



Universidade Federal de Goiás
Instituto de Ciências Biológicas



Programa de Pós-graduação em Ecologia e Evolução

Tese de Doutorado

Efeitos da perda e fragmentação de habitat sobre felinos: ecologia e genética de paisagem como ferramentas para a conservação

Marina Zanin Gregorini

Orientador: Prof. Dr. Daniel de Brito C. da Silva

GOIÂNIA - GO

MARÇO DE 2014

TERMO DE CIÊNCIA E DE AUTORIZAÇÃO PARA DISPONIBILIZAR AS TESES E DISSERTAÇÕES ELETRÔNICAS (TEDE) NA BIBLIOTECA DIGITAL DA UFG

Na qualidade de titular dos direitos de autor, autorizo a Universidade Federal de Goiás (UFG) a disponibilizar, gratuitamente, por meio da Biblioteca Digital de Teses e Dissertações (BDTD/UFG), sem ressarcimento dos direitos autorais, de acordo com a Lei nº 9610/98, o documento conforme permissões assinaladas abaixo, para fins de leitura, impressão e/ou download, a título de divulgação da produção científica brasileira, a partir desta data.

1. Identificação do material bibliográfico: Dissertação Tese

2. Identificação da Tese ou Dissertação

Autor (a):	Marina Zanin Gregorini		
E-mail:	marinazaning@gmail.com		
Seu e-mail pode ser disponibilizado na página?	<input checked="" type="checkbox"/> Sim	<input type="checkbox"/> Não	
Vínculo empregatício do autor			
Agência de fomento: CAPES	Coordenação de Aperfeiçoamento de Pessoal de Nível Superior	Sigla:	CAPES
País:	Brasil	UF: GO	CNPJ:
Título:	Efeitos da perda e fragmentação de habitat sobre felinos: ecologia e genética de paisagem como ferramentas para a conservação		
Palavras-chave:	Fragmentação, perda de habitat, Felidae, viabilidade populacional, fluxo gênico		
Título em outra língua:	Habitat loss and fragmentation effects on felines: landscape ecology and landscape genetics as conservation tools		
Palavras-chave em outra língua:	Fragmentation, habitat loss, Felidae, population viability, gene flow		
Área de concentração:	Ecologia		
Data defesa: (dd/mm/aaaa)	31/03/2014		
Programa de Pós-Graduação:	Ecologia e Evolução		
Orientador (a):	Dr. Daniel de Brito C. da Silva		
E-mail:	brito.dan@gmail.com		

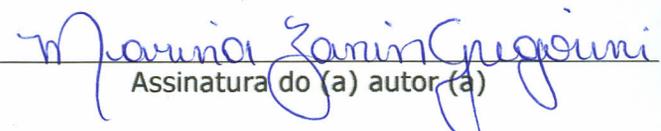
*Necessita do CPF quando não constar no SisPG

3. Informações de acesso ao documento:

Concorda com a liberação total do documento SIM NÃO¹

Havendo concordância com a disponibilização eletrônica, torna-se imprescindível o envio do(s) arquivo(s) em formato digital PDF ou DOC da tese ou dissertação.

O sistema da Biblioteca Digital de Teses e Dissertações garante aos autores, que os arquivos contendo eletronicamente as teses e ou dissertações, antes de sua disponibilização, receberão procedimentos de segurança, criptografia (para não permitir cópia e extração de conteúdo, permitindo apenas impressão fraca) usando o padrão do Acrobat.


Assinatura do (a) autor (a)

Data: 22 / 07 / 2014

¹ Neste caso o documento será embargado por até um ano a partir da data de defesa. A extensão deste prazo suscita justificativa junto à coordenação do curso. Os dados do documento não serão disponibilizados durante o período de embargo.

Universidade Federal de Goiás
Instituto de Ciências Biológicas
Programa de Pós-graduação em Ecologia e Evolução

Tese de Doutorado

Efeitos da perda e fragmentação de habitat sobre felinos: ecologia e genética de paisagem como ferramentas para a conservação

Marina Zanin Gregorini

Tese apresentada à Universidade Federal de Goiás, como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para obtenção do título de doutora.

Orientador: Prof. Dr. Daniel de Brito C. da Silva

GOIÂNIA - GO

MARÇO DE 2014

**Dados Internacionais de Catalogação na Publicação (CIP)
GPT/BC/UFG**

Gregorini, Marina Zanin.
G821e Efeitos da perda e fragmentação do habitat sobre felinos
[manuscrito] : ecologia e genética de paisagem como
ferramentas para a conservação / Marina Zanin Gregorini. -
2014.

205 f. : figs, tabs.

Orientador: Prof. Dr. Daniel de Brito Cândido da Silva.
Tese (Doutorado) – Universidade Federal de Goiás,
Instituto de Estudos Ciências Biológicas, 2014.

Bibliografia.

1. Felinos – Fragmentação de habitat 2. Onça-pintada –
Habitat 3. Onça-parda – Habitat I. Título.

CDU: 599.742.72:591.522



Desenho: Natália Gregorini

Ausência

Por muito tempo achei que a ausência é falta.

E lastimava, ignorante, a falta.

Hoje não a lastimo.

Não há falta na ausência.

A ausência é um estar em mim.

*E sinto-a, branca, tão pegada, aconchegada nos meus braços,
que rio e danço e invento exclamações alegres,
porque a ausência, essa ausência assimilada,
ninguém a rouba mais de mim.*

Dedico esse trabalho aos meus pais (Carmen e Arivaldir) e meu irmão (Willian) que mesmo longe, sempre estiveram ao meu lado. Também, ao meu avô, Natalino Gregorini (in memoriam), pelas doces lembranças dos momentos passado em sua companhia.

AGRADECIMENTOS

Ao meu ver, essa é a parte mais importante de um trabalho, no entanto acredito que sempre destinamos tempo insuficiente para expressar a verdadeira gratidão que sentimos pelas pessoas que fizeram parte desse processo. Primeiramente, quero agradecer a todos os professores do curso de Ecologia e Evolução pelo aprendizado que tive ao longo desses quatro anos de doutoramento, por meio de disciplinas, debates e conversas. Dentre eles, agradeço especialmente ao meu orientador, Daniel Brito, pela liberdade que me deu durante esses quatro anos, permitindo que eu fizesse um trabalho que não se encaixa em sua principal linha de pesquisa.

Quero agradecer à CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, pela bolsa concedida durante o doutorado e o estágio sanduíche. Também, à Fundação O Boticário de Proteção a Natureza, pelo apoio financeiro ao projeto “Dinâmica metapopulacional de felinos simpátricos em uma paisagem do Cerrado: Genética molecular como uma ferramenta para a conservação e manejo”. Aos gestores e técnicos da RPPN Serra do Tombador pelo apoio logístico durante a etapa do projeto realizada na reserva.

Quero agradecer especialmente aos amigos que fiz ao longo dos seis anos que vivi (entre idas e vindas) em Goiânia: Bruno Barreto, Guilherme Oliveira, Lorena Cintra, Geiziane Tessarolo, Nathália Machado, Nayara Rodrigues, Paulina Gordón, Renata Prado, Renato Cirino e Rodolfo Carvalho. Dentre esses, quero agradecer especialmente a Lorena Cintra, Geiziane Tessarolo, Nathália Machado, Renata Prado e Paulina. Vocês foram meu pilar ao longo desses anos. Obrigada pelas conversas, risadas, apoio e puxões-de-orelha. Terei sempre vocês nas minhas melhores lembranças de Goiânia.

Não há como esquecer daqueles que riram e choraram comigo em campo. Por isso, quero agradecer ao Rodolfo Cabral, Grasiela Porfírio e Vânia Foster pelos melhores (e alguns dos piores) momentos em campo. Vocês foram as melhores companhias que poderia ter nos instantes de aventuras e desventuras.

Quero agradecer também ao Francisco Palomares, por ter me recebido na Estación Biológica de Doñana, me orientado e me apoiado nos últimos anos do doutorado. Aprendi muito estando sobre sua orientação e o tenho como um exemplo de pesquisadora que quero ser. Não bastando, foi ainda o responsável por colocar a Esther Alberca na minha vida! À Esther, quero agradecer pela maravilhosa companhia, conversas e ensinamentos ao longo dos meses que moramos juntas em Sevilla. Eu nunca imaginei criar um vínculo de amizade tão profundo em tão pouco tempo com alguém. Você foi mais um dos anjinhos que a vida me deu.

Quero agradecer também à todos os amigos da Estación Biológica de Doñana que, ao longo dos 10 meses que passei em Sevilla, me receberam muito bem. Quero agradecer especialmente a Patricia Martínez, Cande Rodríguez, Begoña Adrados, Clemencia Amaya, Rocío Monsa, David Roiz, Miguel Jácome, Gemma Calvo, Marcello D'Amico e Alvaro Dugo pela boa companhia e risadas, dentro e fora da EBD.

Por fim, mas não menos importante, quero agradecer à minha família (Carmen, Arivaldir e Willian). Já são tantos anos distantes que nem quero contar. Apesar da distância, vocês sempre me apoiaram, me incentivaram, me levantaram quando caí, lamentaram comigo quando estava triste, riram comigo quando estava feliz. À vocês devo tudo que sou. São meus maiores exemplos de força e superação.

SUMÁRIO

INTRODUÇÃO GERAL	2
O estudo da perda e fragmentação do habitat	3
Susceptibilidade à perda e fragmentação do habitat: escolha do grupo focal	5
Conteúdo do trabalho	7
Referências.....	9
CAPÍTULO 1	13
What we (don't) know about the effects of habitat loss and fragmentation on felines	14
2. Introduction	17
3. Methods	18
3.1 Trends in the knowledge about HLF effects on felines	18
3.2 Allocation of research effort	20
3.3 Gap analysis of HLF knowledge on felines	21
4. Results and Discussion	23
4.1 Trends in the knowledge about HLF effects on felines	23
4.1.1 Trends in the attention designated to study HLF effects on felines	23
4.1.2 Taxonomic level of analysis	24
4.1.3 Characteristics of HLF evaluated	25
4.1.4 Methodological approach	25
4.1.5 Differentiation of habitat loss from fragmentation.....	26
4.1.6 Knowledge on the sub-disciplines.....	28
4.2 Allocation of research effort	30
4.3 Gap analysis of HLF knowledge on feline.....	31
5. Conclusion.....	32
6. References	33
Appendix A – Search words used to investigate habitat loss and fragmentation effects on felines and publications found.	52
References	62
Appendix B – Species specific results about effect of habitat loss and fragmentation	82
CAPÍTULO 2	89
The jaguar's patches: the decline of jaguar populations	90
1. Abstract.....	91
2. Introduction	92
3. Methods	94

3.1. Study Area.....	94
3.2. Landscape scenarios.....	94
3.3. Population Viability Analysis	95
3.4. Statistical Analysis	97
4. Results	100
5. Discussion.....	102
6. References	107
Supplementary Material A.....	125
References	129
Supplementary Material B	132
Supplementary Material C	136
CAPÍTULO 3.....	151
Landscape genetics of American felids: from regional to local scales.....	152
1. Abstract.....	153
2. Introduction	155
3. Methods	157
3.1. Sample collection and laboratory procedures	157
3.2. Distance models	158
3.3. Isolation pattern among individuals	160
3.4. Genetic clustering analysis.....	162
3.5. Descriptive statistics of genetic clusters.....	164
4. Results	164
5. Discussion.....	168
6. References	171
Appendix A. Raster creation representing landscape permeability for jaguars and pumas	189
Jaguar	189
DISCUSSÃO GERAL.....	198
Referências.....	201
ANEXOS	202
Anexo 1.....	203
Anexo 2.....	204

INTRODUÇÃO GERAL

O estudo da perda e fragmentação do habitat

A rápida conversão de habitats naturais consiste na principal ameaça à biodiversidade da atualidade, afetando ecossistemas em todo o globo e espécies de todos os taxa (Foley et al. 2005). A substituição de habitats nativos por cobertura antrópica tem acarretado uma perda substancial de espécies (Foley et al. 2005), alcançando proporções somente observadas em eventos de extinção em massa (Johnson 2002). A perda e a fragmentação são processos inerentes da conversão do habitat (Lindenmayer & Fischer 2007; Ewers & Didham 2006; Fischer & Lindenmayer 2007), levando à transformação de manchas de habitat contínuos em fragmentos menores e isolados. Esses processos ocorrem principalmente em escala de paisagem (Fahrig 2003) e geram heterogeneidade espacial, composicional e estrutural no ambiente (Bennett et al. 2006).

Devido à importância e complexidade do tema, tem sido produzido um vasto conhecimento acerca dos efeitos diretos e indiretos das alterações antrópicas sobre a biodiversidade. Tais estudos possuem diferentes enfoques, que podem ser: abordagens experimentais (Mortelliti et al. 2011) ou teóricas (Reed 2004); respostas de espécies (Tian et al. 2011) ou táxons (Smith et al. 2011); padrões estruturais (Rodríguez et al. 2012) e relativos à escala (Hanski 2013); revisões e meta-análises sobre aspectos metodológicos (Debinski & Holt 2000; McGarigal & Cushman 2002), conceituais (Andrén 1994; Fahrig 2003; Fischer & Lindenmayer 2007) e padrões ecológicos (Jenkins et al. 2007; Watling et al. 2011).

A base conceitual e teórica dos efeitos da perda e fragmentação de habitats surgiu, em um primeiro momento, a partir das aplicações da Teoria de Equilíbrio em Biogeografia de Ilhas (TBI) (MacArthur & Wilson 1967) no âmbito da Biologia da Conservação. Nesse

contexto, compreendeu-se que fragmentos de habitat poderiam ser considerados como “ilhas” circundadas por um “oceano” de matriz inóspita. Assim, a dinâmica de colonização e extinção de espécies em comunidades terrestres também seriam explicadas pelos efeitos da área e isolamento previstos pela TBI (Haila 2002; MacArthur & Wilson 1967).

Poucos anos após a publicação de MacArthur e Wilson, Levins propôs um modelo simples para a compreensão da dinâmica de uma única espécie dentro de paisagens fragmentadas (Levins 1970). A partir do trabalho de Levins, surge a teoria de Metapopulação, que se assemelha as previsões gerais da TBI, onde a área e o isolamento são os principais fatores responsáveis pela dinâmica de ocupação de fragmentos em uma paisagem (Hanski & Gilpin 1991; Hanski 1998). O desenvolvimento dessa teoria e dos modelos propostos por ela consistiu em outro marco para a evolução da compreensão dos efeitos da perda e fragmentação de habitat sobre as espécies (Hanski & Gilpin 1991; Hanski 2001; Hanski 2005).

Entretanto, ainda nos anos 70 foi observado que o arcabouço teórico e metodológico da *Teoria de Biogeografia de Ilhas e Metapopulações* eram insuficientes para responder questões relativas à perda e fragmentação do habitat. Assim, entre as décadas de 70 e 80, a Ecologia de Paisagem ganhou destaque por sua abordagem no estudo das causas e consequências da heterogeneidade espacial e suas variações em diferentes escalas (Turner 2005; Turner 1989). A Ecologia de Paisagem permitiu um grande avanço na compreensão dos efeitos da perda e fragmentação de habitat sobre o ambiente, uma vez que as atividades antrópicas relacionadas a conversão de habitats consistem no principal fator de modificação na estrutura e composição das paisagens (Turner 2005; Turner 1989).

Posteriormente, outras disciplinas surgiram com o intuito de explorar novos níveis de resposta dos efeitos da perda e fragmentação do habitat; nesse contexto, a Genética de

Paisagem também se tornou uma poderosa abordagem de estudo, especialmente pelo avanço dos marcadores genéticos (Holderegger & Wagner 2008). A Genética de Paisagem é uma disciplina recente que combina ecologia de paisagem e genética de populações por meio de uma abordagem que possibilita a compreensão de como as características da paisagem afetam processos microevolutivos (Holderegger & Wagner 2008; Manel et al. 2003). Dessa forma, a genética de paisagem permite um melhor entendimento dos efeitos das mudanças da paisagem, simultaneamente, sobre as respostas ecológicas e evolutivas (Wagner & Fortin 2013).

Como exposto, as consequências da perda e fragmentação do habitat sobre a biodiversidade pode ser estudado por meio de várias disciplinas e à luz de diferentes teorias ecológicas ou evolutivas. Em um contexto conservacionista, o uso de diferentes abordagens é a melhor estratégia para dimensionar o real efeito da perda e fragmentação sobre as espécies e/ou paisagens. Nesse contexto, essa tese usa o arcabouço teórico e metodológico da ecologia e genética de paisagem para estudar o efeito da perda e fragmentação do hábitat sobre as espécies.

Susceptibilidade à perda e fragmentação do habitat: escolha do grupo focal

Alguns trabalhos têm destinado esforços em identificar os fatores de risco de extinção das espécies (Cardillo et al. 2005; Cardillo & Bromham 2008; Machado & Loyola 2013), investigando se espécies ameaçadas são vítimas de ‘maus genes ou má sorte’ (Cardillo et al. 2005). A fragmentação aparece em todos os trabalhos como o principal ameaça, independentemente do táxon (Cardillo et al. 2005; Cardillo & Bromham 2008; Machado & Loyola 2013). No entanto, existem atributos intrínsecos às características bionômicas e traços ecológicos das espécies que retro-alimentam o risco de extinção

(Cardillo et al. 2005; Cardillo & Bromham 2008). Dentre eles tais atributos podemos citar: especialização quanto ao uso de habitats, área de vida, capacidade de dispersão, tamanho corporal, densidade, tamanho da distribuição histórica e atual (Fischer & Lindenmayer 2007). A combinação dos fatores ambientais e biológicos em uma paisagem fragmentada pode acarretar no declínio da população e, em níveis mais drásticos, até mesmo em sua extinção por ação de eventos demográficos, genéticos ou estocásticos (Fischer & Lindenmayer 2007).

