird*	1	0.38	2	1.17	Capuchin monkey	-	-	1	2.56
Caiman lizard	1	0.38	-	-	Agouti	-	-	1	2.56
					Tapeti	-	-	1	2.56

* More than one species combined.

ni = unidentified species.

doi:10.1371/journal.pone.0151814.t002

Discussion

The prey community detected in jaguar diet did not differ when analyzed using either method, GPS location clusters or scat analysis. We found a high similarity between both methods in terms of consumed prey, despite some natural variation due to jaguar individual preference [15].

Our findings differ from previous studies that investigated jaguar diet using both methods. Azevedo and Murray [14] detected capybara as the main prey in jaguar kills (31.6%) and in scats (20,8%). However, the second main prey encountered in scats was deer (red-brocket deer and dwarf red-brocket deer) (19.2%) and these species were not recorded as kills. The data Scognamillo and collaborators [30] collected to investigate jaguar diet also included kills and scats. Their study results indicate a difference on prey proportion among both methods, with livestock as the main jaguar kill (33%) opposed to only 7% of occurrence on scats. However, peccaries accounted for 40% of the jaguar diet based on scats and just 16% based on kills. Jaguar preference for large prey (>15kg) was evident in both methods, as expected for the Pantanal. Prey selection can be related to predator size as carnivores exhibit different feeding strategies according to their body mass [55]. The Pantanal jaguar features a high mean weight,

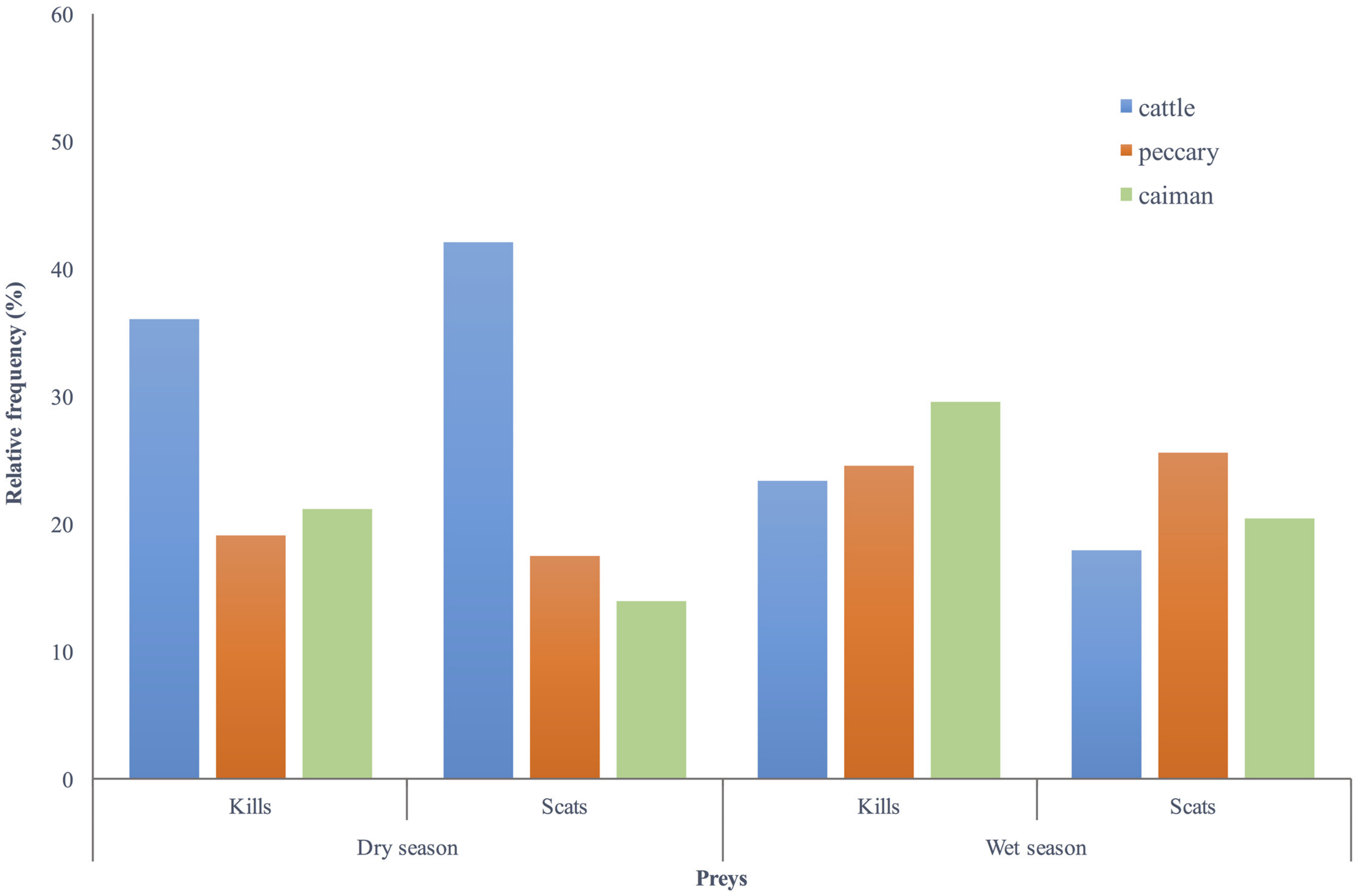

Fig 1. Relative frequency of occurrence of the 3 main prey found in GPS location clusters of 10 radio-collared jaguars (Kills) and in 125 jaguar scats (Scats) during dry and wet seasons from 2001 to 2004. Southern Pantanal, Brazil.

doi:10.1371/journal.pone.0151814.g001

with individuals of >80kg, and have a high energetic demand [15]. Similar to our results, other studies on the Pantanal also showed large prey as the base diet of jaguars, even though the proportion of species was different. Between the years of 1980–1983, Crawshaw and Quigley [56] investigated jaguar kills in the same region of our study. They found the main prey to be cattle, peccaries and capybaras. Azevedo and Murray [14], also in a cattle ranch, found that capybara was the main prey in jaguar diet, followed by cattle, deer and caiman. In Venezuela llanos, male jaguars also weight an average of >80 kg and selected for large prey (capybaras and peccaries) [30].

Conversely, rainforest jaguar show a diet less concentrated on large prey and with a more even composition. Garla and collaborators [27] found 40.5% of jaguar prey base in Brazilian Atlantic Forest to be comprised of medium sized (which they considered 3kg-10kg) species, 27.7% of large sized (>10kg) and 23.4% of small sized species (1-3kg). In Iguaçu National Park, also in the Brazilian Atlantic Forest, 49. 4% of jaguar diet was comprised by medium-sized prey, followed by 46.6% of large-sized prey species [34].

Another explanation for the variation in prey composition in a predator diet is related to prey availability, which can explain the differences between our findings and previous studies.