Felinos como objeto de estudo

Essa tese teve como grupo focal os felinos (Carnivora: Felidae), grupo composto por 36 espécies selvagens, separados filogeneticamente em 12 gêneros. Os felinos podem ser considerado uma das Famílias mais bem sucedidas da Ordem dos Carnívoros, uma vez que possuem uma ampla distribuição (Figura 1), habitando todos os continentes exceto a Antártica (IUCN 2013). Os felinos são mamíferos de hábito alimentar essencialmente carnívoro, frequentemente topo de cadeia alimentar (Wilson & Reeder 2005). Mesmo sendo composto por poucas espécies, o grupo possui grande heterogeneidade de traços ecológicos e história de vida, pois possuem espécies sociais e solitárias, de tamanho corpóreo menor que 1.5 kg a maior que 150 kg, áreas de vida que variam de pouco mais que um quilômetro à quase 300 km², distribuições restritas à continentais, especialistas e generalistas quanto ao habitat e dieta (Wilson & Reeder 2005).

Apesar dessa heterogeneidade, os felinos podem ser generalizados como espécies de altos requerimentos ecológicos, o que os tornam sensíveis às alterações antrópicas em seus ambientes naturais (Cardillo et al., 2005). Morrison et al. (2007) lista cinco felinos (*Acinonyx jubatus*, *Panthera leo*, *Panthera pardus*, *Panthera onca* e *Puma concolor*) entre

as 20 espécies de grandes mamíferos com maior redução na distribuição devido aos impactos antrópicos, demonstrando que esse é um dos grupos de mamíferos mais ameaçados pela conversão do hábitat. Atualmente, todos os felinos estão ameaçados pela perda e fragmentação de hábitats e 16 deles estão classificados sobre algum *status* de ameaça devido primariamente a esses processos (IUCN 2013). Essa situação tende a ser agravada nos próximos anos, pois as regiões de grande diversidade de felinos estão inseridas em países economicamente emergentes que compõem o G-20 de países em desenvolvimento e que apresentam hoje as maiores taxas de conversão habitat (Hugueney 2004; Figura 1). Esse panorama geral revela a urgência em compreender os efeitos da perda e fragmentação do habitat sobre os felinos, motivando e fundamentando sua escolha como grupo focal desse trabalho.

Conteúdo do trabalho

Nosso trabalho teve como objetivo investigar o efeito da perda e fragmentação de habitat sobre os felinos (Carnivora: Felidae), testando hipóteses relacionadas ao tema, bem como fazendo inferências para a conservação. Apresentamos aqui três capítulos no formato de artigo científico e uma breve discussão geral, que consiste na compreensão geral proveniente dos resultados dos três primeiros.

Iniciamos essa tese com uma revisão sistemática e quantitativa da literatura sobre o efeito da perda e fragmentação do habitat sobre felinos. Esse trabalho consistiu no passo inicial dessa tese, pois permitiu identificar as lacunas de conhecimento, tendências gerais e metodologias eficientes a serem aplicadas nas outras etapas do trabalho. No entanto, nossa revisão se estende além da avaliação do “estado da arte”, pois testamos também hipóteses relativas a alocação do esforço de pesquisa.

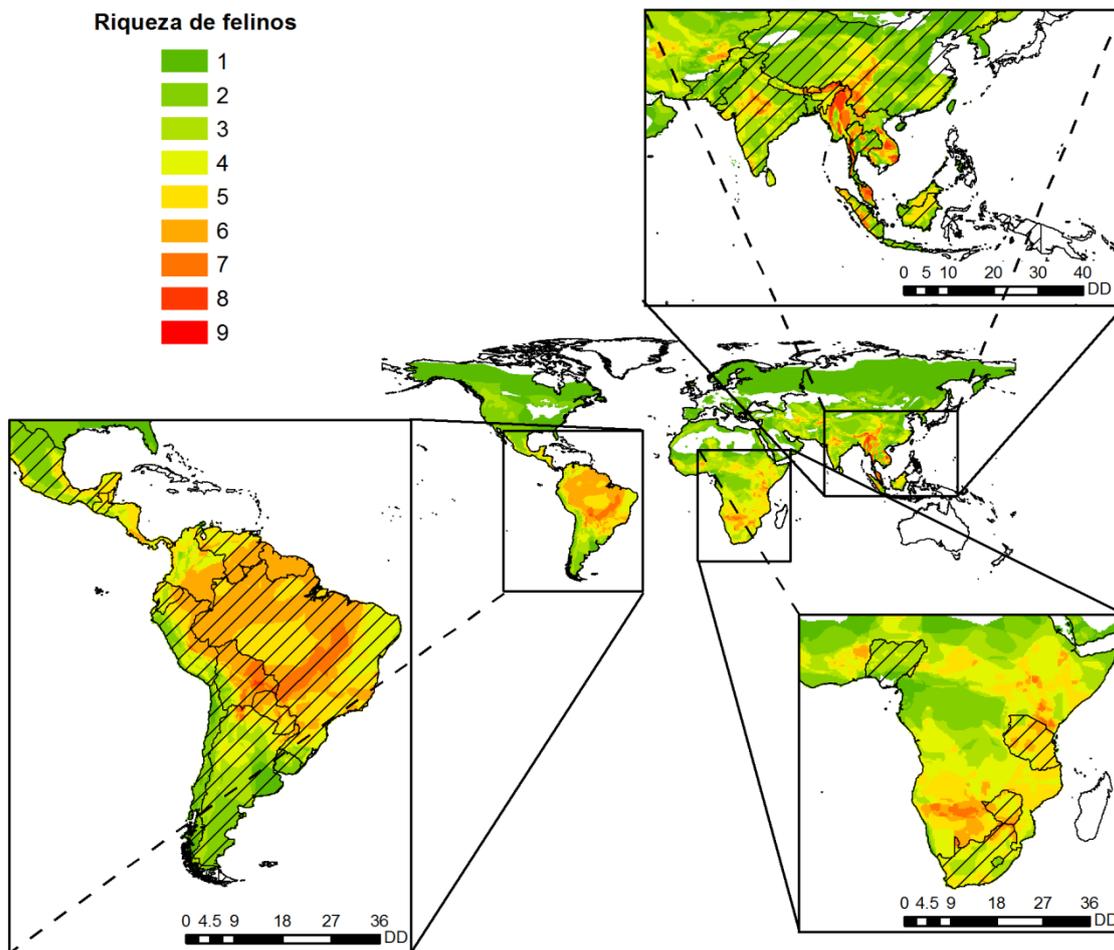


Figura 1. Riqueza de espécies de felinos ao longo do globo (cores quentes denotam uma maior riqueza). Rachurado, destacamos os países que compõem o G-20 de países em desenvolvimento, que constituem em 20 países emergentes de grande desenvolvimento agrícola (Hugueney 2004).

Já no segundo capítulo, avaliamos os efeitos da perda e fragmentação do habitat para uma única espécie, a onça-pintada (*Panthera onca*). Nesse estudo, investigamos o efeito sinérgico e isolado da perda e fragmentação de hábitat sobre a probabilidade de sobrevivência da espécie. Para tal, utilizamos uma abordagem teórica que fez uso de

simulações de dinâmica populacional em paisagens reais e hipotéticas, que nos permitiu também estimar limiares de perda e fragmentação de habitat para as populações.

O terceiro capítulo utiliza uma abordagem mais recente na pesquisa do efeito da perda e fragmentação de habitat, que consiste na genética de paisagem. Nesse trabalho, avaliamos o efeito da complexidade da paisagem na estrutura genética de duas espécies, a onça-pintada e a onça-parda (*Puma concolor*), testando hipóteses sobre o efeito da capacidade de dispersão no fluxo gênico.

Referências

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos*, 71(3), pp.355–366.
- Bennett, A.F., Radford, J.Q. & Haslem, A., 2006. Properties of land mosaics: Implications for nature conservation in agricultural environments. *Biological Conservation*, 133(2), pp.250–264.
- Cardillo, M. et al., 2005. Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738), pp.1239–1241.
- Cardillo, M. & Bromham, L., 2008. Body Size and Risk of Extinction in Australian Mammals. *Conservation Biology*, 15(5), pp.1435–1440.
- Debinski, D.M. & Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14(2), pp.342–355.
- Ewers, R.M. & Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, 81(1), pp.117–142.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), pp.487–515.

- Fischer, J. & Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography*, 16(3), pp.265–280.
- Foley, J.A. et al., 2005. Global consequences of land use. *Science*, 309(5734), pp.570–574.
- Haila, Y., 2002. A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications*, 12(2), pp.321–334.
- Hanski, I., 2013. Extinction debt at different spatial scales. *Animal Conservation*, 16(1), pp.12–13.
- Hanski, I., 2005. Landscape fragmentation, biodiversity loss and the societal response. *EMBO Reports*, 6(5), pp.388–392.
- Hanski, I., 1998. Metapopulation dynamics. *Nature*, 396(6706), pp.41–49.
- Hanski, I., 2001. Spatially realistic theory of metapopulation ecology. *Naturwissenschaften*, 88(9), pp.372–381.
- Hanski, I. & Gilpin, M., 1991. Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42(1-2), pp.3–16.
- Holderegger, R. & Wagner, H.H., 2008. Landscape Genetics. *BioScience*, 58(3), p.199.
- Hugueney, C., 2004. The G-20: Passing phenomenon or here to stay? *Friedrich Eberto Stiftung*, March, pp.1–5.
- IUCN, 2013. The IUCN red list of threatened Species. Available at: <http://www.iucnredlist.org/> [Accessed December 1, 2013].
- Jenkins, D.G. et al., 2007. Does size matter for dispersal distance? *Global Ecology and Biogeography*, 16(4), pp.415–425.
- Johnson, C.N., 2002. Determinants of loss of mammal species during the Late Quaternary “megafauna” extinctions: life history and ecology, but not body size. *Proceedings. Biological sciences / The Royal Society*, 269(1506), pp.2221–2227.

- Levins, R., 1970. Extinction. In M. Gerstenhaber, ed. *Some Mathematical Problems in Biology*. Providence: American Mathematical Society, pp. 77–107.
- Lindenmayer, D.B. & Fischer, J., 2007. Tackling the habitat fragmentation pantheon. *Trends in ecology & evolution*, 22(3), pp.127–32.
- MacArthur, R.H. & Wilson, E.O., 1967. *The theory of island biogeography*, Princeton University Press.
- Machado, N. & Loyola, R.D., 2013. A comprehensive quantitative assessment of bird extinction risk in Brazil. *PloS one*, 8(8), p.e72283.
- Manel, S. et al., 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18(4), pp.189–197.
- McGarigal, K. & Cushman, S.A., 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, 12(2), pp.335–345.
- Morrison, J.C. et al., 2007. Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy*, 88(6), pp.1363–1380.
- Mortelliti, A. et al., 2011. Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. *Journal of Applied Ecology*, 48(1), pp.153–162.
- Reed, D.H., 2004. Extinction risk in fragmented habitats. *Animal Conservation*, 7(2), pp.181–191.
- Rodríguez, N. et al., 2012. Patterns and trends of forest loss in the Colombian Guyana. *Biotropica*, 44(1), pp.123–132.

- Smith, A.C., Fahrig, L. & Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, 34(1), pp.103–113.
- Tian, Y. et al., 2011. Population viability of the Siberian Tiger in a changing landscape: Going, going and gone? *Ecological Modelling*, 222(17), pp.3166–3180.
- Turner, M., 1989. Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics*, 20, pp.171–197.
- Turner, M.G., 2005. Landscape ecology: What is the state of the science? *Annual Review of Ecology, Evolution, and Systematics*, 36(1), pp.319–344.
- Wagner, H.H. & Fortin, M.-J., 2013. A conceptual framework for the spatial analysis of landscape genetic data. *Conservation Genetics*, 14(2), pp.253–261.
- Watling, J.I. et al., 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography*, 20(2), pp.209–217.
- Wilson, D.E. & Reeder, D.M., 2005. *Mammal Species of the World. A Taxonomic and Geographic Reference* 3rd ed. D. E. Wilson & D. M. Reeder, eds., Baltimore: Johns Hopkins University Press.

CAPÍTULO 1

Esse artigo segue o padrão de formatação da revista Oryx, na qual foi aceito para publicação (Anexo 1).

1 **What we (don't) know about the effects of habitat loss and fragmentation on**
2 **felines**

3

4 **Marina Zanin*** Departamento de Ecologia, Universidade Federal de Goiás, Caixa
5 Postal 131, CEP 74001-970, Goiania, Goiás, Brazil. E-mail: marinazaning@gmail.com

6

7 **Francisco Palomares** Department of Conservation Biology, Estación Biológica de
8 Doñana CSIC; Avenida Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla,
9 Spain. E-mail: ffpaloma@ebd.csic.es

10

11 **Daniel Brito** Departamento de Ecologia, Universidade Federal de Goiás, Caixa Postal
12 131, CEP 74001-970, Goiania, Goiás, Brazil. E-mail: brito.dan@gmail.com

13

14 * Corresponding author

15

16 Word count: 6,969

17 **What we (don't) know about the effects of habitat loss and fragmentation on**
18 **felines**

19

20 **HLF effects on felines**

21

22 **1. Abstract**

23 Habitat loss and fragmentation (HLF) are among the main threats to biodiversity.
24 However, some taxa are more susceptible to HLF due to intrinsic ecological traits,
25 leading to local extinctions and range contractions. The goal of this study was to
26 compile the current knowledge of HLF effects on felines, by describing trends,
27 investigating research effort allocation, and identifying knowledge gaps. We searched
28 the scientific literature in scientific databases and classified the articles according to
29 conceptual and methodological approaches. We reviewed a total of 162 articles and
30 observed that scientific knowledge is unevenly distributed among important topics and
31 species. Habitat suitability and patch-landscape configuration are the most studied
32 topics, comprising 56% of studies. The allocation of research effort is unrelated to
33 variables that describe conservation priorities, such as threat status and habitat
34 availability within the species range. However, it is related to body size, suggesting that
35 charismatic attributes influence the choice of target species. Moreover, the countries
36 with lower research effort are also those with lower economic development, making
37 North America and Europe the centers of knowledge generation on HLF studies on
38 felines. The responses of sixteen felines to HLF remain unknown. Among these,
39 *Leopardus jacobita*, *Pardofelis badia*, *Prionailurus planiceps*, and *Prionailurus*
40 *viverrinus* have the highest urgency of research because they are threatened with
41 extinction. We suggest that theoretical approaches, through modeling exercises, as a

42 first step to decrease the lack of information about HLF effects on felines, especially
43 those species with larger knowledge gaps.

44

45 **Keywords:** Felidae, fragmentation, gap analysis, habitat loss, landscape,

46 metapopulation

47 **2. Introduction**

48 Habitat loss and fragmentation are rising at an alarming rate due to the growth of
49 human activities that convert natural landscapes into human-modified mosaics (Lord &
50 Norton, 1990; Ritters et al., 2000). Habitat loss and fragmentation (HLF) reduce
51 wildlife-adequate habitat and create dispersion barriers; they affect the size and spatial
52 configuration of fragments (Fahrig, 1997; Ewers & Didham, 2006) from the local (Lord
53 & Norton, 1990) to the global scale (Ritters et al., 2000). Not surprisingly, they are
54 listed as the main threats to biodiversity and have become central issues in conservation
55 biology (Foley et al., 2005). Due to the importance of these issues, many reviews and
56 meta-analyses have been published with the objective of clarifying terms (e.g. Andr n
57 1994, Fahrig 2003, Fischer & Lindenmayer 2007), methodological aspects (Debinski &
58 Holt, 2000; McGarigal & Cushman, 2002), ecological processes (Jenkins et al., 2007;
59 Watling et al., 2011), and their effects on target taxa (Mortelliti et al., 2010).

60 Susceptibility to human alteration of the environmental is related to life-history
61 and ecological traits of species (Davidson et al., 2009; Ockinger et al., 2010; Thornton
62 et al., 2011). Therefore, it is expected that certain evolutionary lineages are more
63 vulnerable to HLF than others. Felines (Carnivore: Felidae) are a phylogenetically and
64 ecologically homogeneous taxon composed of 36 wild species (Johnson et al., 2006;
65 Morales & Giannini, 2010). These taxa share traits that potentially make them
66 vulnerable to HLF, such as: high trophic levels, large home ranges, low population
67 densities (Sunquist & Sunquist, 2002), and continued persecution by humans
68 (Woodroffe & Ginsberg, 1998; Inskip & Zimmermann, 2009). Felines are an interesting
69 model to study HLF impacts on wildlife populations due to their high susceptibility to
70 such impacts, their key ecological roles within ecosystems, and their charisma.

71 Our objective was to review the global literature about HLF effects on felines,
72 investigating biases and trends in knowledge. To achieve this goal, our study focuses on
73 three targets. First, we charted the state of knowledge concerning feline HLF studies,
74 discussing weak points and potential solutions to correct such weaknesses. Second, we
75 identified the allocation of research effort across species and countries, providing a
76 global picture of feline HLF studies; we choose these taxonomic and geopolitical scales
77 because they are the levels for which conservation actions could be planned a later
78 implemented on the ground. In a species-specific context, we expected species with
79 higher conservation priorities (e.g. threatened species) to be better studied, and those
80 with high rates of habitat reduction would be studied more extensively. On other hand,
81 charismatic attributes and logistic easiness could be influencing in the choice of target
82 felid species, making large-bodied and widespread species to be more studied.
83 Considering the allocation of research effort across countries, we expected that
84 countries with better economic development would have a greater research effort,
85 whereas research in less-developed countries would have been led mainly by
86 investigators from developed countries. Finally, we created an index based on our
87 results, which allowed for the ranking of species and required studies according to the
88 lack of information associated with them.

89

90 **3. Methods**

91

92 **3.1 Trends in the knowledge about HLF effects on felines**

93 We searched the scientific literature for articles that quantify or describe HLF
94 effects on felines, through a combination of search strings in three scientific publication
95 databases: ISI Web of Science, Cat Library, and Google Scholar (see Appendix A for a

96 complete list of search keywords). All articles published up to and including November
97 2012 were analyzed and classified according to their conceptual and methodological
98 information. We based this classification in key points previously appointed by
99 Mortelliti et al. 2010 in a review of the state of knowledge to European mammals, but
100 modified for felids necessities.

101 The key points studied were: (1) the attention designated to study HLF effects on
102 felines, which can be expressed through total number of publication, the intention to
103 evaluate directly their effects on felines (which considered those articles with a clear
104 objective centered on the topic and the inclusion of variables that measure such
105 processes within a statistical framework), and temporal trends in the publications; (2)
106 taxonomical level of analyses; (3) characteristic of HLF evaluated (habitat reduction or
107 subdivision *per se*, human buildings as barriers, and climatic changes; see Table 1); (4)
108 methodological approach (review, theoretical or empiric; see Table 1); (5) ability to
109 separate habitat loss from fragmentation processes; and (6) sub-discipline studied
110 (conservation medicine, demographic viability, genetic viability, habitat selection,
111 landscape genetic, movement ecology, patch-landscape configuration, road ecology, and
112 systematic conservation plan; see Table 1 for definitions of the sub-disciplines).
113 Poaching of felines or their prey could have been included as a sub-discipline due to the
114 indirect effects of HLF. However, this topic is more complex and commonly studied in
115 the context of conservation conflicts and should be evaluated in an independent study;
116 so, we decided do not considered the poaching in this study.

117 In order to investigate temporal trends in feline reviewed publications, we
118 divided the number of articles investigating HLF on felines by the total number of
119 articles published each year, assessing the relative growth of knowledge in this area in
120 relation to the advancement of science in general. We used the total number of articles

121 indexed in ISI Web of Science in each year as an estimate of the annual total number of
122 publications.

123

124 **3.2 Allocation of research effort**

125 We investigate whether research effort was allocated across species according to
126 ecological and conservation variables, which were: threat status (IUCN 2011), body size
127 (Wilson & Reeder, 2005), range distribution size (IUCN 2011), and suitable habitat
128 within the species range (measured as the absolute area of suitable habitat and the
129 proportion of the range holding suitable habitat). Variables of suitable habitat measure
130 different ecological and conservation attributes, since a species could have a large
131 absolute area of remaining habitat, but also a low proportion of suitable habitat within
132 the range. The proportion of suitable habitat was calculated as the suitable habitat area
133 inside the range distribution relative to total range size. We considered as suitable
134 habitat types those listed by IUCN (IUCN, 2011), and the total area was calculated from
135 available land cover maps (Bontemps et al., 2011).

136 We performed an analysis of covariance (ANCOVA) to evaluate if the number of
137 publications is equal among groups of threat status (categorical variables), measuring
138 and controlling the effect of the others (continuous variables). The results of ANCOVA
139 clarify about the relation of response variable and each one of descriptive variables;
140 even same one or more descriptive variables are not interacting to predict the response
141 variable (Zar, 2010). Research effort across the countries was measured in two different
142 ways: the proportion of felines studied relative to the national feline richness; and the
143 proportion of the range distribution studied. These metrics evaluate different aspects of
144 national research effort; the first represents the knowledge of HLF effects on species
145 while the second may provide information regarding populations that can suffer distinct

146 HLF pressure. We mapped the locations of research article study areas to obtain a
147 global distribution of the studies. We divided species ranges using a 0.25 decimal
148 degree grid and selected grid cells that overlapped with study areas, creating a presence
149 and absence matrix of the studies. Using this matrix, we calculated the number of
150 species and the area studied in each country; the feline richness and range distribution
151 area of countries were calculated through range distribution maps (IUCN 2011).

152 We categorized the countries into classes according to their economic
153 development, which were described by the annual Gross National Income per capita –
154 GNI (World Bank, 2010). The classes were ≤ 10 , > 10 and ≤ 30 , and > 30 times the
155 income needed to live at the poverty line (\$ 540.5 person/year; Ravallion et al., 2009).
156 We compare the research effort variables to the economic development classes through
157 non-parametric methods. Thus, Kruskal-Wallis was performed to evaluate the mean
158 variation among groups and a Nemenyi test was performed to identify the different
159 groups. Nemenyi test is an analog of the Turkey test to non-parametric analysis, which
160 does *a posteriore* comparison of the groups (Zar, 2010).

161 The influence of researchers from developed countries, in other hand, was
162 investigated though the economic power of the paper's authorship. We divided the
163 publication into the economic classes based in the GNI of the country where the study
164 area is located; we evaluated the GNI from the country of the first author and the author
165 from the country with the highest economic power (highest GNI).

166

167 **3.3 Gap analysis of HLF knowledge on felines**

168 Gap analysis is a term conventionally used to identify 'gaps' in the protected
169 areas network by classification of biodiversity and its demands (Jennings, 2000), which
170 results in information used to plan conservation priorities. In this study, we adapted the

171 objective of traditional gap analysis to investigate the ‘gaps’ of knowledge concerning
 172 HLF effects on felines. These results could clarify the information needed for planning
 173 conservation actions.

174 To that end, we converted the relevant topics to be studied (see below, Figure
 175 3A-P) into an index that ranks species by lack of information. The basic index of Gap
 176 Knowledge (GK) consisted of the sum of ‘knowledge distance’ - the difference between
 177 the maximum number of articles for a given issue and the number of articles for species
 178 for the same issue. The variables were linearly transformed (varying from zero to one)
 179 to have the same weight in the index. Therefore, the index was calculated according the
 180 following equation:

$$181 \quad GK = \sum_{i=1}^n 1 - \left(\frac{x_{ij}}{x_{j \max}} \right) \quad \text{Equation 1}$$

182 where i are felids species; j are the key points. The gap analysis regards only those
 183 articles evaluating directly the effect of HLF on felines. This index rates the gap of
 184 information for each species

185 To create a more realistic rank of species according their priority to be studied,
 186 we included in this index other items that affect species knowledge and conservation
 187 following equations

$$188 \quad GK_{PR} = \left(\sum_{i=1}^n 1 - \left(\frac{x_{ij}}{x_{j \max}} \right) \right) * PR \quad \text{Equation 2}$$

$$189 \quad GK_{TS} = \left(\sum_{i=1}^n 1 - \left(\frac{x_{ij}}{x_{j \max}} \right) \right) * TS \quad \text{Equation 3}$$

$$190 \quad GK_{PR/TS} = \left(\sum_{i=1}^n 1 - \left(\frac{x_{ij}}{x_{j \max}} \right) \right) * PR * TS \quad \text{Equation 4}$$

191 where PR is proportion of species range not studied and TS is the threat status of
 192 species. The inclusion of proportion of species range not studied is a way to include the

193 spatial gap of information in the score and, with this, an indirect representation of the
194 regions or populations not studied until now. In the equations, TS assume values
195 hierarchically distributed to IUCN threat status (Least Concern – 0.2; Near Threatened –
196 0.4; Vulnerable – 0.6; Endangered – 0.8; Critically Endangered – 1.0), representing the
197 current species susceptibility to extinction and the urgency of study for the species. The
198 last equation (*Equation 4*), which considers both the proportion of range studied and the
199 threat status, provide a final rank regarding the knowledge gap on the topic and the
200 urgency of study the species.

201

202 **4. Results and Discussion**

203

204 **4.1 Trends in the knowledge about HLF effects on felines**

205

206 **4.1.1 Trends in the attention designated to study HLF effects on felines**

207 We found a total of 162 published articles concerning HLF on felines
208 (Appendix A). This is a relatively small number, considering the number of feline
209 species, the threat that these processes represent to the taxa, and the charisma of the
210 group. If we analyze the objectives and methodologies of these studies, we observe that
211 the effective number of articles is less than half (Figure 1A), as many of them only
212 provide indirect inferences of these anthropogenic alteration on felines. Consequently,
213 the knowledge about HLF effects on felines is small, even though felids are among the
214 best studied mammal groups (Amori & Gippoliti, 2000).

215 The modest attention given to the topic is also demonstrated by the date of the
216 first publications (Ferrerias et al., 1992; Rodríguez & Delibes, 1992), since the
217 popularization of HLF as a conservation research theme took place in the 1970s (Haila,

218 2002). However, the number of publications has grown throughout the years (Figure 2),
219 showing that researchers have paid more attention on the topic recently, probably due to
220 its importance to feline conservation.

221

222 **4.1.2 Taxonomic level of analysis**

223 Most articles have a single-species approach (Figure 1B); however, the effects
224 of HLF on felines have not been studied using a single species approach for 61% felines
225 (Figure 3A). When that is not the case, the focus group of the research was frequently
226 carnivores (13.9%) or mammals in general (19.6%), and only two studies investigated
227 HLF effects on sympatric felines (e.g. Hunter et al. 2003, Moisés Gallas & Silveira
228 2011). However, both articles had only an indirect approach of HLF effects and do not
229 direct inferences of its consequences on felines.

230 Studies considering felines as target species can help elucidate species-specific
231 or taxonomic patterns, which is important given the ecological functions these species
232 perform within ecosystems. Felids are the top predators in many ecosystems (Ritchie &
233 Johnson 2009) and their extirpation may affect community structure through a process
234 known as mesopredator release. Mesopredator release impacts the ecosystem due to the
235 increase of small predator abundance, the decline of prey populations, and the
236 consequent species extinctions (Prugh et al., 2009).

237 Felines may occupy partially overlapping niches, competing for resources
238 (Caro & Stoner, 2003; Foster et al., 2010); considering that felines are territorial
239 species, they can compete for the habitat available in a landscape. Habitat loss and
240 fragmentation can favor different species according to the predominant matrix type
241 given that the species differ in their environmental plasticity and their ability to use
242 suboptimum habitat. Thus, we could expect that land cover change alters the

243 competitive relationship among sympatric felines. It is a relevant topic for feline
244 conservation planning, but this topic remains unexplored (Figure 3B).

245

246 **4.1.3 Characteristics of HLF evaluated**

247 Habitat reduction or subdivision effects on species were the themes most often
248 investigated (Figure 1C). Only a few studies addressed exclusively the effects of human
249 infrastructures on felines, and the least studied topic was habitat loss due to climate
250 change (Figure 1C). According to the IUCN Red List (IUCN, 2011), HLF affects all 36
251 wild felines; for 21 of them, it is a primary threat. Currently, climate change does not
252 represent a threat to felid species (IUCN, 2011), but studies focusing on the synergies
253 among climate change and habitat loss for felines are scarce (Figure 3C-E), impairing
254 our comprehension of its consequences (Heller & Zavaleta, 2009).

255

256 **4.1.4 Methodological approach**

257 There is a clear bias for empirical approaches in the reviewed literature (Figure
258 1D), but the imbalance among theoretical and empirical publications does not constitute
259 a gap. It is possible to generate good data and generalizations about HLF effects on
260 felines by adopting each type of approach, but it would be interesting to have theoretical
261 approaches providing suggestions to be tested in the field (McGarigal & Cushman,
262 2002). In this way, theoretical and empirical studies could be considered with two parts
263 of investigation process, the first find pattern and process to be tested by the second.

264 Theoretical studies can permit manipulations through a variety of conditions
265 helping to understand the species response in a large range of human interferences on
266 the landscape, which could be impossible to perform for ethical or logistical reasons due
267 to the obvious difficulties to do field manipulations on rare large-bodied wide-ranging

268 species. In this way, theoretical approaches could have two main functions on HLF
269 studies with felines, simulations of species responses in a large-range of environmental
270 conditions and help to plan empirical studies.

271 As example of manipulative approaches in HLF studies with felines, Reed
272 (2004) investigates the HLF effects on population of many species evaluating the
273 importance of dispersal among subpopulation to long term survival of population.
274 Brook et al. (2002) also investigated HLF effects on a set of species, but in an
275 inbreeding depression context, which increase the extinction risk. Tian et al. (2011), by
276 the way, used a more robust field data to investigate the HLF effects on long-term
277 survival of the Amur tiger. These are the only manipulative studies among the reviewed
278 articles and all are into theoretical approach of population viability. As described, the
279 objectives of these studies were simulates the species responses in different
280 environmental conditions; however, no one used the theoretical approach as a way to
281 plan empirical studies as a strategy to better design field work.(Brook et al., 2002; Reed,
282 2004; Tian et al., 2011)

283

284 **4.1.5 Differentiation of habitat loss from fragmentation**

285 To conduct an efficient separation of the processes of habitat loss and
286 fragmentation, landscape scale studies and true replicas are needed (McGarigal &
287 Cushman, 2002); however, most of the studies reviewed were conducted at the local
288 scale. The distinction of habitat loss from fragmentation should support management
289 strategies for species (Fischer & Lindenmayer, 2007; Mortelliti et al., 2011), but only
290 one article tackles the differences between such processes (Tian et al., 2011) (Figure
291 3F). Of course, it is difficult to define landscape boundaries and true independent
292 replicas in a real world landscape, especially for species with large dispersion ability

293 like felines. Theoretical approaches could allow for the differentiation of habitat loss
294 from fragmentation for some species through modeling of hypothetical landscapes.

295 Many articles discuss the use of movement corridors as a mechanism to maintain
296 or reestablish population dynamics (e.g. Carroll & Miquelle 2006, Hetherington et al.
297 2008, Morrison & Boyce 2009), solving or minimizing the fragmentation problem.
298 Corridors might be a coherent conservation strategy for felids due to the difficulty of
299 finding large and connected habitat areas, which is needed to felines conservation
300 (Boitani et al., 2011); however, dispersion corridors could have negative consequences
301 to species conservation, making species susceptible to contagious diseases from
302 domestic animals and retaliatory hunting due to human-predator-prey conflicts
303 (Chetkiewicz et al., 2006). Among the reviewed articles, only a few were designed to
304 actually evaluate corridor function for felid conservation (Figure 1E). We believe this
305 topic needs more attention from the felid conservationist community to determine
306 whether such statements are truly supported by data, elucidating the real effects of
307 corridors and which species might benefit from such a strategy.

308 A set of specific data are essential for designing corridors and evaluating their
309 efficiency, such as dispersal rates of different sexes and ages, considering also different
310 spatial and temporal scales. The spatial data necessary to discuss these issues is
311 relatively frequent among the reviewed publications (Figure 1F), but it was adequately
312 explored for only a few species (Figure 3I and also section 4.1.7 for further details
313 concerning the movement ecology sub-discipline).

314 Even the correct definition of processes (habitat loss and fragmentation *per se*)
315 was found only in a small number of articles, given that 'habitat fragmentation' was
316 commonly used to represent both processes (Figure 1G). For many years there was a
317 confusion regarding HLF concepts and nomenclature until Andr n (1994) provided a

318 review of habitat loss and fragmentation effects and defined the terminology. This lack
319 of differentiation between processes has been generated, in part, by a delay in the
320 adoption of a widespread scientific terminology by the feline scientific community.

321

322 **4.1.6 Knowledge on the sub-disciplines**

323 Knowledge about HLF is concentrated in only a few sub-disciplines as habitat
324 selection and patch-landscape configuration account for 56% of all publications (Figure
325 4). *P. concolor* and *L. rufus* were the focal species in 44% (Figure 3G) of habitat
326 selection studies and had similar responses to HLF, such as the ability to use landscapes
327 with some level of anthropogenic disturbance (Johnson et al., 2010; Burdett et al., 2010)
328 (see Appendix B - Table S.B1 for general results of HLF on felines). This trend is also
329 observed in the second most studied sub-discipline, patch-landscape configuration
330 (Figure 4), in which three species (*P. concolor*, *L. rufus*, and *Leopardus pardalis*)
331 comprise 48% of the articles (Figure 3H).

332 Knowledge on movement ecology is fundamental to understand spatial
333 dynamics at the landscape level, which is a key aspect to the conservation of large-
334 bodied wide-ranging species. This research theme has been well-explored only for *Lynx*
335 *pardinus* through studies of habitat selection on dispersion phases (Palomares et al.,
336 2000), landscape structure (Ferrerias, 2001), and matrix heterogeneity effects on
337 dispersion (Revilla et al., 2004). There are also a large number of articles about
338 movement ecology for *L. lynx* and *L. rufus* (Figure 3I), but the ecological questions do
339 not address as many issues as in *L. pardinus* studies.