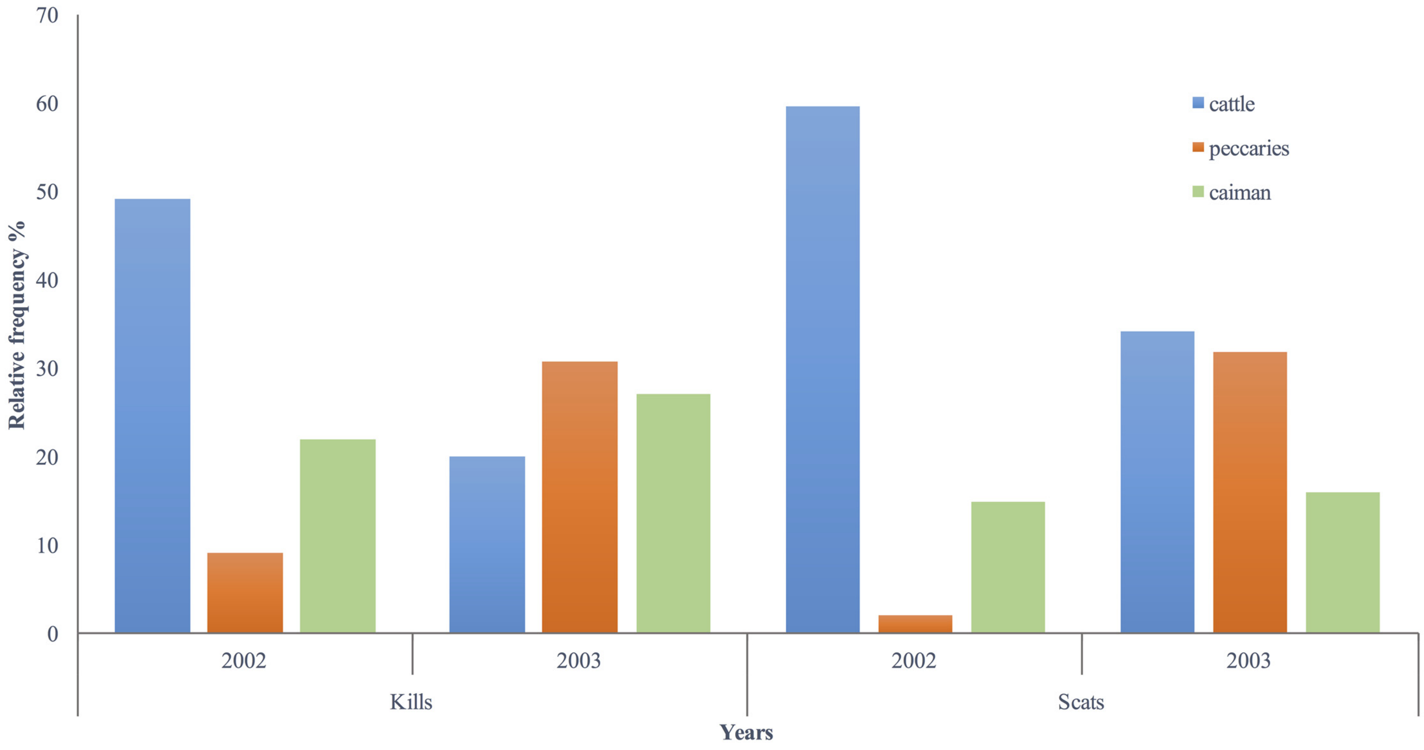

Fig 2. Relative frequency of occurrence of the 3 main prey found in GPS telemetry clusters of 10 radio-collared jaguars (Kills) and in 125 jaguar scats (Scats) during the years of 2001 and 2002. Southern Pantanal, Brazil.

doi:10.1371/journal.pone.0151814.g002

Rabinowitz and Notthingham [19] found that the occurrence of prey in jaguar scats was associated with the availability of prey species in Guam Bank (Belize), showing the opportunist nature of jaguars as predators. Also in Guam Bank, Weckel and colleagues [57] confirmed the previous observations, but noted a tendency to large prey selection.

Some large prey species where detected only by the GPS location cluster method, namely maned wolves, crab-eating foxes and tapirs. Quigley and Crawshaw [56] monitored jaguars with radio-telemetry in the same area of our study and also recorded tapir as a jaguar prey. However, other studies that used only scats to describe jaguar diet did not record tapir, even though its occurrence in the study areas were known (e.g. [19,20,34,57]). Beside the low occurrence of tapirs on jaguar diet, the difficulty in detecting tapirs on scats may be due the small surface to volume ratio of tapirs [35,58]. That associated with the species shortage of hair, can produce scats without identifiable remains [35].

Jaguars tend to remain feeding on the carcasses of large animals for a long time, returning frequently [15]. Monitored individuals remained for an average of 23.3 hours at the carcasses of prey weighing 45–200 kg [15]. Consequently, an individual prey may be associated with several scat samples, and we expected the method of scat collection to overestimate predation on large prey. However, we did not observe that overestimation in our study. It is important to emphasize that we took care to avoid the collection of multiple scats from a single jaguar that fed on a single prey over several meals. When several scats were found in close proximity during a single occasion, and contained the same food item, we selected only one sample for the analysis, thereby minimizing the risk of bias due to pseudo-replication of large prey.

We also assessed whether the GPS location cluster method was biased towards larger prey and missed detection of smaller prey [15,59,60]. As opposed to our expectations, the direct method of locating kills (GPS) enabled us to encounters maller prey species as well. Some medium-sized species such as red-footed tortoise (*Chelonoidis carbonaria*) and armadillos (*Dasypus novencinctus* and *Euphractus sexcinctus*) were located due to their carapace, which is not eaten by the jaguar. The direct method enabled us to record also two small prey: a boat-billed heron (*Cochlearius cochlearius*) and an egret (*Ardea alba*). However, small prey found in scats (but not in GPS clusters) represented less than 5% of the diet. Missing smaller prey may be more problematic in areas where they are more representative of jaguar diet, as in forested areas. Some small prey found in scats, such as crab and small rodent, are probably consumed during rare encounters between jaguars and vulnerable animals, or they are consumed indirectly as the stomach contents of larger prey [20].

Additionally, given the comparable results in terms of species occurrence in the diet, we were able to detect similar patterns of variation in the frequency of main prey consumed in wet and dry seasons, as well as among the years of 2002 and 2003. The remarkable patterns revealed by both methods show a peak of predation on livestock in dry seasons and in the driest year (2002) and an increase in the consumption of peccaries in the wettest year (2003). This peak in livestock consumption may be a reflection of an increase in livestock availability during the dry season, as the cattle herds can be found spread in large portions of the ranch. In addition, the dry season also coincides with the livestock calving season, which increases the availability of calves. A dominance of calves in jaguar kills was observed, as from the 135 cattle records in GPS clusters, 94 (69.63%) were of calves. Furthermore, during the dry season, natural prey move toward the remaining bodies of water, while cattle remains confined within fenced pastures. In contrast, during the wet season, large portions of the study area remain flooded and cattle herds group together at higher ground pastures, while native prey like caiman can be found widely dispersed through the landscape and available to more jaguars [15]. Indeed, the proportion of caiman in jaguar kills and scats increased during the wet season.

The increasing consumption of peccaries coincided with a decrease in predation of domestic livestock, which suggests the importance of maintaining native prey species in order to minimize jaguar-human conflicts that result from predation on livestock [26]. Important jaguar prey such as peccaries can be associated with forested areas, where most fruit are produced [51]. The conversion of forested landscapes into grasslands, for cattle grazing, can severely threaten vertebrate communities and trophic processes [51].

Despite the large number of studies that used scat analysis to examine jaguar diet, to our knowledge none focused on evaluating the efficiency of this method. Together, the direct and indirect methods we present here allowed the construction of a comprehensive diet database, with about 33 recorded taxa. Thus, our results also indicate the importance of joint and complementary studies for dietary descriptions. Given there are concerns over perceived versus real threats jaguars pose to livestock producers, data on the feeding habits of the species are important to subsidize jaguar conservation actions. Furthermore, considering the conflict caused by livestock predation, an accurate estimation of jaguar feeding habits is essential for the long-term conservation of the species.

Acknowledgments

We thank I. and L. Klabin for support and permission to conduct research on Fazenda Sete. MLLP and SMCC thank J. da Silva, A. Porfirio, R. Costa, S. Aquino, E. Ramalho, S. Romeiro, E. Vilalba, J. A. Silveira, R. Minillo, and M. Soisalo for their invaluable field assistance and help in scat collection. MLLP and FL thank M. Vancine for the discussions on data analysis. We thank

J. Polisar, M. King and the anonymous reviewers for the valuable revision and suggestions for this manuscript.

Author Contributions

Conceived and designed the experiments: MLLP SMCC. Performed the experiments: MLLP SMCC. Analyzed the data: MLLP FL. Contributed reagents/materials/analysis tools: FHGR. Wrote the paper: MLLP SMCC FL FHGR.

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RESEARCH ARTICLE

Implications of Fine-Grained Habitat Fragmentation and Road Mortality for Jaguar Conservation in the Atlantic Forest, Brazil

Laury Cullen, Jr.[1]*, Jessica C. Stanton[2¤], Fernando Lima[1,3], Alexandre Uezu[1], Miriam L. L. Perilli[4,5], H. Reşit Akçakaya[2]

1 IPÊ –Instituto de Pesquisas Ecológicas, Nazaré Paulista, São Paulo, Brazil, **2** Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York, United States of America, **3** Programa de Pós-graduação em Ecologia e Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista–UNESP, Rio Claro, São Paulo, Brazil, **4** Instituto para a Conservação dos Carnívoros Neotropicais–Pró-Carnívoros, Atibaia, São Paulo, Brazil, **5** Programa de Pós-graduação em Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa—UFV, Viçosa, Minas Gerais, Brazil

¤ Current address: Upper Midwest Environmental Sciences Center, U.S. Geological Survey, La Crosse, Wisconsin, United States of America.
* laurycullen@gmail.com

OPEN ACCESS

Citation: Cullen L, Jr., Stanton JC, Lima F, Uezu A, Perilli MLL, Akçakaya HR (2016) Implications of Fine-Grained Habitat Fragmentation and Road Mortality for Jaguar Conservation in the Atlantic Forest, Brazil. PLoS ONE 11(12): e0167372. doi:10.1371/journal.pone.0167372

Editor: Sam C Banks, Australian National University, AUSTRALIA

Received: August 9, 2016

Accepted: November 11, 2016

Published: December 14, 2016

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: Funding for field work was provided by the Boticário Group Foundation in Brazil (http://www.fundacaogrupoboticario.org.br/en/), The Scott Neotropical Fund of the Lincoln Park Zoological Society (http://www.clevelandmetroparks.com/Main/Home.aspx), The Species Survival Fund from Wildlife Trust, IdeaWild Grant Program (http://www.ideawild.org/), World Wildlife Fund/U.S, DICE Small Grant Program, The

Abstract

Jaguar (*Panthera onca*) populations in the Upper Paraná River, in the Brazilian Atlantic Forest region, live in a landscape that includes highly fragmented areas as well as relatively intact ones. We developed a model of jaguar habitat suitability in this region, and based on this habitat model, we developed a spatially structured metapopulation model of the jaguar populations in this area to analyze their viability, the potential impact of road mortality on the populations' persistence, and the interaction between road mortality and habitat fragmentation. In more highly fragmented populations, density of jaguars per unit area is lower and density of roads per jaguar is higher. The populations with the most fragmented habitat were predicted to have much lower persistence in the next 100 years when the model included no dispersal, indicating that the persistence of these populations are dependent to a large extent on dispersal from other populations. This, in turn, indicates that the interaction between road mortality and habitat fragmentation may lead to source-sink dynamics, whereby populations with highly fragmented habitat are maintained only by dispersal from populations with less fragmented habitat. This study demonstrates the utility of linking habitat and demographic models in assessing impacts on species living in fragmented landscapes.

Introduction

Loss of natural vegetation cover often leads to a fragmented distribution of habitat. How this habitat fragmentation affects species depends on the spatial scale and pattern of the fragmentation in relation to how the species uses the landscape [1]. One level of fragmentation may result in an environment perceived as "coarse-grained" by a small species with limited home

Liz Claiborne Art Ortenberg Foundation (http://www.lcaof.org/), The Ashoka Foundation (http://brasil.ashoka.org/), Conservation, Food and Health Foundation (http://cfhfoundation.grantsmanagement08.com/), 100% Fund from Fauna and Flora International, The Woodland Park Zoo (http://www.zoo.org/), The Whitley Awards (http://whitleyaward.org/), The Rolex Awards (http://www.rolexawards.com/), Durrell Wildlife Conservation Trust (https://www.durrell.org/wildlife/), The Rufford Small Grant Program (http://www.rufford.org/) and Ridgeway Trust. All the above mentioned funding was received by LC. Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior (CAPES) provided support during LC PhD and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Center for Latin American Studies (University of Florida) during the post-doctoral studies of LC. LC, FL, AU and MLLP received financial support for data and metadata management, curation and analysis from Fundo Brasileiro para a Biodiversidade – Tropical Forest Conservation Act agreement (FUNBio/TFCA). Contributions of HRA and JCS were supported in part by the National Aeronautics and Space Administration under Grant No. NNX09AK19G awarded through the NASA Biodiversity Program, and the National Science Foundation under Grant No. DEB-1146198. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: Our initiative was granted by The Rolex Awards, a prize aimed to recognize outstanding conservation initiatives and is not related to employment, consultancy, patents, products in development, marketed products, etc. Thus, this does not alter our adherence to PLOS ONE policies on sharing data and materials.

range and dispersal [2]. In this case, each fragment may be large enough to contain a subpopulation, or a part of it. Thus, fragmentation divides a large population into multiple subpopulations, with a total carrying capacity less than that of the original single population. The same level of fragmentation may result in an environment perceived as "fine-grained" by a larger, more mobile species. In this case each population (even each territory) may extend to multiple fragments [3,4]. The population-level effects in this case are likely to be more complex. The fragmentation may or may not result in population subdivision, but will likely affect the carrying capacity of the population as the habitat area is decreased [5]. Also, if the species is territorial there may be fewer territories available. In addition, vital rates and behavior of the individuals may also be affected, e.g., due to edge effects [6]. The home range of each individual in the fragmented landscape may include multiple fragments, forcing the individual to move among them through the human-modified landscape. Depending on the characteristics of the non-habitat (i.e., "matrix") areas of the landscape, this may result in higher levels of human-wildlife conflict and higher mortality due to hunting, poaching and collisions with vehicles [7]. From the perspective of species, like jaguar, that have very large home ranges, most habitat fragmentation would be fine-grained [8–12]. The impact of such fragmentation may not be loss of populations, but a more subtle interaction between habitat fragmentation and road mortality such that populations with more fragmented habitat suffer higher mortality.

In this paper, we analyze the factors affecting the viability of a top predator in a fine-grained fragmented landscape. The use of selected species as a basis for site-based conservation has been widely used for designing landscape conservation (e.g. [13–15]), building on the concept of umbrella species, whose protection indirectly causes the protection of several other species. Large carnivores, such as jaguars, can act as umbrella species because of their large area requirements [16]. In addition, as top predators they play an important role in maintaining healthy ecosystems [17].

Remaining jaguar (*Panthera onca*) populations are becoming increasingly fragmented and isolated throughout the species' range [18]. The Upper Paraná River, in the Brazilian Atlantic Forest region, provides a unique opportunity to study jaguars in a landscape that includes highly fragmented areas as well as relatively intact ones. Jaguar populations may exhibit a metapopulation structure, and an important step in assessing the status of jaguars is to determine the spatial structure of its populations in this region. The Pontal do Paranapanema Region, together with the upper Rio Paraná ecosystem still maintains approximately 50,000 km^2 of relatively connected and well-preserved semi-deciduous Atlantic forests and marshlands, surrounded by a mosaic of agriculture, extensive cattle ranching, and agrarian settlements [19]. It is among the few areas where large carnivores such as jaguars, pumas and ocelots persist [20]. There are several protected areas in the region, including the Morro do Diabo and Ivinhema state parks in Brazil, Ilha Grande national park and Iguaçu national park in Brazil and Argentina. In this region, jaguar is identified as one of a handful of umbrella species whose long-term viability is a conservation priority [1,21]. In the broader context of the species' range, the populations in the Upper Paraná ecosystem are considered to be of highest conservation concern [22]. These populations are threatened by several factors, including habitat loss, habitat fragmentation, and consequential mortality from interactions with livestock [9,19,23–25] and proximity to roads. These populations are also relatively isolated from populations in other regions such as the Pantanal and the Coastal Atlantic forests [8].