340 Landscape genetics has been investigated in a large number of species (Figure
341 3), resulting in interesting conclusions about HLF effects on population genetic
342 structure (Ernest et al., 2003; Janečka et al., 2008; Schmidt et al., 2011), inbreeding

343 depression (Björklund, 2003; Johnson et al., 2004; Loxterman, 2011), and their long-
344 term consequences (Singh & Gibson, 2011; Schnitzler, 2011). Landscape genetics has
345 become more popular than both demographic viability and genetic viability (Figure 3J-
346 L and Figure 4), which are older conservation issues. Studies concerning HLF impacts
347 on population genetics are relevant because demographic data might be unrealistic from
348 a conservation standpoint, due to their long generation times and lengthy time-lags in
349 population responses (Jackson & Sax, 2010; Krauss et al., 2010); however, not a single
350 article measured the time delay of felids in response to HLF (Figure 3M). Additionally,
351 there is difficulty in “putting ‘landscape’ in landscape genetics” (Storfer et al., 2007),
352 and thus the majority of studies are based on population genetics and make indirect
353 inferences about HLF.

354 Conservation medicine is the only sub-discipline with a higher number of
355 species than publications (Deem et al., 2001; Aguirre & Tabor, 2008). However, the
356 lack of *in situ* data is still considerable (Figure 3N), probably due to the interdisciplinary
357 nature of conservation medicine studies that combines landscape ecology and veterinary
358 approaches.

359 The least studied disciplines are systematic conservation plan and road ecology
360 (Figure 4). The selection of priority areas can be a difficult task for feline conservation
361 because HLF studies are conducted mainly at the local or landscape scale, whereas site-
362 selection studies are commonly carried out at a macroecological scale (Loyola et al.,
363 2009; Mortelliti et al., 2010; Rondinini et al., 2011). Consequently, inserting HLF into
364 feline site-selection schemes may be a challenge, especially if includes connectivity and
365 dispersal data (Hodgson et al., 2011; Lourival et al., 2011; Crooks et al., 2011); we can
366 observe this in our results, as only one species received an adequate approach (Figure
367 3O). Road ecology studies attempt to quantify the impacts of vehicle collision on

368 animals. Only a few of these studies, however, measure quantitatively the relationship
369 between traffic, mortality and its consequences for the population (Kerley et al., 2002;
370 Riley et al., 2006; Schwab & Zandbergen, 2011). Roadkill threatens some felines
371 (Appendix B - Table S.B1 and Figure 3), but the studies are not focused on these
372 species (Appendix B - Table S.B1).

373

374 **4.2 Allocation of research effort**

375 The allocation of research effort is unevenly distributed among felids, in which
376 more than 80% of published studies concerned with only seven species, and 11 species
377 have not yet been studied (Figure 3). Conservation priorities did not motivate effort
378 allocation, as threat status and range distribution contraction were unrelated to the
379 number of publications (Table 2). As a consequence, five threatened species do not have
380 a single publication pertaining to HLF; if we consider only the studies investigating
381 directly HLF effects, the number of threatened species without scientific publication
382 increases to eight (Figure 3). In addition, among the five felines listed as large mammals
383 with high range contraction (Morrison et al. 2007), three of them are poorly studied
384 (*Panthera leo*, *Panthera pardus*, and *Acinonyx jubatus*) (Figure 3).

385 We also expected species with larger distributions to have more publications
386 given that their wide distribution could provide field researchers more options for
387 selecting study sites. However, our results did not support this prediction (Table 2).
388 Instead, large bodied felines are more studied (Table 2), suggesting that researcher
389 choice may be associated with charismatic characteristics, rather than conservation
390 priorities (see also Brodie 2009). Another explanation could be the ease of studying
391 large cats through camera trapping, as larger body sizes have higher chances to be
392 detected by sensors (Karanth et al., 2004), and the coat patterns used to identify

393 individuals (Karanth et al., 2006) are most common in large cats (Brodie, 2009).
394 However, camera trapping techniques are used in only a few of the articles reviewed
395 (Figure 1F) and, consequently, cannot be responsible for the difference in effort
396 allocated between large and small cats.

397 As expected, countries with higher economic development possess greater
398 knowledge of HLF effects on their felines than countries with lower economic
399 development (Figure 5). As a consequence, the effort allocation of felid HLF studies is
400 also disproportional across countries (see Appendix B - Figure S.B1 for a map depicting
401 study area locations), in which the majority of research are concentrated in North
402 America and Europe. The studies realized on countries with lower economic
403 development are frequently conducted by researcher from the region; however, it is not
404 rare these studies have as coauthor researches from countries with higher economic
405 development (Figure 6A). Therefore, in general, economically developed countries
406 contribute to the knowledge about HLF on felines, as they also lead research in less
407 developed countries (Figure 6A), and the inverse association is rarely the case (Figure
408 6B-C). This result shows a collaborative relation of researches probable due to the
409 funding provided by developed countries and the gap knowledge of the less developed
410 countries.

411

412 **4.3 Gap analysis of HLF knowledge on feline**

413 Many felines have a large knowledge gap concerning HLF effects (Figure 3Q-
414 T). In a general context, only *L. rufus* has been adequately studied, as it has publications
415 regarding the majority of issues discussed here (Figure 3Q). Conversely, sixteen species
416 are still without precise information about HLF effects on them. The proportion of
417 range unstudied decreases the knowledge gap for a few species (Figure 3R); this occurs

418 due to theoretical studies regarding large proportion of range distribution of species
419 (Forrest et al., 2012; Trisurat et al., 2012). However, if we weight the species by threat
420 status, four species display higher gaps (*Leopardus jacobita*, *Pardofelis badia*,
421 *Prionailurus planiceps*, and *Prionailurus viverrinus* – Figure 3S), and thus these species
422 could be considered the ones with the most urgent need of study. The index value for
423 few species changes if we weight the gap index by both threat status and proportion of
424 range studied compared with only threat status, given that, in general (Figure 3T), the
425 proportion of species range studied is low.

426

427 **5. Conclusion**

428 The results of our analyses demonstrate that the knowledge gap concerning HLF
429 effects on felids varies greatly among species. Many species are poorly studied and
430 those with a reasonable number of publications are lacking in sub-disciplines and
431 generality of results. Feline research urgently needs larger-scale investigations and
432 generalizations to better improve the preservation of biodiversity of this group. A
433 strategy to decrease of gap knowledge on felines could be focus in theoretical
434 approaches of some topics appointed in this study, such as: (i) differentiation of habitat
435 loss from fragmentation effects through theoretical scenarios; (ii) selection of priority
436 areas for conservation considering land cover types and configuration on a range
437 distribution scale; and (iii) consequences of habitat loss due to climatic changes that had
438 its effects largely unknown. These studies are not the only ones necessary to understand
439 HLF effects on felines and, maybe, they is not even same the most urgent; however,
440 these topics are a good first step to decrease the knowledge gaps concerning HLF
441 effects on felines since they will help discern general patterns and will cover a large
442 portion of a range distribution.

443 **6. References**

- 444 AGUIRRE, A. & TABOR, G.M. (2008) Global factors driving emerging infectious
445 diseases. *Annals of the New York Academy of Sciences*, 1149, 1–3.
- 446 AMORI, G. & GIPPOLITI, S. (2000) What do mammalogists want to save? Ten years of
447 mammalian conservation biology. *Biodiversity and Conservation*, 9, 785–793.
- 448 ANDRÉN, H. (1994) Effects of habitat fragmentation on birds and mammals in
449 landscapes with different proportions of suitable habitat: a review. *Oikos*, 71, 355–
450 366.
- 451 BJÖRKLUND, M. (2003) The risk of inbreeding due to habitat loss in the lion (*Panthera*
452 *leo*). *Conservation Genetics*, 4, 515–523.
- 453 BOITANI, L., MAIORANO, L., BAISERO, D., FALCUCCI, A., VISCONTI, P. & RONDININI, C.
454 (2011) What spatial data do we need to develop global mammal conservation
455 strategies? *Philosophical Transactions of the Royal Society of London. Series B,*
456 *Biological Sciences*, 366, 2623–2632.
- 457 BONTEMPS, S., DEFOURNY, P., BOGAERT, E. VAN, KALOGIROU, V. & PEREZ, J.R. (2011)
458 GLOBCOVER 2009. UCLouvain & ESA Team.
- 459 BRODIE, J.F. (2009) Is research effort allocated efficiently for conservation? Felidae as a
460 global case study. *Biodiversity and Conservation*, 18, 2927–2939.
- 461 BROOK, B.W., TONKYN, D.W., O'GRADY, J.J. & FRANKHAM, R. (2002) Contribution of
462 inbreeding to extinction risk in threatened species. *Conservation Ecology*, 6.
- 463 BURDETT, C.L., CROOKS, K.R., THEOBALD, D.M., WILSON, K.R., BOYDSTON, E.E.,
464 LYREN, L.M., ET AL. (2010) Interfacing models of wildlife habitat and human
465 development to predict the future distribution of puma habitat. *Ecosphere*, 1, 1–21.
- 466 CARO, T.. & STONER, C.. (2003) The potential for interspecific competition among
467 African carnivores. *Biological Conservation*, 110, 67–75.

- 468 CARROLL, C. & MIQUELLE, D.G. (2006) Spatial viability analysis of Amur tiger
469 *Panthera tigris altaica* in the Russian Far East: the role of protected areas and
470 landscape matrix in population persistence. *Journal of Applied Ecology*, 43, 1056–
471 1068.
- 472 CHETKIEWICZ, C.-L.B., ST. CLAIR, C.C. & BOYCE, M.S. (2006) Corridors for
473 conservation: integrating pattern and process. *Annual Review of Ecology,*
474 *Evolution, and Systematics*, 37, 317–342.
- 475 CROOKS, K.R., BURDETT, C.L., THEOBALD, D.M., RONDININI, C. & BOITANI, L. (2011)
476 Global patterns of fragmentation and connectivity of mammalian carnivore habitat.
477 *Philosophical Transactions of the Royal Society of London. Series B, Biological*
478 *Sciences*, 366, 2642–2651.
- 479 DAVIDSON, A.D., HAMILTON, M.J., BOYER, A.G., BROWN, J.H. & CEBALLOS, G. (2009)
480 Multiple ecological pathways to extinction in mammals. *Proceedings of the*
481 *National Academy of Sciences of the United States of America*, 106, 10702–10705.
- 482 DEBINSKI, D.M. & HOLT, R.D. (2000) A survey and overview of habitat fragmentation
483 experiments. *Conservation Biology*, 14, 342–355.
- 484 DEEM, S.L., KARESH, W.B. & WEISMAN, W. (2001) Putting theory into practice: wildlife
485 health in conservation. *Conservation Biology*, 15, 1224–1233.
- 486 ERNEST, H., BOYCE, W., BLEICH, V., MAY, B., STIVER, S.J. & TORRES, S.G. (2003)
487 Genetic structure of mountain lion (*Puma concolor*) populations in California.
488 *Conservation Genetics*, 4, 353–366.
- 489 EWERS, R.M. & DIDHAM, R.K. (2006) Confounding factors in the detection of species
490 responses to habitat fragmentation. *Biological Reviews*, 81, 117–142.
- 491 FAHRIG, L. (1997) Relative effects of habitat loss and fragmentation on population
492 extinction. *The Journal of Wildlife Management*, 61, 603–610.

493 FAHRIG, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of*
494 *Ecology, Evolution, and Systematics*, 34, 487–515.

495 FERRERAS, P., ALDAMA, J.J., BELTRÁN, J.F. & DELIBES, M. (1992) Rates and causes of
496 mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck,
497 1824. *Biological Conservation*, 61, 197–202.

498 FISCHER, J. & LINDENMAYER, D.B. (2007) Landscape modification and habitat
499 fragmentation: a synthesis. *Global Ecology and Biogeography*, 16, 265–280.

500 FOLEY, J.A., DEFRIES, R., ASNER, G.P., BARFORD, C., BONAN, G., CARPENTER, S.R., ET
501 AL. (2005) Global consequences of land use. *Science*, 309, 570–574.

502 FORREST, J.L., WIKRAMANAYAKE, E., SHRESTHA, R., AREENDRAN, G., GYELTSHEN, K.,
503 MAHESHWARI, A., ET AL. (2012) Conservation and climate change: assessing the
504 vulnerability of snow leopard habitat to treeline shift in the Himalaya. *Biological*
505 *Conservation*, 150, 129–135.

506 FOSTER, R.J., HARMSSEN, B.J. & DONCASTER, C.P. (2010) Habitat use by sympatric
507 jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica*,
508 42, 724–731.

509 HAILA, Y. (2002) A conceptual genealogy of fragmentation research: from island
510 biogeography to landscape ecology. *Ecological Applications*, 12, 321–334.

511 HELLER, N.E. & ZAVALETA, E.S. (2009) Biodiversity management in the face of climate
512 change: a review of 22 years of recommendations. *Biological Conservation*, 142,
513 14–32. Elsevier Ltd.

514 HETHERINGTON, D.A., MILLER, D.R., MACLEOD, C.D. & GORMAN, MA.L. (2008) A
515 potential habitat network for the Eurasian lynx *Lynx lynx* in Scotland. *Mammal*
516 *Review*, 38, 285–303.

517 HODGSON, J.A., MOILANEN, A., WINTLE, B.A. & THOMAS, C.D. (2011) Habitat area,
518 quality and connectivity: striking the balance for efficient conservation. *Journal of*
519 *Applied Ecology*, 48, 148–152.

520 HUNTER, R.D., FISHER, R.F. & CROOKS, K.R. (2003) Landscape-level connectivity in
521 coastal southern California, USA, as assessed through carnivore habitat suitability.
522 *Natural Areas Journal*, 23, 302–314.

523 INSKIP, C. & ZIMMERMANN, A. (2009) Human-felid conflict: a review of patterns and
524 priorities worldwide. *Oryx*, 43, 18–34.

525 IUCN (2011) The IUCN red list of threatened Species. [Http://www.iucnredlist.org/](http://www.iucnredlist.org/).

526 JACKSON, S.T. & SAX, D.F. (2010) Balancing biodiversity in a changing environment:
527 extinction debt, immigration credit and species turnover. *Trends in Ecology &*
528 *Evolution*, 25, 153–160.

529 JANEČKA, J.E., TEWES, M.E., LAACK, L.L., GRASSMAN, L.I., HAINES, A.M. &
530 HONEYCUTT, R.L. (2008) Small effective population sizes of two remnant ocelot
531 populations (*Leopardus pardalis albescens*) in the United States. *Conservation*
532 *Genetics*, 9, 869–878.

533 JENKINS, D.G., BRESCACIN, C.R., DUXBURY, C. V., ELLIOTT, J. A., EVANS, J. A.,
534 GRABLOW, K.R., ET AL. (2007) Does size matter for dispersal distance? *Global*
535 *Ecology and Biogeography*, 16, 415–425.

536 JENNINGS, M. (2000) Gap analysis: concepts, methods, and recent results. *Landscape*
537 *ecology*, 15, 5–20.

538 JOHNSON, S.A., WALKER, H.D. & HUDSON, C.M. (2010) Dispersal characteristics of
539 juvenile bobcats in South-Central Indiana. *Journal of Wildlife Management*, 74,
540 379–385.

541 JOHNSON, W.E., EIZIRIK, E., PECON-SLATTERY, J., MURPHY, W.J., ANTUNES, A.,
542 TEELING, E. & O'BRIEN, S.J. (2006) The late Miocene radiation of modern Felidae:
543 a genetic assessment. *Science*, 311, 73–77.

544 JOHNSON, W.E., GODOY, J.A., PALOMARES, F., DELIBES, M., REVILLA, E. & O'BRIEN,
545 S.J. (2004) Phylogenetic and phylogeographic analysis of Iberian lynx populations.
546 *Journal of Heredity*, 95, 19–28.

547 KARANTH, K.U., NICHOLS, J.D., KUMAR, N.S. & HINES, J.E. (2006) Assessing tiger
548 population dynamics using photographic capture-recapture sampling. *Ecology*, 87,
549 2925–2937.

550 KARANTH, K.U., NICHOLS, J.D., KUMAR, N.S., LINK, W.A. & HINES, J.E. (2004) Tigers
551 and their prey: predicting carnivore densities from prey abundance. *Proceedings of*
552 *the National Academy of Sciences of the United States of America*, 101, 4854–
553 4858.

554 KERLEY, L.L., GOODRICH, J.M., MIQUELLE, D.G., SMIRNOV, E.N., QUIGLEY, H.B. &
555 HORNOCKER, M.G. (2002) Effects of roads and human disturbance on Amur tigers.
556 *Conservation Biology*, 16, 97–108.

557 KRAUSS, J., BOMMARCO, R., GUARDIOLA, M., HEIKKINEN, R.K., HELM, A., KUUSSAARI,
558 M., ET AL. (2010) Habitat fragmentation causes immediate and time-delayed
559 biodiversity loss at different trophic levels. *Ecology Letters*, 13, 597–605.

560 LORD, J.M. & NORTON, D.A. (1990) Scale and the spatial concept of fragmentation.
561 *Conservation Biology*, 4, 197–202.

562 LOURIVAL, R., DRECHSLER, M., WATTS, M.E., GAME, E.T. & POSSINGHAM, H.P. (2011)
563 Planning for reserve adequacy in dynamic landscapes; maximizing future
564 representation of vegetation communities under flood disturbance in the Pantanal
565 wetland. *Diversity and Distributions*, 17, 297–310.

566 LOXTERMAN, J.L. (2011) Fine scale population genetic structure of pumas in the
567 Intermountain West. *Conservation Genetics*, 12, 1049–1059.