We developed a habitat-based metapopulation model to estimate the viability of jaguars in the Upper Paraná Region and the contribution of road mortality to the risk of decline of this species. We analyzed the simulation results to identify interaction between the effects of road mortality and habitat fragmentation. We interpreted these results in terms of landscape management and corridor restoration in a human-dominated landscape, with the hope that this approach will contribute to future state and national government efforts and well-founded conservation policies in the Upper Paraná ecosystem, and provide the basis for long-term landscape conservation planning within the region.

Materials and Methods

Overview of the model

We modeled the metapopulation dynamics of the jaguar in an approximately 340 km x 660 km region of the upper Paraná-Paranapanema region, along the Paraná and Paranapanema Rivers in Brazil (Fig 1). We developed the model using the software RAMAS GIS [26], which uses spatial data (such as habitat maps) to determine the spatial structure of a metapopulation (i.e., number and location of its populations) and simulates metapopulation dynamics with an age- or stage-structured (matrix) model for each population. RAMAS GIS can incorporate stochasticity, density dependence, and other factors, and has been used to analyze the viability of a variety of species (e.g., see [27]), including large carnivores such as ocelot [28], cougar [29], Florida panther [30], grizzly bear [31] and Iberian lynx [32].

We developed a habitat model using data on land cover and habitat selection of jaguars, and used this model to calculate the spatial structure of the metapopulation. We used a combination of our own data and data from the literature to estimate demographic parameters and combined these parameters with the spatial structure to build a stage-structured, stochastic, spatially explicit metapopulation model. Finally, we used this model to simulate the dynamics of the jaguar metapopulation and to estimate its viability under various scenarios. The components of the model are detailed below.

Habitat Model

The spatial structure of the jaguar metapopulation in the upper Paraná-Paranapanema ecoregion was based on a habitat map that we developed using logistic regression. Presences included 1223 locations at which jaguars were recorded using a variety of methods including radio collars, camera traps, animal tracks, and personal observations. Predictor variables included land cover maps with 7 categorical variables, which we converted to percentages by reducing the spatial resolution. The most important variables were primary and secondary forest and marshlands. Information about the data and the maps that formed the basis of this analysis, and the details of the habitat model are described in S1 Appendix.

We used the habitat map to determine the spatial structure of the metapopulation, including size and location of main habitat patches and the distances between them. The link between the habitat map and the jaguar metapopulation was characterized by two parameters. *Neighborhood distance* was used to identify nearby grid cells that belong to the same patch (i.e., population) and may represent the mean foraging distance of the species or the size of the home range. Based on the average home range area of 125 km^2 [33], the diameter of a circle shaped home range was calculated as 47 cells (1 cell = 270 meters), which was used as the *Neighborhood distance* parameter. *Threshold habitat suitability* is the minimum habitat suitability value below which the habitat is not suitable for reproduction and/or survival. As the threshold is increased, the number of populations identified by the program increases. We adjusted this parameter so as to identify the four populations that were determined to be genetically distinct populations by Haag and colleagues [34] as separate populations of the model. This was achieved by setting *Threshold habitat suitability* to 0.75. The proportion of the study area with habitat suitability (HS) at or above 0.75 is 3.8%. This represents a conservative (precautionary) value, because only a small portion of the landscape is assumed to be suitable.

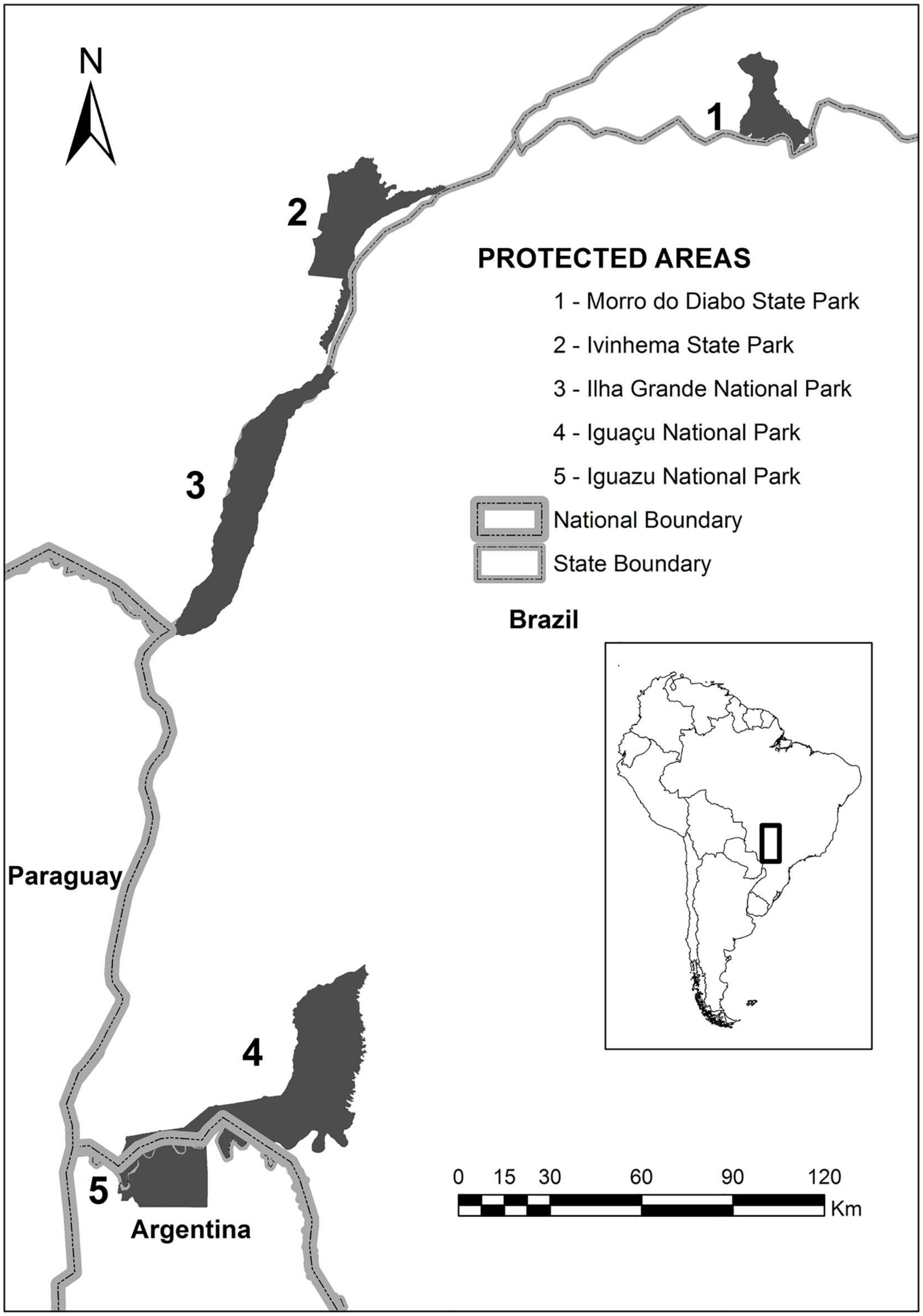

Fig 1. Some important protected sites in the study area, along the upper and the lower Paraná River. The inside frame indicates the location of the study.

doi:10.1371/journal.pone.0167372.g001

Based on the habitat map and these two parameters, RAMAS GIS [26] identified the spatial structure of the metapopulation (i.e., the size and location of habitat patches that support populations). Each patch supports one population (or "subpopulation") of the metapopulation. This method of patch identification is described elsewhere ([35], [36]).

Carrying capacity and Initial Abundance

After the populations (habitat patches) were identified, the carrying capacity (K) and initial number of individuals were calculated for each patch, using the total habitat suitability (HS) value of each patch (see [26,36] for a detailed description). Based on home range sizes and the camera trapping results [33], the carrying capacity was estimated for the Morro do Diabo population as 13 animals (including only adults and sub-adults of both sexes). The carrying capacity was then scaled to the other populations based on the total HS of the Morro do Diabo population (i.e., the sum of the habitat suitability values of all grid cells identified by the model as belonging to this population), which was 3311. Thus, the carrying capacities of the other populations were calculated by multiplying their total HS value by 0.003926 (13/3311). We excluded fragments with a carrying capacity of 2 or less. Initial abundance was assumed to be equal to carrying capacity for all populations, and distributed by age classes according to a stable age distribution (SAD). Carrying capacity in this model is the equilibrium population size under density dependence (see below). Although a recent, major disturbance could have reduced the abundance below the carrying capacity (and pushed the age distribution away from SAD), there is no evidence for such an event.

Demographic Structure and Vital Rates

We developed a stochastic, age- and sex-structured model with 15 annual age classes for each sex; thus a total of 30 age classes. We based the main demographic parameters of the model on the model developed in a workshop [37] in which experts reviewed all the available field and captive data on jaguars and related species. Although the model is based on data from a large variety of sources, data are not available to estimate all parameters independently. Thus, the model includes a number of simplifying assumptions—equal sex ratio at birth, fecundity independent of age after age 3 (the age of first reproduction), annual survival (S) in ages 3 to 10 is the same—which reduce the number of parameters.

The matrix model is parameterized according to pre-reproductive census. Thus, we calculated fecundity (i.e., the elements of the matrix representing reproduction) as $F = m \cdot S_0$, where S_0 is survival rate from birth to age 1, and m is the number of cubs per female per year. We assumed the same survival rates as used in the workshop report [37], and we set m to 1.0, assuming a litter size of 2, and that only 50% of females breed at any one year (because of birth interval of 2 years). We then divided the resulting fecundity into fecundity representing daughters and sons. The population growth rate (i.e., the finite rate of population increase as determined by the eigenvalue of the matrix) is 1.06, representing population growth of 6% per year. We analyzed the sensitivity of results to the matrix by changing survival rate by ±0.03 and fecundities by ±0.05 such that the population growth rate ranged from 1.025 to 1.095 (i.e., 2.5% to 9.5% per year).

Density Dependence

We assumed that at high densities, the proportion of females breeding decreases as a function of the ratio of population size to carrying capacity [37]. However, we used a function that is different than the one used by [37], who assumed that the proportion changed according to the function (50-((50–40*((N/K)^15))). We changed this function for two reasons. First, it

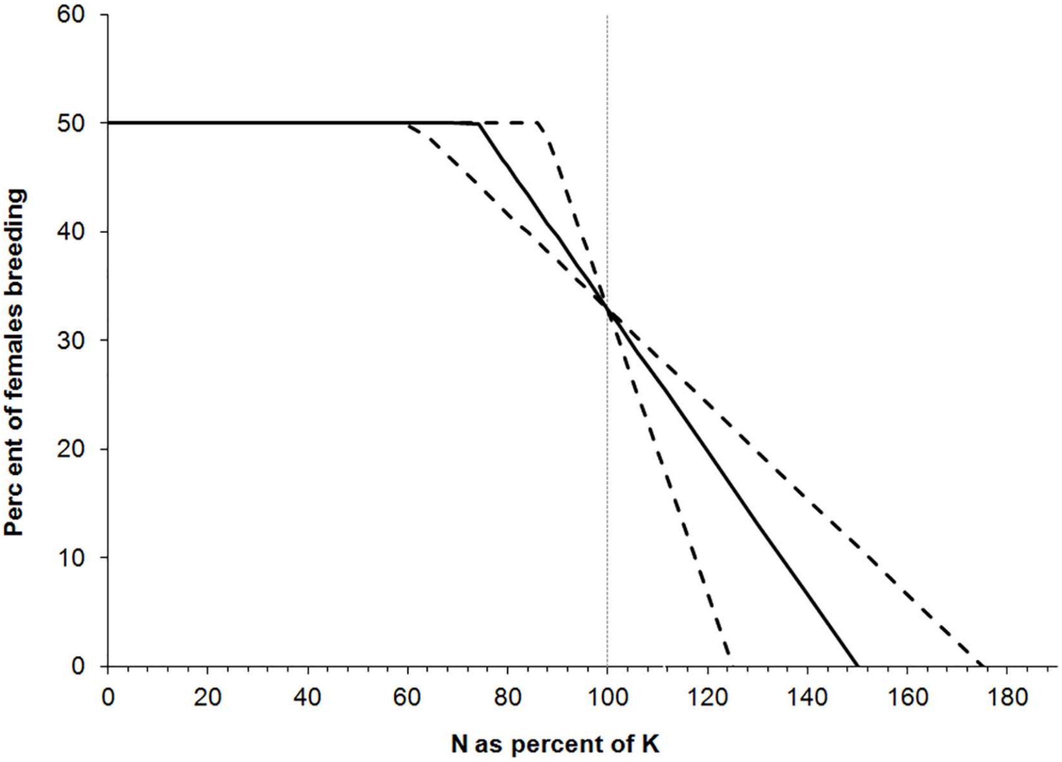

Fig 2. Density dependence function used in this model (solid line) and its uncertainty limits used in the sensitivity analysis (dashed lines). In all models, the proportion of females that are breeding is 50% when population size (N) is small relative to carrying capacity. At carrying capacity, the proportion breeding is 32.9% (which gives an eigenvalue of 1.0; see text for details). The percent breeding declines as N increases, dropping to zero when N = 1.5·K (1.25 to 1.75 used in the sensitivity analysis).

doi:10.1371/journal.pone.0167372.g002

results in 40% of females breeding at carrying capacity. This percentage results in a population growth rate of 1.027. However, by definition, growth rate at carrying capacity should be 1.0 (i.e., no population growth or decline), which in this case can be obtained by setting the percentage of females breeding to 32.9% at carrying capacity. Second, the function used by [37] represents an extreme form of density dependence, in which the proportion of females breeding decreases to 0 when the population size is only about 11% over the carrying capacity (Fig 2). Instead, we used a function in which this proportion declined linearly for N/K>0.8, such that it reached 0 only when N/K>1.5 (Fig 2). In other words, breeding does not cease until the population size increases 50% beyond the carrying capacity. We analyzed the sensitivity of results to this function, by varying it between the uncertainty limits depicted in Fig 2.

Dispersal Rates

Dispersal rate between populations was modeled as a negative exponential function of distance, with distances between populations measured from the center of the source population to the edge of the target population. Centre-to-edge distances are used to model asymmetric rates of dispersal expected between two habitat patches that are substantially different in size [38]. The function was parameterized based on information from [39] which calculated dispersal rates among some of these jaguar populations. From 3 populations in close proximity to each other, the total dispersal (emigration) rate from each population averaged about 20% per generation, corresponding to about 2.5% per year. Thus, we set the dispersal-distance function such that the total dispersal from each population (i.e., sum of all dispersal rates from this population to all other populations) ranged from 1.9% to 3.9%, with an overall average of about 2.5%. This resulted in a dispersal matrix with 0.0 to 1.5% dispersal rate between pairs of populations (Table A in S2 Appendix). Dispersal was modeled as a density-dependent process for each population, with the dispersal rate being directly proportional to population size. Under density-dependent dispersal, when the population size (*N*) is lower than the carrying capacity (K), the proportion dispersing is lower in proportion to the ratio of *N*/*K* [40]. We analyzed the sensitivity of results to dispersal rates by changing them by ± 100% (i.e., from no dispersal to twice the values in Table A in S2 Appendix). Because of lack of quantitative information about age- and sex-specific dispersal rates, we assumed an equal probability of dispersal from all stages.

Stochasticity

Environmental stochasticity was modeled by sampling mortality (1-*S*), fecundity and dispersal rates from log-normal random distributions with coefficients of variation of 20% (we sample mortality instead of *S* to eliminate truncation of sampled values over 1, because most S values in this model are close to 1; see [26]). This value of coefficients of variation is similar to the variability of mortality included in the models of [37] and [41]. We analyzed the sensitivity of results to variability by changing the standard deviations of vital rates by ±20%.