568 LOYOLA, R.D., OLIVEIRA-SANTOS, L.G.R., ALMEIDA-NETO, M., NOGUEIRA, D.M.,
569 KUBOTA, U., DINIZ-FILHO, J.A.F. & LEWINSOHN, T.M. (2009) Integrating economic
570 costs and biological traits into global conservation priorities for carnivores. *PloS*
571 *ONE*, 4, e6807.

572 MCGARIGAL, K. & CUSHMAN, S.A. (2002) Comparative evaluation of experimental
573 approaches to the study of habitat fragmentation effects. *Ecological Applications*,
574 12, 335–345.

575 MOISÉS GALLAS & SILVEIRA, E.F. DA (2011) Mesocestoides sp. (Eucestoda,
576 Mesocestoididae) parasitizing four species of wild felines in Southern Brazil.
577 *Revista Brasileira de Parasitologia Veterinaria de Jaboticabal*, 20, 168–170.

578 MORALES, M.M. & GIANNINI, N.P. (2010) Morphofunctional patterns in Neotropical
579 felids: species co-existence and historical assembly. *Biological Journal of the*
580 *Linnean Society*, 100, 711–724.

581 MORRISON, J.C., SECHREST, W., DINERSTEIN, E., WILCOVE, D.S. & LAMOREUX, J.F.
582 (2007) Persistence of large mammal faunas as indicators of global human impacts.
583 *Journal of Mammalogy*, 88, 1363–1380.

584 MORRISON, S.A. & BOYCE, W.M. (2009) Conserving connectivity: some lessons from
585 mountain lions in southern California. *Conservation Biology*, 23, 275–285.

586 MORTELLITI, A., AMORI, G., CAPIZZI, D., CERVONE, C., FAGIANI, S., POLLINI, B. &
587 BOITANI, L. (2011) Independent effects of habitat loss, habitat fragmentation and
588 structural connectivity on the distribution of two arboreal rodents. *Journal of*
589 *Applied Ecology*, 48, 153–162.

590 MORTELLITI, A., AMORI, G., CAPIZZI, D., RONDININI, C. & BOITANI, L. (2010)
591 Experimental design and taxonomic scope of fragmentation studies on European
592 mammals: current status and future priorities. *Mammal Review*, 40, 125–154.

593 OCKINGER, E., SCHWEIGER, O., CRIST, T.O., DEBINSKI, D.M., KRAUSS, J., KUUSSAARI,
594 M., ET AL. (2010) Life-history traits predict species responses to habitat area and
595 isolation: a cross-continental synthesis. *Ecology letters*, 13, 969–979.

596 PALOMARES, F., DELIBES, M., FERRERAS, P., FEDRIANI, J.M., CALZADA, J. & REVILLA, E.
597 (2000) Iberian lynx in a fragmented landscape: predispersal, dispersal, and
598 postdispersal habitats. *Conservation Biology*, 14, 809–818.

599 PRUGH, L.R., STONER, C.J., EPPS, C.W., BEAN, W.T., RIPPLE, W.J., LALIBERTE, A.S. &
600 BRASHARES, J.S. (2009) The rise of the mesopredator. *BioScience*, 59, 779–791.

601 RAVALLION, M., CHEN, S. & SANGRAULA, P. (2009) Dollar a day revisited. *The World*
602 *Bank Economic Review*, 23, 163–184.

603 REED, D.H. (2004) Extinction risk in fragmented habitats. *Animal Conservation*, 7, 181–
604 191.

605 REVILLA, E., WIEGAND, T., PALOMARES, F., FERRERAS, P. & DELIBES, M. (2004) Effects
606 of matrix heterogeneity on animal dispersal: from individual behavior to
607 metapopulation-level parameters. *The American Naturalist*, 164, E130–E153.

608 RILEY, S.P.D., POLLINGER, J.P., SAUVAJOT, R.M., YORK, E.C., BROMLEY, C., FULLER,
609 T.K. & WAYNE, R.K. (2006) A southern California freeway is a physical and social
610 barrier to gene flow in carnivores. *Molecular ecology*, 15, 1733–1741.

611 RITCHIE, E.G. & JOHNSON, C.N. (2009) Predator interactions, mesopredator release and
612 biodiversity conservation. *Ecology Letters*, 12, 982–998.

613 RITTERS, K., WICKHAM, J., O’NEILL, R., JONES, B. & SMITH, E. (2000) Global-scale
614 patterns of forest fragmentation. *Conservation Ecology*, 4.

615 RODRÍGUEZ, A. & DELIBES, M. (1992) Current range and status of the Iberian lynx *Felis*
616 *pardina* Temminck, 1824 in Spain. *Biological Conservation*, 61, 189–196.

617 RONDININI, C., DI MARCO, M., CHIOZZA, F., SANTULLI, G., BAISERO, D., VISCONTI, P.,
618 ET AL. (2011) Global habitat suitability models of terrestrial mammals.
619 *Philosophical Transactions of the Royal Society of London. Series B, Biological*
620 *Sciences*, 366, 2633–2641.

621 SCHMIDT, K., RATKIEWICZ, M. & KONOPÍNSKI, M.K. (2011) The importance of genetic
622 variability and population differentiation in the Eurasian lynx *Lynx lynx* for
623 conservation, in the context of habitat and climate change. *Mammal Review*, 41,
624 112–124.

625 SCHNITZLER, A.E. (2011) Past and present distribution of the North African-Asian lion
626 subgroup: a review. *Mammal Review*, 41, 220–243.

627 SCHWAB, A.C. & ZANDBERGEN, P.A. (2011) Vehicle-related mortality and road crossing
628 behavior of the Florida panther. *Applied Geography*, 31, 859–870. Elsevier Ltd.

629 SINGH, H.S. & GIBSON, L. (2011) A conservation success story in the otherwise dire
630 megafauna extinction crisis: the Asiatic lion (*Panthera leo persica*) of Gir forest.
631 *Biological Conservation*, 144, 1753–1757. Elsevier Ltd.

632 STORFER, A., MURPHY, M.A., EVANS, J.S., GOLDBERG, C.S., ROBINSON, S., SPEAR, S.F.,
633 ET AL. (2007) Putting the “landscape” in landscape genetics. *Heredity*, 98, 128–
634 142.

635 SUNQUIST, M. & SUNQUIST, F. (2002) Wild cats of the world. The University of Chicago
636 Press, Chicago.

637 THORNTON, D., BRANCH, L. & SUNQUIST, M. (2011) Passive sampling effects and
638 landscape location alter associations between species traits and response to
639 fragmentation. *Ecological Applications*, 21, 817–829.

- 640 TIAN, Y., WU, J., SMITH, A.T., WANG, T., KOU, X. & GE, J. (2011) Population viability
641 of the Siberian Tiger in a changing landscape: going, going and gone? *Ecological*
642 *Modelling*, 222, 3166–3180.
- 643 TRISURAT, Y., BHUMPAKPHAN, N., REED, D.H. & KANCHANASAKA, B. (2012) Using
644 species distribution modeling to set management priorities for mammals in
645 northern Thailand. *Journal for Nature Conservation*, 20, 264–273.
- 646 WATLING, J.I., NOWAKOWSKI, A. J., DONNELLY, M. A. & ORROCK, J.L. (2011) Meta-
647 analysis reveals the importance of matrix composition for animals in fragmented
648 habitat. *Global Ecology and Biogeography*, 20, 209–217.
- 649 WILSON, D.E. & REEDER, D.M. (2005) Mammal species of the world. A taxonomic and
650 geographic reference, 3rd edition. Johns Hopkins University Press, Baltimore.
- 651 WOODROFFE, R. & GINSBERG, J.J.R. (1998) Edge effects and the extinction of
652 populations inside protected areas. *Science*, 280, 2126–2128.
- 653 WORLD BANK (2010) Global Economy: GNI per capita 2000 - 2009, atlas method.
654 *Geohive*. <http://www.geohive.com/default.aspx>.
- 655 ZAR, J.H. (2010) Biostatistical analysis. Fifth Edit. Prentice Hall, Upper Saddle River,
656 New Jersey.

657 Table 1. Definitions of terms used in this review

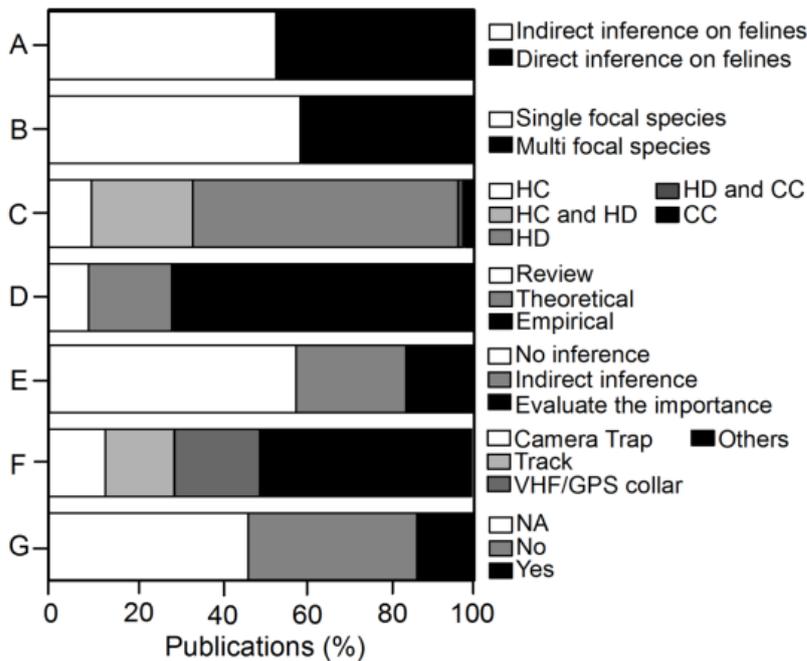
Term	Definition
<i>Process evaluated</i>	
Habitat reduction	Loss in the total area of habitat available to a species
Habitat subdivision	Habitat partition into smaller patches
Human buildings as barrier	Non-natural barriers such as roads, dams, urban areas that make animal movement in the landscape difficult
Climate change	Reduction of the total area of habitat available to a species through the increase of global average temperature
<i>Approach</i>	
Review	A survey paper about a particular subject
Empirical	Use of observed data to report a result
Theoretical	A paper that uses a simulated environment and data base to investigate a pattern or test a hypothesis
<i>Sub-discipline</i>	
Conservation medicine	Investigates wildlife health in response to anthropogenic pressure and habitat conversion
Demographic viability	Investigation of population viability through the number of individuals in a population or metapopulation
Genetic viability	Investigation of population viability through the genetic diversity of a population or metapopulation
Habitat selection	Evaluation of habitat suitability through the

Term	Definition
	hierarchy of space, which can be based on variegation or contour models
Landscape genetics	The influence of the landscape on gene flow and spatial genetic variation
Movement ecology	Concerned with the movement of an organism in a landscape, dispersal ability, and its choice on non- optimal habitats
Patch-landscape configuration	Measure habitat loss and fragmentation effects on species through the use of fragmentation metrics
Road ecology	Road network effects on wildlife
Systematic conservation plan	Selection of priority areas for species conservation through systematic planning

659 Table 2. Results of analysis of covariance performed to identify patterns in the
 660 allocation of research effort for publications about habitat loss and fragmentation effects
 661 on felines.

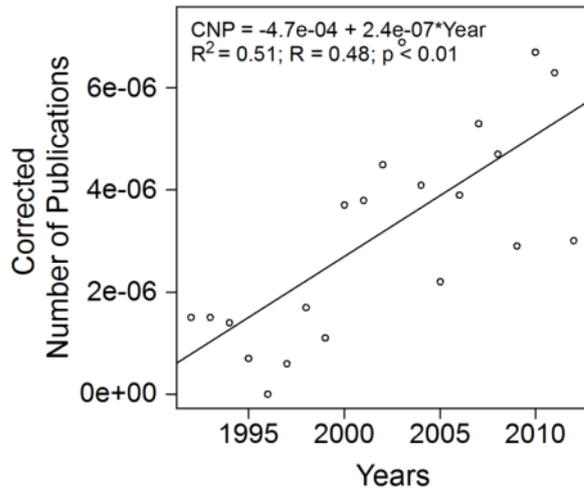
Effect	Degree of Freedom	F
Intercept	1	2.31
IUCN threat status	4	2.18
Body size	1	10.78*
Range size	1	<0.01
Total habitat area	1	0.38
Proportion of habitat in the range	1	0.29
Error	27	

662 * p < 0.05



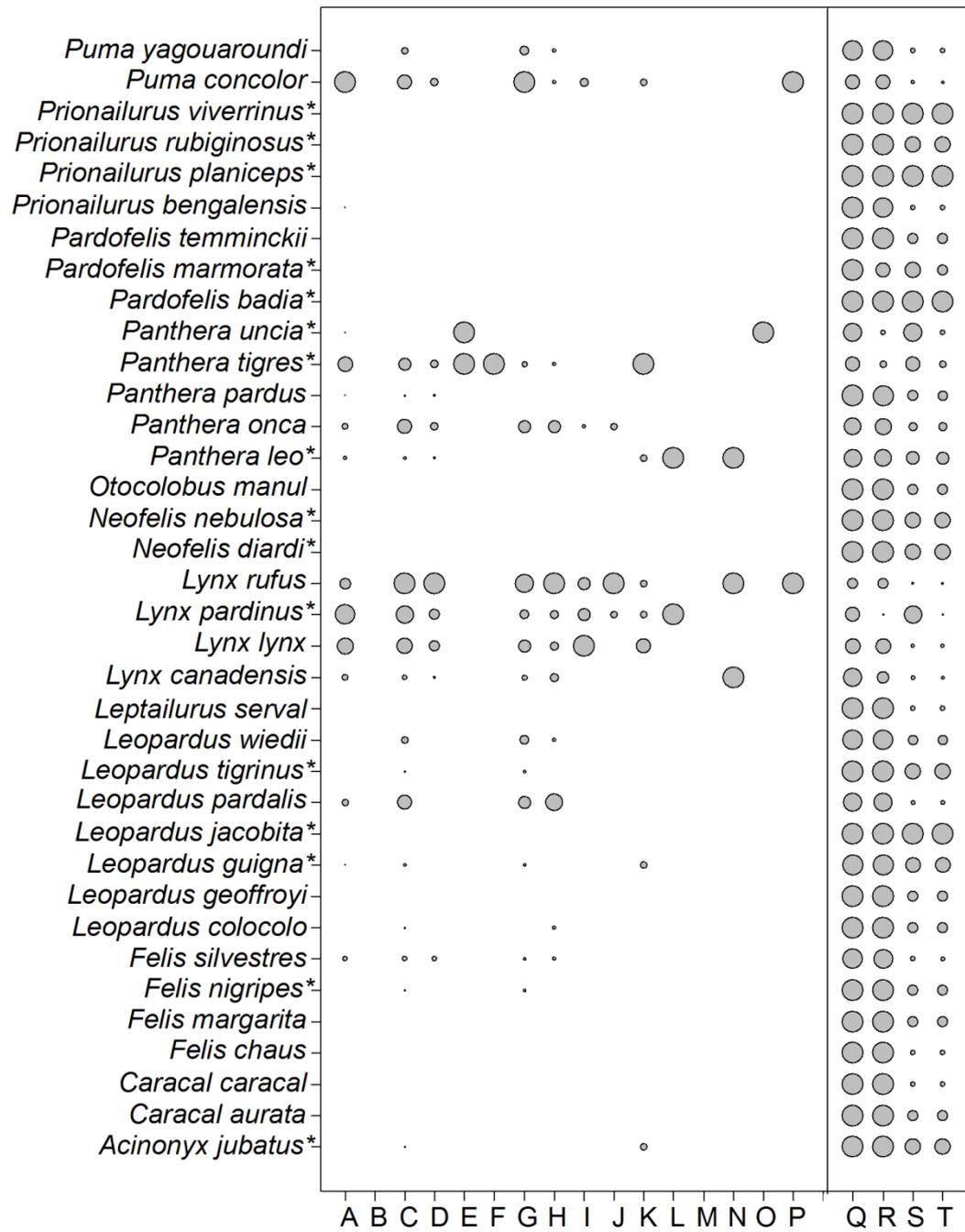
663

664 Figure 1. Proportion of published articles (N=162) classified according to the study
 665 approaches. (A) Articles that evaluate indirectly or directly the effects of habitat loss
 666 and fragmentation (HLF) on felines; those studies with a clear objective and variables
 667 focused on HLF processes or consequences were considered as direct inferences about
 668 HLF on felines. (B) Number of target species investigated in the study (focal taxa). (C)
 669 Studies which evaluate the influences of human infrastructures (roads, dams, buildings,
 670 and other physical barriers - HC) and their effects on habitat destruction (HD), and
 671 habitat loss due to climatic changes (CC) on felines. (D) Methodological approach to
 672 investigating HLF effects. (E) Inference about dispersion corridors for the conservation
 673 of felines in fragmented landscapes. “No inference”: no reference made to this issue;
 674 “Indirect inference”: mentioned the importance but did not test it; “Evaluate the
 675 importance”: made direct inferences about dispersion corridors. (F) Methods of data
 676 sampling. (G) Studies that differentiate conceptually habitat loss from habitat
 677 fragmentation. NA represents articles in which this differentiation is unnecessary
 678 because, based on its objectives, it is not relevant.



679

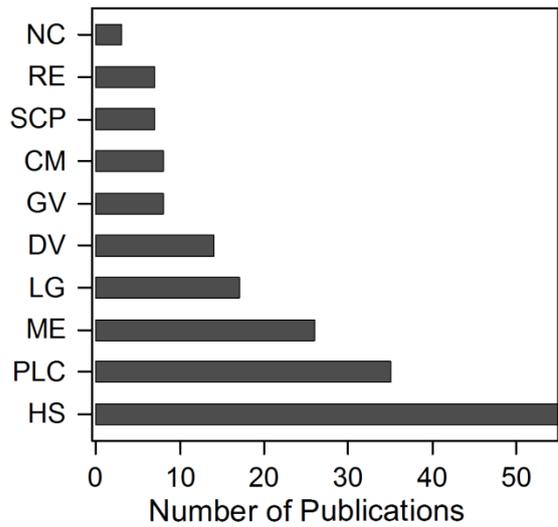
680 Figure 2. Relative growth of knowledge about HLF effects on felids over time, taking
 681 into account the increase of publications in all areas of science indexed on ISI Web of
 682 Science for the year.



683

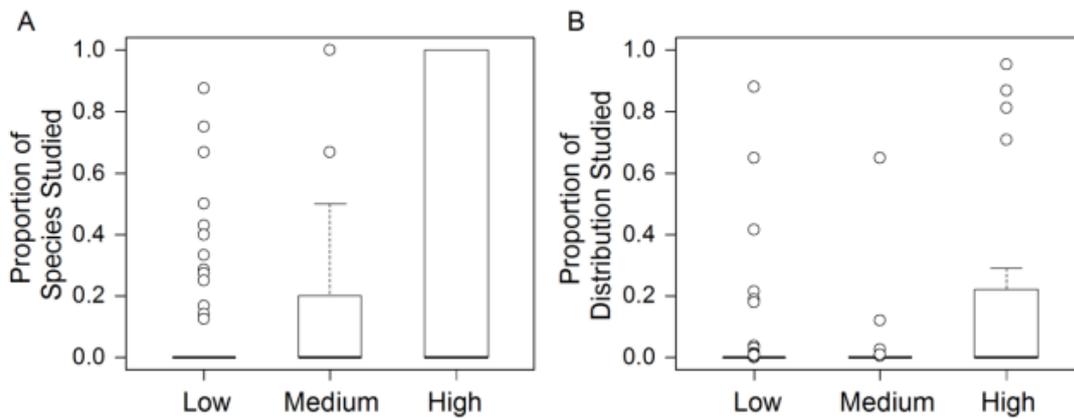
684 Figure 3. Chart of habitat loss and fragmentation (HLF) effects on felines, which depict
 685 the knowledge state of species. The knowledge of species is expressed by the number of
 686 publications that evaluate directly the effects of HLF; number of articles was linearly
 687 transformed to standardize it in each topic listed, varying from zero (without circle) to
 688 one (largest circle). The topics of knowledge considered were: (A) one feline as the
 689 target species; (B) competitive relationship between sympatric felines; (C) effects of

690 habitat destruction; (D) human infrastructures (roads, dams, buildings, and other
691 physical barriers); (E) habitat loss due to climatic change; (F) differentiation between
692 the effects of habitat loss and fragmentation; (G) habitat suitability studies; (H) patch-
693 landscape configuration; (I) movement ecology; (J) landscape genetics; (K)
694 demographic viability; (L) genetic viability; (M) time delay of response to habitat loss
695 and fragmentation; (N) conservation medicine; (O) systematic conservation plan; (P)
696 road ecology. These topics were summarized into indexes (Q-T) that express the gap of
697 knowledge (GK) concerning HLF effects, which also vary from zero (smallest circle –
698 maximum knowledge) to one (largest circle – maximum knowledge gap). (Q) Basic GK
699 index based on topics cited in Figure 3. (R) GK weighted by the proportion of range
700 distribution unstudied. (S) GK weighted by values hierarchically distributed to represent
701 threat status (Least Concern – 0.2; Near Threatened – 0.4; Vulnerable – 0.6; Endangered
702 – 0.8; Critically Endangered – 1.0). (T) GK weighted by both the proportion of range
703 distribution unstudied and threat status. *Threatened species.



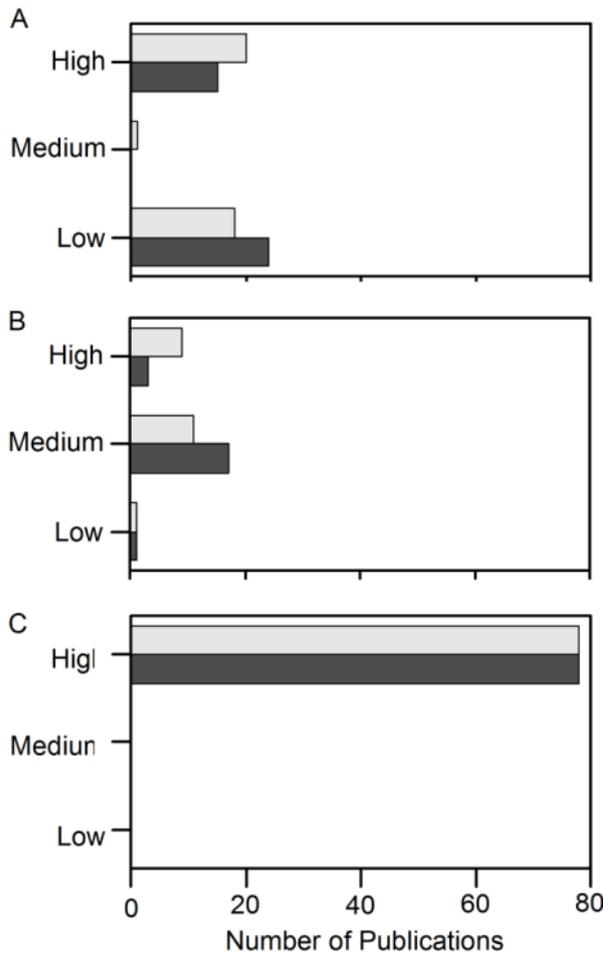
704

705 Figure 4. Number of publications in sub-disciplines considered in this study. HS –
 706 habitat suitability studies; PLC – patch-landscape configuration; ME – movement
 707 ecology; LG – landscape genetics; DV – demographic viability; GV – genetic viability;
 708 CM – conservation medicine; SCP – systematic conservation plan; RE – road ecology;
 709 and NC – non-classified.



710

711 Figure 5. Comparison of research effort between countries with low annual Gross
 712 National Income *per capita* (GNI - ≤ 10 times the income needed to live at the poverty
 713 line), medium GNI (> 10 and ≤ 30 times), and high GNI (> 30 times). The research
 714 effort of countries was represented by: (A) the proportion of felines studied, considering
 715 the national feline richness (Kruskal- Wallis test: $\chi^2 = 12.56$, $p < 0.01$; Nemenyi test for
 716 low and high classes: $p = 0.01$); and (B) the proportion of the range distribution studied
 717 (Kruskal- Wallis test: $\chi^2 = 10.98$, $p < 0.01$; Nemenyi test for low and high classes: $p =$
 718 0.04). In both cases, the countries with intermediary GNI (between 10 and 30 times) is
 719 not different from the countries with low and high GNI.



720

721 Figure 6. Economic power of the country of residence for authors that researched the
 722 effects of habitat loss and fragmentation on felines. Firstly, the papers were classified
 723 into three groups, according to the Gross National Income *per capita* (GNI) of the
 724 country in which the study area is located: GNI lower than 10 (A), between 10 and 30
 725 (B), and higher than 30 (C) times the annual income needed to live at the poverty line.
 726 The economic power of the authors was expressed by the same categories in the
 727 graphics abscissas (low, medium, and high respectively) according to the GNI of the
 728 countries in which they reside. Dark gray represents the nationality of first author and
 729 light gray represents the nationality of the author from the most developed country.

Appendix A – Search words used to investigate habitat loss and fragmentation effects on felines and publications found.

- Habitat loss and fragmentation key words: fragmentation OR “habitat fragmentation” OR “habitat loss” OR “habitat destruction” OR “habitat alteration” OR “human alteration”.
- Taxonomical groups of felines: mammal OR mammalia OR Carnivore OR felid OR feline OR Felidae
- Search string to felid studied and list of publications on habitat loss and fragmentation effects to each species.

Species	Search string	References
<i>Acinonyx jubatus</i>	“Acinonyx jubatus” OR “hunting leopard” OR cheetah	Reed, 2004
<i>Caracal aurata</i>	“Caracal aurata” OR “Profelis aurata” OR “Felis aurata” OR “African golden cat” OR “golden cat”	N/A
<i>Caracal caracal</i>	“Caracal caracal” OR “Felis caracal” OR caracal OR “African caracal” OR “Asian caracal” OR “desert lynx”	N/A
<i>Felis chaus</i>	“Felis chaus” OR “jungle cat” OR “reed cat” OR “swamp cat”	N/A

Species	Search string	References
<i>Felis margarita</i>	“Felis margarita” OR “sand cat” OR “sand dune cat”	N/A
<i>Felis nigripes</i>	“Felis nigripes” OR “black-footed cat” OR “small-spotted cat”	Blaum et al., 2007
<i>Felis silvestres</i>	“Felis silvestres” OR “wildcat”	Virgós, 2001; Virgós et al., 2002; Mata et al., 2005; Ascensão & Mira, 2006; Klar et al., 2008, 2009, 2012; Santos et al., 2008; Meinig & Boye, 2009; Say et al., 2012
<i>Leopardus colocolo</i>	“Leopardus colocolo” OR “Felis colocolo” OR “Oncifelis colocolo” OR “pampas cat” OR “Chilean pampa cat”	Carvalho et al., 2009; Medina-Vogel, 2010; Moisés Gallas & Silveira, 2011; Pereira et al., 2011
<i>Leopardus geoffroyi</i>	“Leopardus geoffroyi” OR “Oncifelis geoffroyi” OR “Felis geoffroyi” OR “geoffoy’s cat”	Canepuccia et al., 2008; Andrade-Núñez & Aide, 2010; Medina-Vogel, 2010; Moisés Gallas & Silveira, 2011; Pereira et al., 2011; Lantschner et al., 2012
<i>Leopardus guigna</i>	“Leopardus guigna” OR “Oncifelis guigna” OR “Felis guigna” OR “kodkod” OR “guiña” OR “Chilean cat”	Acosta-Jamett et al., 2003; Acosta-Jamett & Simonetti, 2004; Farias & Jaksic, 2011

Species	Search string	References
<i>Leopardus jacobita</i>	<p>“Leopardus jacobita” OR “Oreailurus jacobita” OR</p> <p>“Felis jacobita” OR “Oreailurus jacobitus” OR</p> <p>“Andean mountain cat” OR “Andean Cat” OR</p> <p>“Mountain Cat”</p>	Medina-Vogel, 2010
<i>Leopardus pardalis</i>	<p>“Leopardus pardalis” OR “Felis pardalis” OR</p> <p>“ocelot”</p>	<p>Bisbal, 1993; Estrada et al., 1994; Medellin & Equihua, 1998;</p> <p>Chiarello, 1999; Mora et al., 2000; Cuarón, 2000; Jacson et al., 2005; Dillon & Kelly, 2007; Dotta & Verdade, 2007, 2011; Janečka et al., 2008, 2007; Whiteman et al., 2007; Michalski & Peres, 2007; Lyra-Jorge et al., 2008, 2010; Cáceres et al., 2010; Sampaio et al., 2010; Thornton et al., 2010; D. H. Thornton et al., 2011</p>
<i>Leopardus tigrinus</i>	<p>“Leopardus tigrinus” OR “Felis tigrinus” OR</p> <p>“oncilla” OR “little spotted cat” OR “little tiger cat”</p> <p>OR “tiger cat”</p>	<p>Bisbal, 1993; Chiarello, 1999; Coelho et al., 2008; Moisés Gallas & Silveira, 2011; Dotta & Verdade, 2011</p>

Species	Search string	References
<i>Leopardus wiedii</i>	“Leopardus wiedii” OR margay OR “tree ocelot”	Bisbal, 1993; Estrada et al., 1994; Medellin & Equihua, 1998; Chiarello, 1999; Cuarón, 2000; Andrade-Núñez & Aide, 2010; Dotta & Verdade, 2011; D. Thornton et al., 2011; D. H. Thornton et al., 2011
<i>Leptailurus serval</i>	“Leptailurus serval” OR “Caracal serval” OR “serval”	N/A
<i>Lynx canadensis</i>	“Lynx canadensis” OR “canada lynx”	Carroll et al., 2001; Schwartz et al., 2003; Hoving et al., 2005; Koehler et al., 2008; Murray et al., 2008; Bayne et al., 2008; Dunne & Quinn, 2009
<i>Lynx lynx</i>	“Lynx lynx” OR “Felis lynx” OR “Eurasian lynx”	Schadt, Revilla, et al., 2002; Schadt, Knauer, et al., 2002; Kramer-Schadt et al., 2004, 2005, 2011; Niedziałkowska et al., 2006; Zimmermann et al., 2007; Breitenmoser et al., 2007; Hetherington et al., 2008; Meinig & Boye, 2009; Schmidt et al., 2009, 2011; Hepcan et al., 2009; Basille et al., 2009; Mortelliti et al., 2010; Huck et al., 2010

Species	Search string	References
<i>Lynx pardinus</i>	“Lynx pardinus” OR “Felis pardinus” OR “Iberian lynx” OR “lynx pardinus” OR “pardel lynx” OR “Spanish lynx”	Rodríguez & Delibes, 1992, 2002, 2003, 2004; Ferreras et al., 1992, 2001, 2004; Gaona et al., 1998; Palomares et al., 2000; Palomares, 2001; Ferreras, 2001; Fernández et al., 2003; Johnson et al., 2004; Revilla et al., 2004; Santos et al., 2008; Revilla & Wiegand, 2008; Medina-Vogel, 2010; Rodríguez et al., 2011
<i>Lynx rufus</i>	“Lynx rufus” OR “Felis rufus” OR “bobcat” OR “bay lynx”	Lomolino & Perault, 2000; Velázquez et al., 2001; Crooks, 2002; Tigas et al., 2002; Hunter et al., 2003; Riley et al., 2003, 2006; Cain et al., 2003; Hilty & Merenlender, 2004; Reed, 2004; Constible et al., 2006; Hilty et al., 2006; George & Crooks, 2006; Riley, 2006; Millions & Swanson, 2007; Preuss & Gehring, 2007; Markovchick-Nicholls et al., 2008; Tucker et al., 2008; Medina-Vogel, 2010; Roberts et al., 2010; Johnson et al., 2010; Ordeñana et al., 2010; Ruell et al., 2012;

Species	Search string	References
		Lee et al., 2012; Linde et al., 2012
<i>Neofelis diardi</i>	“Neofelis diardi” OR “Sunda clouded leopard” OR “enkuli clouded leopard” OR “Sunda islands clouded leopard” OR “Sundaland Clouded Leopard”	N/A
<i>Neofelis nebulosa</i>	“Neofelis nebulosa” OR “clouded leopard”	Laidlaw, 2000; Lau et al., 2010
<i>Otocolobus manul</i>	“Otocolobus manul” OR “Felis manul” OR “manul” OR “Pallas's Cat”	N/A
<i>Panthera leo</i>	“Panthera leo” OR “lion” OR “African Lion”	Brook et al., 2002; Björklund, 2003; Reed, 2004; Alexander et al., 2010; Singh & Gibson, 2011; Schnitzler, 2011
<i>Panthera onca</i>	“Panthera onca” OR “jaguar”	Bisbal, 1993; Medellin & Equihua, 1998; Ortega-Huerta & Medley, 1999; Chiarello, 1999; Cuarón, 2000; Whiteman et al., 2007; Michalski & Peres, 2007; McCain & Childs, 2008; Carvalho et al., 2009; Sampaio et al., 2010; Conde et al., 2010; Haag et al., 2010; Vynne et al., 2011; Colchero et al.,

Species	Search string	References
		2011; D. Thornton et al., 2011
<i>Panthera pardus</i>	“Panthera pardus” OR “Felis pardalis” OR “leopard”	Fleury & Brown, 1997; Pattanavibool & Dearden, 2002; Johnsingh & Negi, 2003; Ngoprasert et al., 2007; Lau et al., 2010; Svengren & Björklund, 2010; Trisurat et al., 2012
<i>Panthera tigris</i>	“Panthera tigris” OR “tiger”	Fleury & Brown, 1997; Wikramanayake et al., 1998; Laidlaw, 2000; Lynam et al., 2001, 2006; Kerley et al., 2002; Pattanavibool & Dearden, 2002; Kawanishi et al., 2003; Kinnaird et al., 2003; Linkie et al., 2003; O’Brien et al., 2003; Johnsingh & Negi, 2003; Reed, 2004; Carroll & Miquelle, 2006; Goodrich et al., 2008; Chauvenet et al., 2010; Lau et al., 2010; Lynam, 2010; Wibisono & Pusparini, 2010; Loucks et al., 2010; Xiaofeng et al., 2011; Tian et al., 2011; Mondal & Nagendra, 2011; Trisurat et al., 2012
<i>Panthera uncia</i>	“Panthera uncia” OR “Uncia uncia” OR “snow	Forrest et al., 2012