An important source of environmental fluctuations is frequent fires, which are more common in years with hotter and drier weather patterns. Because such patterns have the potential to affect many populations simultaneously, environmental fluctuations are expected to be spatially correlated to some extent (such that different populations experience partially synchronous temporal fluctuations). However, the correlation would not be perfect, because there are other, more local, sources of environmental variability, such as hunting and other human disturbances. Thus, we assumed environmental fluctuations to be moderately correlated among populations, based on a correlation-distance function (see [26,36]) that resulted in correlation coefficients ranging from 0.09 (for pairs of distant populations) to 0.76 (for pairs of nearby populations). In addition, demographic stochasticity was used by sampling the annual number of survivors and dispersers from binomial distributions and the number of offspring from Poisson distributions [42].

Road Mortality

There is very little information about mortality, except for anecdotal reports of jaguars killed in various populations, and an estimate of about 1 jaguar killed per year by vehicles in the Morro do Diabo population (based on anecdotal reports and observations of road kills by LC and FL during daily routine around the only road that crosses the park) (Fig 3). In addition to vehicle strikes, roads also allow easier access for hunters to parts of the species' range. This can result in direct mortality of jaguars by poaching or indirect mortality because of the competition with hunters for prey species. We assumed that population-specific road mortality from all these causes (percent of a population killed because of roads) is proportional to the product of the number of linear km of road per jaguar, and human density (which we used as an index of traffic) within the minimum convex polygon around all the habitat patches (fragments) that form that population. Based on this assumption and the estimate mentioned above, we calculated the expected road mortality for all populations. Data on human population density were from the Global Rural-Urban Mapping Project (version 1, [43]). Road lengths were calculated from the Vector Map Level 0 (VMAP0) road layer available through the United States National Imagery and Mapping Agency. We analyzed the sensitivity of results to road mortality by

Fig 3. Radio-collared female jaguar (*Panthera onca)* roadkill, Morro do Diabo State Park, Brazil.

doi:10.1371/journal.pone.0167372.g003

changing the percent mortality by ±100% (i.e., from no mortality to twice the values in Table 1). We assume that the estimates of annual survival used in the model (see above) incorporate sources of mortality other than road mortality, such as natural mortality and poaching.

Simulations, Scenarios, and Sensitivity Analysis

We used a series of simulations to analyze the dynamics of the jaguar population using the habitat-based metapopulation model described above. Each simulation consisted of 1,000 replications and each replication projected the abundance of each population for 100 years, which corresponds to 13–14 generations. To assess the effects of fragmentation through road mortality, we ran simulations with several different levels of mortality, including 0%, 100% and 200% of the mortality calculated as described above. We analyzed simulation results in terms of final metapopulation size (total number of individuals in all populations in year 100, averaged over the 1000 replications), population persistence (number of years a population was extant, i.e., included at least 1 individual, averaged over the 1000 replications), and expected minimum metapopulation size (the minimum metapopulation size during the 100-year projection interval, averaged over the 1000 replications).

Table 1. Properties of jaguar populations in the upper Paraná-Paranapanema, Brazil. Populations were identified by RAMAS GIS (see Fig 4).

	Area km^2						Road Mortality	
Population	**Core (habitat)**	**Minimum convex polygon (MCP)**	**Total road length in MCP (km)**	**Human population density in MCP (km^{-1})**	**Carrying capacity (K; number of jaguars)**	**km road per jaguar at N = K**	**Percent killed**	**Number killed at N = K**
1. Três Lagoas	190	1,615	81	11.8	8	10.1	8.5%	0.7
2. Rio Pardo	145	8,029	741	1.6	6	123.5	13.9%	0.8
3. Ivinhema-Ilha Grande	1,121	16,536	1,143	13.0	48	23.8	22.2%	10.7
4. Morro do Diabo	292	674	90	15.5	13	6.9	7.7%	1.0
5. Itabo-Carapa	201	3,591	87	10.0	9	9.6	7.0%	0.6
6. Morombi	507	11,833	555	18.0	22	25.2	32.7%	7.2
7. Green corridor	5,1	17,288	922	24.6	231	4.0	7.0%	16.3
8. San Rafael	796	2,952	104	17.0	34	3.1	3.8%	1.3
Overall	8,353	62,518	3,722		371	10.0	10.4%	38.5

doi:10.1371/journal.pone.0167372.t001

We analyzed the sensitivity of these results to parameter uncertainty, focusing on the five sets of parameters mentioned above: the stage matrix (survival rates and fecundities), the density dependence function, dispersal rates, environmental variability, and road mortality. We sampled the values of these 5 sets of parameters from uniform random distributions, creating 1000 models. These distributions represent the uncertainty of the parameters due to lack of information or measurement error, not their natural variability (natural variability is discussed above, under *Stochasticity*). Each of these 1000 models were run as described in the previous paragraph (with 1000 replicates each). We summarized the uncertainty as the interquartile range (IQR; the range from the 25th to 75th percentiles) of the results of these 1000 models.

Results

Patch Structure

The habitat model produced the habitat map (see Figure A in S1 Appendix), which was validated using ROC curve (see Figure B in S1 Appendix). We tested a sample of occurrence locations or presences (that were not used for model building) with the map projected to the most recent classification of land cover. This resulted in an omission error rate (false negative rate) of 0.01 at a habitat suitability threshold of 0.75 (3 out of 302 occurrence records). Based on the habitat map resulting from this model, RAMAS GIS identified the spatial structure of the metapopulation as 8 populations (i.e., 8 clusters of suitable cells within the neighborhood distance of each other) with a total habitat area of 8,353 km^2 and a total carrying capacity of 371 individuals (Fig 4, Table 1). The patch structure was realistic considering the remaining habitat, known jaguar occurrences and the location of some protected areas in the upper Paraná-Paranapanema region.

Road Mortality

Based on the estimate of 1 jaguar killed in Morro do Diabo per year, and the assumption that road mortality is a linear function of the road length per jaguar and human density, we estimated overall annual road mortality as 10.4% of the population, resulting in about 39 jaguars killed per year at carrying capacity (Table 1). Estimated annual road mortality varied from 4%