Species	Search string	References
	leopard”	
<i>Pardofelis badia</i>	“Pardofelis badia” OR “Felis badia” OR “Catopuma badia” OR “bay cat” OR “Bornean bay cat” OR “Bornean marbled cat” OR “Borneo bay cat”	N/A
<i>Pardofelis marmorata</i>	“Pardofelis marmorata” OR “Felis marmorata” OR “marbled cat”	Trisurat et al., 2012
<i>Pardofelis temminckii</i>	“Pardofelis temminckii” OR “Catopuma temmincki” OR “Felis temmincki” OR “Asiatic golden cat” OR “golden cat” OR “temminck's cat”	Lau et al., 2010
<i>Prionailurus bengalensis</i>	“Prionailurus bengalensis” OR “Felis bengalensis” OR “rusty-spotted cat” OR “leopard cat”	Rhim & Lee, 2007; Izawa et al., 2009; Lau et al., 2010; Trisurat et al., 2012
<i>Prionailurus planiceps</i>	“Prionailurus planiceps” OR “Felis planiceps” OR “flat-headed cat” OR “flat headed cat”	N/A
<i>Prionailurus rubiginosus</i>	Prionailurus rubiginosus	N/A

Species	Search string	References
<i>Prionailurus viverrinus</i>	“Prionailurus viverrinus” OR “Felis viverrinus” OR “fishing cat”	N/A
<i>Puma concolor</i>	“Puma concolor” OR “Felis concolor” “puma” OR “mountain lion” OR “cougar” OR “deer tiger” OR “red tiger”	Bisbal, 1993; Beier, 1993, 1995; Smallwood, 1994; Estrada et al., 1994; Fleury & Brown, 1997; Chiarello, 1999; Cuarón, 2000; Sweanor et al., 2000; Hctor et al., 2000; Velázquez et al., 2001; Buergelt et al., 2002; Dickson & Beier, 2002; Ernest et al., 2003; Hunter et al., 2003; Daily et al., 2003; Hilty & Merenlender, 2004; Dickson et al., 2005; Hilty et al., 2006; Whiteman et al., 2007; Markovchick-Nicholls et al., 2008; Lyra-Jorge et al., 2008, 2010; Land et al., 2008; Morrison & Boyce, 2009; Medina-Vogel, 2010; Cáceres et al., 2010; Sampaio et al., 2010; Burdett et al., 2010; Mazzolli, 2010; Ordeñana et al., 2010; Vynne et al., 2011; Castilho et al., 2011; Dotta & Verdade, 2011; Schwab & Zandbergen, 2011;

Species	Search string	References
<i>Puma yagouarondi</i>	“Puma yagouarondi” OR “Herpailurus yaguarondi” OR “Herpailurus yagouarondi” OR “jaguarundi”	Loxterman, 2011; D. Thornton et al., 2011; Miotto et al., 2011; Lantschner et al., 2012 Bisbal, 1993; Estrada et al., 1994; Medellin & Equihua, 1998; Chiarello, 1999; Cuarón, 2000; Daily et al., 2003; Sampaio et al., 2010; Moisés Gallas & Silveira, 2011; Dotta & Verdade, 2011; Pereira et al., 2011; D. Thornton et al., 2011; D. H. Thornton et al., 2011

References

- ACOSTA-JAMETT, G. & SIMONETTI, J.A. (2004) Habitat use by *Oncifelis guigna* and *Pseudalopex culpaeus* in a fragmented forest landscape in central Chile. *Biodiversity and Conservation*, 13, 1135–1151.
- ACOSTA-JAMETT, G., SIMONETTI, J.A., BUSTAMANTE, R.O. & DUNSTONE, N. (2003) Metapopulation approach to assess survival of *Oncifelis guigna* in fragmented forest of Central Chile: A theoretical model. *Matozoologia Neotropical*, 10, 217–229.
- ALEXANDER, K.A., MCNUTT, J.W., BRIGGS, M.B., STANDERS, P.E., FUNSTON, P., HEMSON, G., ET AL. (2010) Multi-host pathogens and carnivore management in southern Africa. *Comparative Immunology, Microbiology and Infectious Diseases*, 33, 249–265. Elsevier Ltd.
- ANDRADE-NÚÑEZ, M.J. & AIDE, T.M. (2010) Effects of habitat and landscape characteristics on medium and large mammal species richness and composition in northern Uruguay. *Zoologia*, 27, 909–917.
- ASCENSÃO, F. & MIRA, A. (2006) Factors affecting culvert use by vertebrates along two stretches of road in southern Portugal. *Ecological Research*, 22, 57–66.
- BASILLE, M., HERFINDAL, I., SANTIN-JANIN, H., LINNELL, J.D.C., ODDEN, J., ANDERSEN, R., ET AL. (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography*, 32, 683–691.
- BAYNE, E.M., BOUTIN, S. & MOSES, R.A. (2008) Ecological factors influencing the spatial pattern of Canada lynx relative to its southern range edge in Alberta, Canada. *Canadian Journal of Zoology*, 86, 1189–1197.
- BEIER, P. (1993) Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology*, 7, 94–108. Wiley Online Library.

- BEIER, P. (1995) Dispersal of juvenile cougars in fragmented habitat. *The Journal of Wildlife Management*, 59, 228–237.
- BISBAL, F.J. (1993) Human impact on the carnivores of Venezuela. *Studies on Neotropical Fauna and Environment*, 28, 145–156.
- BJÖRKLUND, M. (2003) The risk of inbreeding due to habitat loss in the lion (*Panthera leo*). *Conservation Genetics*, 4, 515–523.
- BLAUM, N., ROSSMANITH, E., POPP, A. & JELTSCH, F. (2007) Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecologica*, 31, 86–92.
- BREITENMOSER, U., BREITENMOSER-WÜRSTEN, C., CAPT, S., MOLINARI-JOBIN, A., MOLINARI, P. & ZIMMERMANN, F. (2007) Conservation of the lynx *Lynx lynx* in the Swiss Jura Mountains. *Wildlife Biology*, 13, 340–355.
- BROOK, B.W., TONKYN, D.W., O'GRADY, J.J. & FRANKHAM, R. (2002) Contribution of inbreeding to extinction risk in threatened species. *Conservation Ecology*, 6.
- BUERGELT, C.D., HOMER, B.L. & SPALDING, M.G. (2002) Causes of mortality in the Florida Panther. *Annals of New York Academy of Sciences*, 969, 350–353.
- BURDETT, C.L., CROOKS, K.R., THEOBALD, D.M., WILSON, K.R., BOYDSTON, E.E., LYREN, L.M., ET AL. (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. *Ecosphere*, 1, 1–21.
- CÁCERES, N.C., NÁPOLI, R.P., CASELLA, J. & HANNIBAL, W. (2010) Mammals in a fragmented savannah landscape in south-western Brazil. *Journal of Natural History*, 44, 491–512.
- CAIN, A., TUOVILA, V., HEWITT, D. & TEWES, M. (2003) Effects of a highway and mitigation projects on bobcats in Southern Texas. *Biological Conservation*, 114, 189–197.

- CANEPUCCIA, A.D., FARIAS, A.A., ESCALANTE, A.H., IRIBARNE, O., NOVARO, A. & ISACCH, J.P. (2008) Differential responses of marsh predators to rainfall-induced habitat loss and subsequent variations in prey availability. *Canadian Journal of Zoology*, 86, 407–418.
- CARROLL, C. & MIQUELLE, D.G. (2006) Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: The role of protected areas and landscape matrix in population persistence. *Journal of Applied Ecology*, 43, 1056–1068.
- CARROLL, C., NOSS, R.F. & PAQUET, P.C. (2001) Carnivores as focal species for conservation planning in Rocky Mountain region. *Ecological Applications*, 11, 961–980.
- CARVALHO, F.M.V., DE MARCO, P. & FERREIRA, L.G. (2009) The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil. *Biological Conservation*, 142, 1392–1403. Elsevier Ltd.
- CASTILHO, C.S., MARINS-SA, L.G., BENEDET, R.C. & FREITAS, T.O. (2011) Landscape genetics of mountain lions (*Puma concolor*) in southern Brazil. *Mammalian Biology*, 76, 476–483.
- CHAUVENET, A.L.M., BAXTER, P.W.J., McDONALD-MADDEN, E. & POSSINGHAM, H.P. (2010) Optimal allocation of conservation effort among subpopulations of a threatened species: How important is patch quality? *Ecological Applications*, 20, 789–797.
- CHIARELLO, A. (1999) Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation*, 89, 71–82.

- COELHO, I.P., KINDEL, A. & COELHO, A.V.P. (2008) Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. *European Journal of Wildlife Research*, 54, 689–699.
- COLCHERO, F., CONDE, D.A., MANTEROLA, C., CHÁVEZ, C., RIVERA, A. & CEBALLOS, G. (2011) Jaguars on the move: Modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. *Animal Conservation*, 14, 158–166.
- CONDE, D.A., COLCHERO, F., ZARZA, H., CHRISTENSEN, N.L., SEXTON, J.O., MANTEROLA, C., ET AL. (2010) Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, 143, 1980–1988. Elsevier Ltd.
- CONSTIBLE, J.M., CHAMBERLAIN, M.J. & LEOPOLD, B.D. (2006) Relationships between landscape pattern and space use of three mammalian carnivores in Central Mississippi. *The American Midland Naturalist*, 155, 352–362.
- CROOKS, K.R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16, 488–502.
- CUARÓN, A. (2000) Effects of land-cover changes on mammals in a neotropical region: A modeling approach. *Conservation Biology*, 14, 1676–1692.
- DAILY, G.C., CEBALLOS, G., PACHECO, J., SUZÁN, G. & SÁNCHEZ-AZOFEIFA, A. (2003) Countryside biogeography of Neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology*, 17, 1814–1826.
- DICKSON, B.G. & BEIER, P. (2002) Home-range and habitat selection by adult cougars in Southern California. *The Journal of Wildlife Management*, 66, 1235.
- DICKSON, B.G., JENNESS, J.S. & BEIER, P. (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management*, 69, 264–276.

- DILLON, A. & KELLY, M.J. (2007) Ocelot *Leopardus pardalis* in Belize: The impact of trap spacing and distance moved on density estimates. *Oryx*, 41, 1–9.
- DOTTA, G. & VERDADE, L.M. (2007) Trophic categories in a mammal assemblage: Diversity in an agricultural landscape. *Biota Neotropica*, 7, 287–292.
- DOTTA, G. & VERDADE, L.M. (2011) Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil. *Mammalia*, 75, 345–352.
- DUNNE, B.M. & QUINN, M.S. (2009) Effectiveness of above-ground pipeline mitigation for moose (*Alces alces*) and other large mammals. *Biological Conservation*, 142, 332–343. Elsevier Ltd.
- ERNEST, H., BOYCE, W., BLEICH, V., MAY, B., STIVER, S.J. & TORRES, S.G. (2003) Genetic structure of mountain lion (*Puma concolor*) populations in California. *Conservation Genetics*, 4, 353–366.
- ESTRADA, A., COATES-ESTRADA, R. & MERITT, D. (1994) Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography*, 17, 229–241.
- FARIAS, A.A. & JAKSIC, F.M. (2011) Low functional richness and redundancy of a predator assemblage in native forest fragments of Chiloe island, Chile. *The Journal of Animal Ecology*, 80, 809–817.
- FERNÁNDEZ, N., DELIBES, M., PALOMARES, F. & MLADENOFF, D.J. (2003) Identifying breeding habitat for the iberian lynx: Inferences from a fine-scale spatial analysis. *Ecological Applications*, 13, 1310–1324.
- FERRERAS, P. (2001) Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation*, 100, 125–136.

- FERRERAS, P., ALDAMA, J.J., BELTRÁN, J.F. & DELIBES, M. (1992) Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck, 1824. *Biological Conservation*, 61, 197–202.
- FERRERAS, P., DELIBES, M., PALOMARES, F., FEDRIANI, J.M., CALZADA, J. & REVILLA, E. (2004) Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behavioral Ecology*, 15, 31–40.
- FERRERAS, P., GAONA, P., PALOMARES, F. & DELIBES, M. (2001) Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx. *Animal Conservation*, 4, 265–274.
- FLEURY, A.M. & BROWN, R.D. (1997) A framework for the design of wildlife conservation corridors with specific application to southwestern Ontario. *Landscape and Urban Planning*, 37, 163–186.
- FORREST, J.L., WIKRAMANAYAKE, E., SHRESTHA, R., AREENDRAN, G., GYELTSHEN, K., MAHESHWARI, A., ET AL. (2012) Conservation and climate change: Assessing the vulnerability of snow leopard habitat to treeline shift in the Himalaya. *Biological Conservation*, 150, 129–135.
- GAONA, P., FERRERAS, P. & DELIBES, M. (1998) Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs*, 68, 349–370.
- GEORGE, S.L. & CROOKS, K.R. (2006) Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, 133, 107–117.
- GOODRICH, J.M., KERLEY, L.L., SMIRNOV, E.N., MIQUELLE, D.G., McDONALD, L., QUIGLEY, H.B., ET AL. (2008) Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *Journal of Zoology*, 276, 323–329.

- HAAG, T., SANTOS, A.S., SANA, D.A., MORATO, R.G., CULLEN, L., CRAWSHAW, P.G., ET AL. (2010) The effect of habitat fragmentation on the genetic structure of a top predator: Loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (*Panthera onca*). *Molecular Ecology*, 19, 4906–4921.
- HEPCAN, Ş., HEPCAN, Ç.C., BOUWMA, I.M., JONGMAN, R.H.G. & ÖZKAN, M.B. (2009) Ecological networks as a new approach for nature conservation in Turkey: A case study of İzmir Province. *Landscape and Urban Planning*, 90, 143–154.
- HETHERINGTON, D.A., MILLER, D.R., MACLEOD, C.D. & GORMAN, M.A.L. (2008) A potential habitat network for the Eurasian lynx *Lynx lynx* in Scotland. *Mammal Review*, 38, 285–303.
- HILTY, J.A., BROOKS, C., HEATON, E. & MERENLENDER, A.M. (2006) Forecasting the effect of land-use change on native and non-native mammalian predator distributions. *Biodiversity and Conservation*, 15, 2853–2871.
- HILTY, J.A. & MERENLENDER, A.M. (2004) Use of riparian corridors and vineyards by mammalian predators in Northern California. *Conservation Biology*, 18, 126–135.
- HOCTOR, T.S., CARR, M.H. & ZWICK, P.D. (2000) Identifying a linked reserve system using a regional landscape approach: The Florida ecological network. *Conservation Biology*, 14, 984–1000.
- HOVING, C.L., HARRISON, D.J., KROHN, W.B., JOSEPH, R.A. & O'BRIEN, M. (2005) Broad-scale predictors of Canada lynx in Eastern North America. *Journal of Wildlife Management*, 69, 739–751.
- HUCK, M., JĘDRZEJEWSKI, W., BOROWIK, T., MIŁOSZ-CIELMA, M., SCHMIDT, K., JĘDRZEJEWSKA, B., ET AL. (2010) Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. *Acta Theriologica*, 55, 177–192.

- HUNTER, R.D., FISHER, R.F. & CROOKS, K.R. (2003) Landscape-level connectivity in coastal southern California, USA, as assessed through carnivore habitat suitability. *Natural Areas Journal*, 23, 302–314.
- IZAWA, M., DOI, T., NAKANISHI, N. & TERANISHI, A. (2009) Ecology and conservation of two endangered subspecies of the leopard cat (*Prionailurus bengalensis*) on Japanese islands. *Biological Conservation*, 142, 1884–1890. Elsevier Ltd.
- JACSON, V.L., LAACK, L.L. & ZIMMERMAN, E.G. (2005) Landscape metrics associated with habitat use by ocelots in South Texas. *Journal of Wildlife Management*, 69, 733–738.
- JANEČKA, J.E., TEWES, M.E., LAACK, L.L., GRASSMAN, L.I., HAINES, A.M. & HONEYCUTT, R.L. (2008) Small effective population sizes of two remnant ocelot populations (*Leopardus pardalis albescens*) in the United States. *Conservation Genetics*, 9, 869–878.
- JANEČKA, J.E., WALKER, C.W., TEWES, M.E., CASO, A., LAACKAND, L.L. & HONEYCUTT, R.L. (2007) Phylogenetic relationships of ocelot (*Leopardus pardalis albescens*) populations from the tamaulipan biotic province and implications for recovery. *The Southwestern Naturalist*, 52, 89–96.
- JOHNSINGH, A.J.T. & NEGI, A.S. (2003) Status of tiger and leopard in Rajaji–Corbett Conservation Unit, northern India. *Biological Conservation*, 111, 385–393.
- JOHNSON, S.A., WALKER, H.D. & HUDSON, C.M. (2010) Dispersal characteristics of juvenile bobcats in South-Central Indiana. *Journal of Wildlife Management*, 74, 379–385.
- JOHNSON, W.E., GODOY, J.A., PALOMARES, F., DELIBES, M., REVILLA, E. & O'BRIEN, S.J. (2004) Phylogenetic and phylogeographic analysis of Iberian lynx populations. *Journal of Heredity*, 95, 19–28.