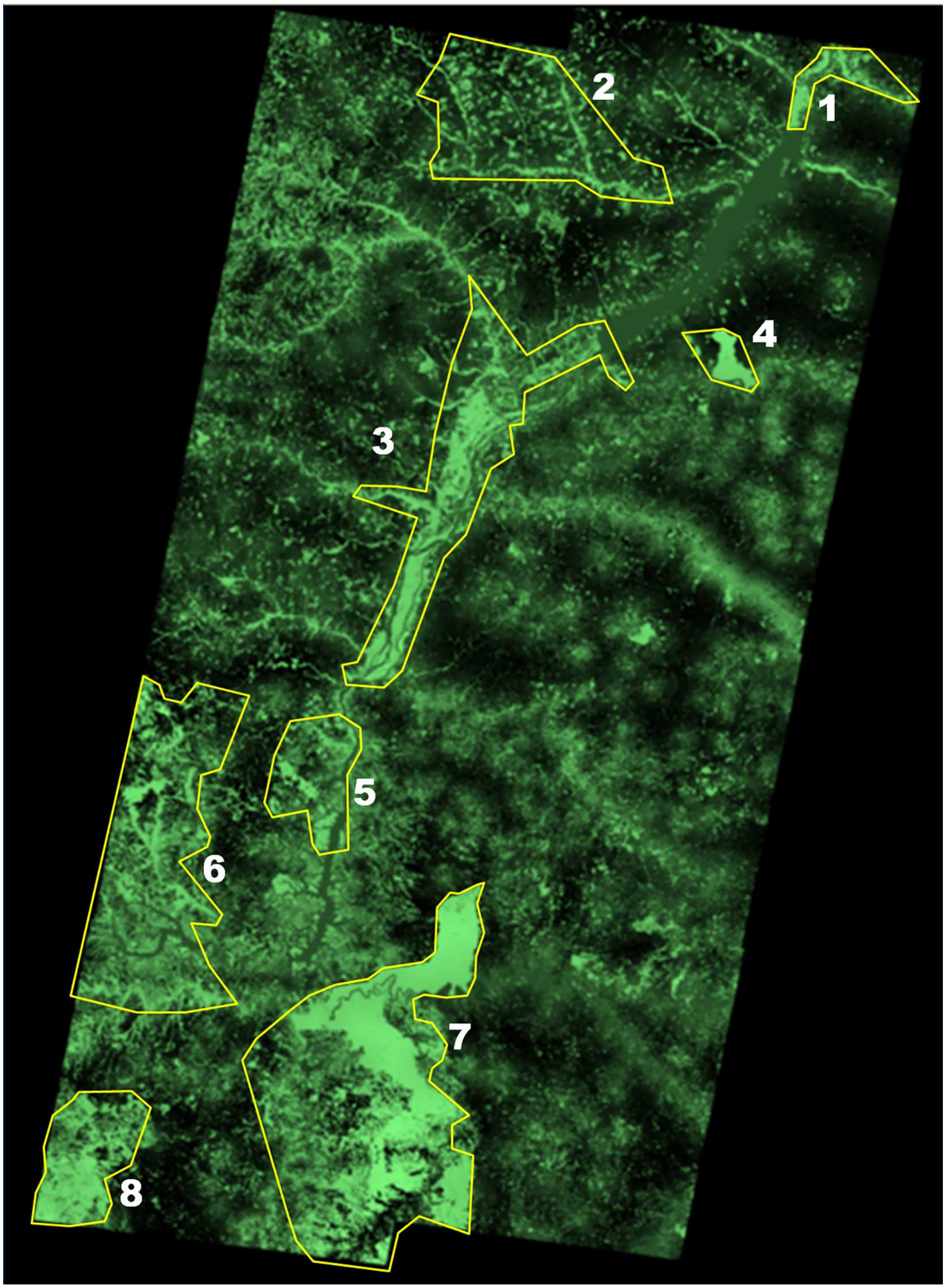

Fig 4. Spatial structure of jaguar populations identified by the model in the upper Paraná region. Lighter shading indicates greater habitat suitability as given in Figure A in S1 Appendix. The polygons outline the populations. The population numbers correspond to those in Table 1, and in Figs 5 and 6.

doi:10.1371/journal.pone.0167372.g004

to 33% for different populations, and was largest for populations with higher number of km of road per jaguar (esp. Rio Pardo, Ivinhema and Morombi; Table 1).

Population Size and Trends

At the end of the 100-year simulation, the average predicted metapopulation size was about 197 individuals (IQR 105–299), down from an initial size of 371, representing a decline of about 47% (19% - 72%). The average number of extant populations (occupied patches) was 5.7 (4.5–7.1), down from 8. Expected minimum metapopulation size was about 155 individuals (82–236). Additional results of the sensitivity analysis are presented in S2 Appendix.

Effect of Road Mortality on Population Dynamics

Road mortality affected the population size and persistence (Table 2; Fig 5). Changing road mortality rate from 0 to the rates in Table 1 ("1x" in Table 2 and Fig 5) and to twice these rates ("2x") resulted in about 80% reduction in final metapopulation size and expected minimum abundance, and 45% reduction in the number of extant populations in year 100 (Table 2). Population persistence was substantially reduced for populations 1 (Tres Lagoas) 2 (Rio Pardo) and 6 (Morombi) due to road mortality (Fig 5). For these populations, persistence was strongly sensitive to dispersal: a model with no dispersal resulted in much lower persistence than the model with dispersal (Fig 6).

Discussion

Our results indicate that jaguars in the upper Paraná-Paranapanema region exist in eight populations with varying sizes and subject to varying degrees of human disturbance. Road mortality is likely impacting the jaguar populations in this region, decreasing both the abundance and the distribution of the species. Our analysis assumed that populations most affected by road mortality would be those with more roads and higher human populations. However, in our model, these factors interacted with the fragmented habitat such that populations in more fragmented areas are more impacted by road mortality. This is because in these populations (e.g., population 2, Rio Pardo; and population 6 Morombi), the fragmentation of habitat results in lower density of habitat (see Fig 4) and consequently lower density of jaguars. Thus, a population in highly fragmented habitat would have higher density of road per jaguar (compared to populations in less fragmented habitat), even if the road density per unit area is the same as in other populations. For example, in population 6, Morombi, road density is about 0.047 km^{-1}, less than the overall average of 0.06km^{-1} for all populations. However, because of fragmented habitat, jaguar density is low, and km road per jaguar is 2.5 times the overall average (Table 1). The nature of this interaction between habitat fragmentation and road mortality

Table 2. Effects of road mortality rate for jaguar population.

	Road mortality rate*		
	0	**1x**	**2x**
Metapopulation size at year 100	351	226	73
Number of extant populations at year 100	7.5	6.6	4.1
Expected minimum abundance	321	173	55
Total road mortality** (average)	0	1062	642.3
Total road mortality (range)	0–0	514–1608	376–980

* Road mortality rate is the percentage of jaguars killed; 0: no road mortality; 1X: the percentages in Table 1; 2X: twice the percentages in Table 1.

** Total road mortality is the number of jaguars killed over 100 years in all populations, averaged over 1000 replications of the model with mid values of all parameters other than road mortality rate.

doi:10.1371/journal.pone.0167372.t002

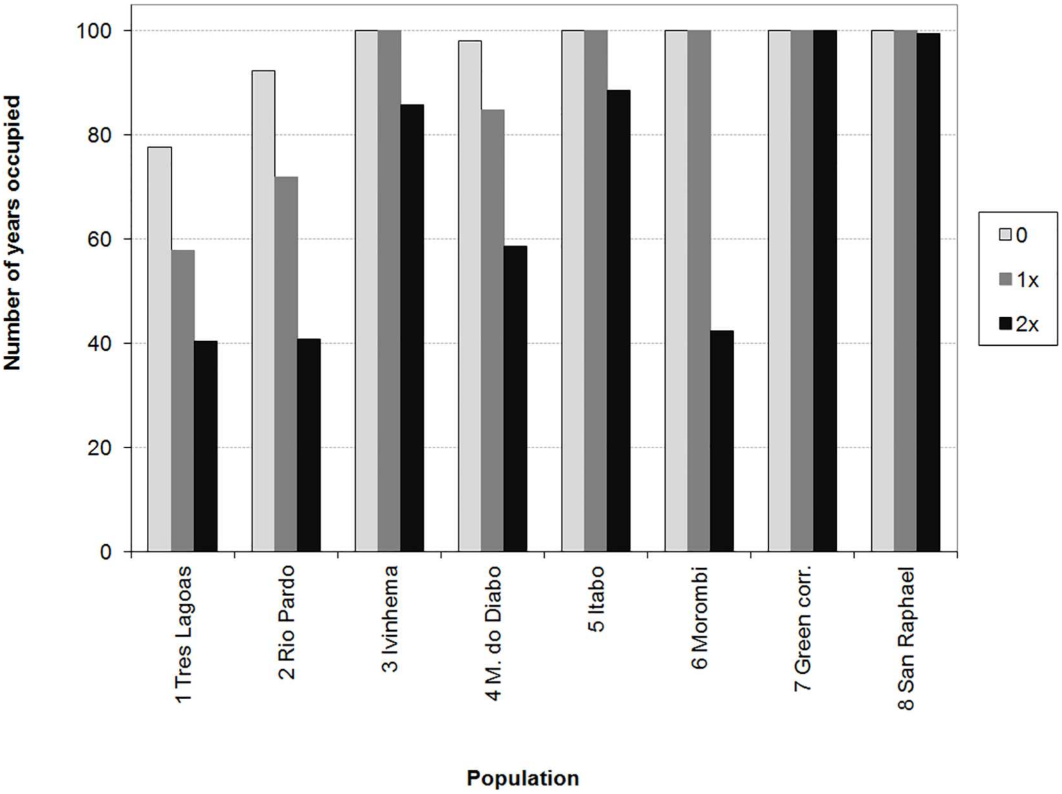

Fig 5. Impact of road mortality on jaguar population persistence: Number of years out of 100 that each population was extant, under no road mortality (0; light gray bars); estimated mortality (1x; dark gray bars); and twice the estimated mortality (2x; black bars).

doi:10.1371/journal.pone.0167372.g005

is determined by the way jaguars perceive the pattern of fragmentation. Because of the large home range size of jaguars, the fragmentation (especially in population 2 and parts of population 6 and 7) is fine-grained from the perspective of this species. These findings corroborate one of the main conclusions of a comprehensive review on road impacts on animal populations[44] that species "with large movement ranges, low reproductive rates, and low natural densities" (a profile that jaguar fits well) would be negatively impacted by roads, regardless of their behavioral response to roads.

Previous research has shown that impact of roads may be at least as great as the impact of habitat loss [45]. Our study shows that habitat loss (which often results in fragmentation of remaining habitat) and road mortality may interact synergistically such that road impacts are higher in fragmented landscapes. In extreme cases, the interaction between road mortality and fine-grained habitat fragmentation may lead to source-sink dynamics, whereby populations with highly fragmented habitat are maintained only by dispersal from populations with less fragmented habitat. There is some indication in our model results that this may already be happening in the upper Paraná-Paranapanema region. The populations with the most fragmented habitat remained extant for much less of the simulated 100 years when the model included no dispersal (Fig 6), indicating that the persistence of these populations are dependent to a large extent on dispersal from other populations. The possibility of source-sink dynamics must be considered when evaluating conservation options for species in fragmented landscapes. For example, even though increasing connectivity by developing and maintaining

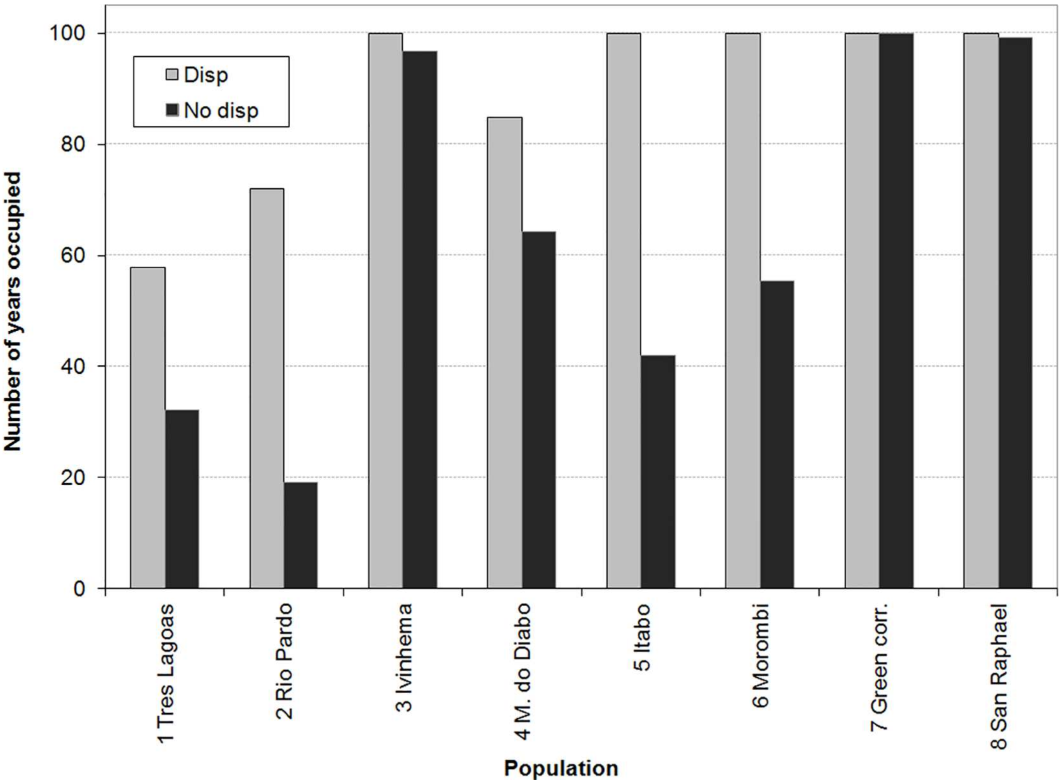

Fig 6. Effect of dispersal on population persistence: Number of years out of 100 that each population was extant under estimated mortality. For several populations, model with no dispersal (black bars) resulted in much lower persistence than model with dispersal (gray bars).

doi:10.1371/journal.pone.0167372.g006

corridors in general can increase the viability of species, they can also exacerbate the negative effects of source-sink dynamics on species viability.

Our study demonstrates the utility of linking habitat and demographic models to assess impacts on species living in fragmented landscapes, as well the importance of assessing impacts with models at different spatial scales. Although range-wide models based on habitat (e.g., [8]) are useful in planning overall conservation strategies, effects and interactions at the local level (such as the interaction between habitat fragmentation and road mortality) are better analyzed with models that combine habitat and demography.

The threats, ecology, distribution, and management options of the jaguars in the Upper Paraná Paranapanema region necessitate the use of models that combine habitat and demography. In this study, we focused only on road mortality and its interaction with habitat fragmentation. However, jaguars in this region are threatened by several factors that we did not explicitly model, such as habitat loss and mortality resulting from their interaction with livestock. Each of these factors affects a different aspect of the jaguar metapopulation. Incorporating these factors into our model would require developing scenarios of future land use, based on past trends and patterns of land-use change, current ownership maps, and plans for future development. Although such information is not available at the moment, when it becomes available, models that link habitat and demography, such as the one presented here, will allow assessing the cumulative effects of these threat factors. Similarly, a number of assumptions in our model (such as equal dispersal rates for all stages) were necessitated by lack of quantitative information. When relevant information becomes available, it can be used to modify these assumptions. However, we believe that such improvements to the model would not alter our main conclusions about the interacting effects of road mortality and fine-grained fragmentation.

There are several types of management actions that may benefit these populations, including habitat protection, increasing connectivity, decreasing road mortality, habitat enhancement or restoration [8–12,19,41], which can also be studied with the type of spatially explicit model we developed. For example, an evaluation of habitat management options can be based on the eight large suitable patches identified in this study, which together were about 8,400 km^2 in area or equivalent to 4% of the potential habitat in the study area. Such an evaluation would require overlaying the habitat map we developed in this study with detailed maps of land ownership (and availability for conservation). This would allow identifying options for establishment of new protected-areas at different intensities of management (such as intensive use areas, buffer zones or intermediate use areas, strictly protected areas, and wildlife corridors). Each option would then be simulated as a set of changes to the spatial structure of the model, and each option would be evaluated in terms of the viability of the species. The viability result for each option can also be combined with the cost of that option, if such cost information is available (see [46] for an example of such an analysis). We believe that the results of such a detailed analysis could lead to specific recommendations for habitat conservation actions in this human-dominated landscape.

Supporting Information

S1 Appendix. Habitat Suitability Model for Jaguar in the Upper Paraná River Corridor.
(PDF)

S2 Appendix. Sensitivity Analysis.
(PDF)

Acknowledgments

We thank Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and Instituto Florestal de São Paulo for the institutional support provided during field studies in Morro do Diabo State Park, and Secretaria de Estado do Meio Ambiente do Mato Grosso do Sul (SEMA- MS) for the support during the field work in Ivinhema State Park. HRA and JCS were supported in part by the National Science Foundation under Grant No. DEB-1146198 and the National Aeronautics and Space Administration under Grant No. NNX09AK19G awarded through the NASA Biodiversity Program.

Author Contributions

Conceptualization: LC.

Data curation: FL.

Formal analysis: JCS AU HRA.

Funding acquisition: LC.

Investigation: LC FL.

Methodology: LC JCS FL AU.

Project administration: LC.

Resources: LC HRA.

Software: JCS HRA.

Supervision: LC.

Visualization: LC JCS FL AU MLLP.

Writing – original draft: LC JCS.

Writing – review & editing: LC JCS FL AU MLLP HRA.

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