- KAWANISHI, K., HAWA, Y.S., KADIR, A.H.A. & RAHMAT., T. (2003) Distribution and potential population size of the tiger in Peninsular Malaysia. *Journal of Wildlife and Parks*, 21, 29–50.
- KERLEY, L.L., GOODRICH, J.M., MIQUELLE, D.G., SMIRNOV, E.N., QUIGLEY, H.B. & HORNOCKER, M.G. (2002) Effects of roads and human disturbance on amur tigers. *Conservation Biology*, 16, 97–108.
- KINNAIRD, M.F., SANDERSON, E.W., O'BRIEN, T.G., WIBISONO, H.T. & WOOLMER, G. (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, 17, 245–257.
- KLAR, N., FERNÁNDEZ, N., KRAMER-SCHADT, S., HERRMANN, M., TRINZEN, M., BÜTTNER, I. & NIEMITZ, C. (2008) Habitat selection models for European wildcat conservation. *Biological Conservation*, 141, 308–319.
- KLAR, N., HERRMANN, M., HENNING-HAHN, M., POTT-DÖRFER, B., HOFER, H. & KRAMER-SCHADT, S. (2012) Between ecological theory and planning practice: (Re) Connecting forest patches for the wildcat in Lower Saxony, Germany. *Landscape and Urban Planning*, 105, 376–384.
- KLAR, N., HERRMANN, M. & KRAMER-SCHADT, S. (2009) Effects and mitigation of road impacts on individual movement behavior of wildcats. *Journal of Wildlife Management*, 73, 631–638.
- KOEHLER, G., MALETZKE, B.T., KIENAST, J.A. VON, AUBRY, K.B., WIELGUS, R.B. & NANEY, R.H. (2008) Habitat fragmentation and the persistence of lynx populations in Washington State. *The Journal of Wildlife Management*, 72, 1518–1524.
- KRAMER-SCHADT, S., KAISER, T., FRANK, K. & WIEGAND, T. (2011) Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. *Landscape Ecology*, 26, 501–513.

- KRAMER-SCHADT, S., REVILLA, E. & WIEGAND, T. (2005) Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? *Biological Conservation*, 125, 169–182.
- KRAMER-SCHADT, S., REVILLA, E., WIEGAND, T. & BREITENMOSER, U. (2004) Fragmented landscapes, road mortality and patch connectivity: Modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, 41, 711–723.
- LADLAW, R.K. (2000) Effects of habitat disturbance and protected areas on mammals of Peninsular Malaysia. *Conservation Biology*, 14, 1639–1648.
- LAND, E.D., SHINDLE, D.B., KAWULA, R.J., BENSON, J.F., LOTZ, M.A. & ONORATO, D.P. (2008) Florida panther habitat selection analysis of concurrent GPS and VHF telemetry data. *Journal of Wildlife Management*, 72, 633–639.
- LANTSCHNER, M.V., RUSCH, V. & HAYES, J.P. (2012) Habitat use by carnivores at different spatial scales in a plantation forest landscape in Patagonia, Argentina. *Forest Ecology and Management*, 269, 271–278.
- LAU, M.W.-N., FELLOWES, J.R. & CHAN, B.P.L. (2010) Carnivores (Mammalia: Carnivora) in South China: A status review with notes on the commercial trade. *Mammal Review*, 40, 247–292.
- LEE, J.S., RUELL, E.W., BOYDSTON, E.E., LYREN, L.M., ALONSO, R.S., TROYER, J.L., ET AL. (2012) Gene flow and pathogen transmission among bobcats (*Lynx rufus*) in a fragmented urban landscape. *Molecular ecology*, 21, 1617–1631.
- LINDE, S.A., ROBERTS, S.D., GOSSELINK, T.E. & CLARK, W.R. (2012) Habitat modeling used to predict relative abundance of bobcats in Iowa. *The Journal of Wildlife Management*, 76, 534–543.

- LINKIE, M., MARTYR, D.J., HOLDEN, J., YANUAR, A., HARTANA, A.T., SUGARDJITO, J. & LEADER-WILLIAMS, N. (2003) Habitat destruction and poaching threaten the Sumatran tiger in Kerinci Seblat National Park, Sumatra. *Oryx*, 37, 41–48.
- LOMOLINO, M. V. & PERAULT, D.R. (2000) Assembly and disassembly of mammal communities in a fragmented temperate rain forest. *Ecology*, 81, 1517–1532.
- LOUCKS, C., BARBER-MEYER, S., HOSSAIN, M.A.A., BARLOW, A. & CHOWDHURY, R.M. (2010) Sea level rise and tigers: Predicted impacts to Bangladesh's Sundarbans mangroves. *Climatic Change*, 98, 291–298.
- LOXTERMAN, J.L. (2011) Fine scale population genetic structure of pumas in the Intermountain West. *Conservation Genetics*, 12, 1049–1059.
- LYNAM, A.J. (2010) Securing a future for wild Indochinese tigers: Transforming tiger vacuums into tiger source sites. *Integrative Zoology*, 5, 324–334.
- LYNAM, A.J., KHAING, S.T. & ZAW, K.M. (2006) Developing a national tiger action plan for The Union of Myanmar. *Environmental Management*, 37, 30–39.
- LYNAM, A.J., KREETIYUTANONT, K. & MATHER, R. (2001) Conservation status and distribution of the Indochinese tiger (*Panthera tigris corbetti*) and other large mammals in a forest complex in Northeastern Thailand. *Natural History Bulletin of the Siam Society*, 49, 61–75.
- LYRA-JORGE, M.C., CIOCHETI, G. & PIVELLO, V.R. (2008) Carnivore mammals in a fragmented landscape in northeast of São Paulo State, Brazil. *Biodiversity and Conservation*, 17, 1573–1580.
- LYRA-JORGE, M.C., RIBEIRO, M.C., CIOCHETI, G., TAMBOSI, L.R. & PIVELLO, V.R. (2010) Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. *European Journal of Wildlife Research*, 56, 359–368.

- MARKOVCHICK-NICHOLLS, L., REGAN, H.M., DEUTSCHMAN, D.H., WIDYANATA, A., MARTIN, B., NOREKE, L. & HUNT, T.A. (2008) Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conservation Biology*, 22, 99–109.
- MATA, C., HERVÁS, I., HERRANZ, J., SUÁREZ, F. & MALO, J.E. (2005) Complementary use by vertebrates of crossing structures along a fenced Spanish motorway. *Biological Conservation*, 124, 397–405.
- MAZZOLLI, M. (2010) Mosaics of exotic forest plantations and native forests as habitat of pumas. *Environmental Management*, 46, 237–253.
- MCCAIN, E.B. & CHILDS, J.L. (2008) Evidence of resident jaguars (*Panthera onca*) in the southwestern United States and the implications for conservation. *Journal of Mammalogy*, 89, 1–10.
- MEDELLIN, R.A. & EQUIHUA, M. (1998) Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. *Journal of Applied Ecology*, 35, 13–23.
- MEDINA-VOGEL, G. (2010) Ecology of emerging infectious diseases and wild species conservation. *Archivos de Medicina Veterinaria*, 42, 11–24.
- MEINIG, H.U. & BOYE, P. (2009) A review of negative impact factors threatening mammal populations in Germany. *Folia Zoologica*, 58, 279–290.
- MICHALSKI, F. & PERES, C.A. (2007) Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. *Conservation Biology*, 21, 1626–1640.
- MILLIONS, D.G. & SWANSON, B.J. (2007) Impact of natural and artificial barriers to dispersal on the population structure of bobcats. *Journal of Wildlife Management*, 71, 96–102.

- MIOTTO, R.A., CERVINI, M., FIGUEIREDO, M.G., BEGOTTI, R.A. & GALETTI, P.M. (2011) Genetic diversity and population structure of pumas (*Puma concolor*) in southeastern Brazil: implications for conservation in a human-dominated landscape. *Conservation Genetics*, 12, 1447–1455.
- MOISÉS GALLAS & SILVEIRA, E.F. DA (2011) *Mesocestoides* sp. (Eucestoda, Mesocestoididae) parasitizing four species of wild felines in Southern Brazil. *Revista Brasileira de Parasitologia Veterinaria de Jaboticabal*, 20, 168–170.
- MONDAL, P. & NAGENDRA, H. (2011) Trends of forest dynamics in tiger landscapes across Asia. *Environmental Management*, 48, 781–794.
- MORA, M., LAACK, L., LEE, M.C., SERICANO, J., PRESLEY, R., GARDINALI, P.R., ET AL. (2000) Environmental contaminants in blood, hair, and tissues of ocelots from the lower Rio Grande Valley, Texas, 1986–1997. *Environmental Monitoring and Assessment*, 64, 477–492.
- MORRISON, S.A. & BOYCE, W.M. (2009) Conserving connectivity: Some lessons from mountain lions in southern California. *Conservation Biology*, 23, 275–285.
- MORTELLITI, A., AMORI, G., CAPIZZI, D., RONDININI, C. & BOITANI, L. (2010) Experimental design and taxonomic scope of fragmentation studies on European mammals: Current status and future priorities. *Mammal Review*, 40, 125–154.
- MURRAY, D.L., STEURY, T.D. & ROTH, J.D. (2008) Assessment of Canada lynx research and conservation needs in the Southern range: Another kick at the cat. *Journal of Wildlife Management*, 72, 1463–1472.
- NGOPRASERT, D., LYNAM, A.J. & GALE, G. A. (2007) Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx*, 41, 343–351.

- NIEDZIAŁKOWSKA, M., JĘDRZEJEWSKI, W., MYŚLAJEK, R.W., NOWAK, S.,
JĘDRZEJEWSKA, B. & SCHMIDT, K. (2006) Environmental correlates of Eurasian lynx occurrence in Poland – Large scale census and GIS mapping. *Biological Conservation*, 133, 63–69.
- O'BRIEN, T.G., KINNAIRD, M.F. & WIBISONO, H.T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.
- ORDEÑANA, M.A., CROOKS, K.R., BOYDSTON, E.E., FISHER, R.N., LYREN, L.M., SIUDYLA, S., ET AL. (2010) Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy*, 91, 1322–1331.
- ORTEGA-HUERTA, M.A. & MEDLEY, K.E. (1999) Landscape analysis of jaguar (*Panthera onca*) habitat using sighting records in the Sierra de Tamaulipas, Mexico. *Environmental Conservation*, 26, 257–269.
- PALOMARES, F. (2001) Vegetation structure and prey abundance requirements of the Iberian lynx: Implications for the design of reserves and corridors. *Journal of Applied Ecology*, 38, 9–18.
- PALOMARES, F., DELIBES, M., FERRERAS, P., FEDRIANI, J.M., CALZADA, J. & REVILLA, E. (2000) Iberian lynx in a fragmented landscape: Predispersal, dispersal, and postdispersal habitats. *Conservation Biology*, 14, 809–818.
- PATTANAVIBOOL, A. & DEARDEN, P. (2002) Fragmentation and wildlife in montane evergreen forests, northern Thailand. *Biological Conservation*, 107, 155–164.
- PEREIRA, J.A., DI BITETTI, M.S., FRACASSI, N.G., PAVIOLO, A., DE ANGELO, C.D., DI BLANCO, Y.E. & NOVARO, A.J. (2011) Population density of Geoffroy's cat in scrublands of central Argentina. *Journal of Zoology*, 283, 37–44.

- PREUSS, T.S. & GEHRING, T.M. (2007) Landscape analysis of bobcat habitat in the Northern lower Peninsula of Michigan. *Journal of Wildlife Management*, 71, 2699–2706.
- REED, D.H. (2004) Extinction risk in fragmented habitats. *Animal Conservation*, 7, 181–191.
- REVILLA, E. & WIEGAND, T. (2008) Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19120–19125.
- REVILLA, E., WIEGAND, T., PALOMARES, F., FERRERAS, P. & DELIBES, M. (2004) Effects of matrix heterogeneity on animal dispersal: From individual behavior to metapopulation-level parameters. *The American Naturalist*, 164, E130–E153.
- RHIM, S.-J. & LEE, W.-S. (2007) Influence of forest fragmentation on the winter abundance of mammals in Mt. Chirisan National Park, South Korea. *Journal of Wildlife Management*, 71, 1404–1408.
- RILEY, S.P.D. (2006) Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *Journal of Wildlife Management*, 70, 1425–1435.
- RILEY, S.P.D., POLLINGER, J.P., SAUVAJOT, R.M., YORK, E.C., BROMLEY, C., FULLER, T.K. & WAYNE, R.K. (2006) A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular ecology*, 15, 1733–1741.
- RILEY, S.P.D., SAUVAJOT, R.M., FULLER, T.K., YORK, E.C., KAMRADT, D.A., BROMLEY, C. & WAYNE, R.K. (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in Southern California. *Conservation Biology*, 17, 566–576.

- ROBERTS, S.B., JORDAN, J.D., BETTINGER, P. & WARREN, R.J. (2010) Using bobcat habitat suitability to prioritize habitat preservation on a suburbanizing barrier island. *Journal of Wildlife Management*, 74, 386–394.
- RODRÍGUEZ, A. & DELIBES, M. (1992) Current range and status of the Iberian lynx *Felis pardina* Temminck, 1824 in Spain. *Biological Conservation*, 61, 189–196.
- RODRÍGUEZ, A. & DELIBES, M. (2002) Internal structure and patterns of contraction in the geographic range of the Iberian lynx. *Ecography*, 25, 314–328.
- RODRÍGUEZ, A. & DELIBES, M. (2003) Population fragmentation and extinction in the Iberian lynx. *Biological Conservation*, 109, 321–331.
- RODRÍGUEZ, A. & DELIBES, M. (2004) Patterns and causes of non-natural mortality in the Iberian lynx during a 40-year period of range contraction. *Biological Conservation*, 118, 151–161.
- RODRÍGUEZ, R., RAMÍREZ, O., VALDIOSERA, C.E., GARCÍA, N., ALDA, F., MADURELL-MALAPEIRA, J., ET AL. (2011) 50,000 years of genetic uniformity in the critically endangered Iberian lynx. *Molecular Ecology*, 20, 3785–3795.
- RUELL, A.E.W., RILEY, S.P.D., DOUGLAS, M.R., ANTOLIN, M.F., POLLINGER, J.R., TRACEY, J.A., ET AL. (2012) Urban habitat fragmentation and genetic population structure of bobcats in coastal Southern California. *The American Midland Naturalist*, 168, 265–280.
- SAMPAIO, R., LIMA, A.P., MAGNUSSON, W.E. & PERES, C.A. (2010) Long-term persistence of midsized to large-bodied mammals in Amazonian landscapes under varying contexts of forest cover. *Biodiversity and Conservation*, 19, 2421–2439.
- SANTOS, M.J., PEDROSO, N.M., FERREIRA, J.P., MATOS, H.M., SALES-LUÍS, T., PEREIRA, I., ET AL. (2008) Assessing dam implementation impact on threatened carnivores:

- The case of Alqueva in SE Portugal. *Environmental monitoring and assessment*, 142, 47–64.
- SAY, L., DEVILLARD, S., LÉGER, F., PONTIER, D. & RUETTE, S. (2012) Distribution and spatial genetic structure of European wildcat in France. *Animal Conservation*, 15, 18–27.
- SCHADT, S., KNAUER, F., KACZENSKY, P., REVILLA, E., WIEGAND, T. & TREPL, L. (2002) Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological Applications*, 12, 1469–1483.
- SCHADT, S., REVILLA, E., WIEGAND, T., KNAUER, F., KACZENSKY, P., BREITENMOSER, U., ET AL. (2002) Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology*, 39, 189–203.
- SCHMIDT, K., KOWALCZYK, R., OZOLINS, J., MÄNNIL, P. & FICKEL, J. (2009) Genetic structure of the Eurasian lynx population in north-eastern Poland and the Baltic states. *Conservation Genetics*, 10, 497–501.
- SCHMIDT, K., RATKIEWICZ, M. & KONOPÍNSKI, M.K. (2011) The importance of genetic variability and population differentiation in the Eurasian lynx *Lynx lynx* for conservation, in the context of habitat and climate change. *Mammal Review*, 41, 112–124.
- SCHNITZLER, A.E. (2011) Past and present distribution of the North African-Asian lion subgroup: a review. *Mammal Review*, 41, 220–243.
- SCHWAB, A.C. & ZANDBERGEN, P.A. (2011) Vehicle-related mortality and road crossing behavior of the Florida panther. *Applied Geography*, 31, 859–870. Elsevier Ltd.
- SCHWARTZ, M.K., MILLS, L.S., ORTEGA, Y., RUGGIERO, L.F. & ALLENDORF, F.W. (2003) Landscape location affects genetic variation of Canada lynx (*Lynx canadensis*). *Molecular Ecology*, 12, 1807–1816.

- SINGH, H.S. & GIBSON, L. (2011) A conservation success story in the otherwise dire megafauna extinction crisis: The Asiatic lion (*Panthera leo persica*) of Gir forest. *Biological Conservation*, 144, 1753–1757. Elsevier Ltd.
- SMALLWOOD, K.S. (1994) Trends in California mountain lion populations. *The Southwestern Naturalist*, 39, 67.
- SVENNGREN, H. & BJÖRKLUND, M. (2010) An assessment of the density of a large carnivore using a non-invasive method adapted for pilot studies. *South African Journal of Wildlife Research*, 40, 121–129.
- SWEANOR, L.L., LOGAN, K.A. & HORNOCKER, M.G. (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology*, 14, 798–808.
- THORNTON, D., BRANCH, L. & SUNQUIST, M. (2011) Passive sampling effects and landscape location alter associations between species traits and response to fragmentation. *Ecological Applications*, 21, 817–829.
- THORNTON, D.H., BRANCH, L.C. & SUNQUIST, M.E. (2010) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology*, 26, 7–18.
- THORNTON, D.H., BRANCH, L.C. & SUNQUIST, M.E. (2011) The relative influence of habitat loss and fragmentation: Do tropical mammals meet the temperate paradigm? *Ecological Applications*, 21, 2324–2333.
- TIAN, Y., WU, J., SMITH, A.T., WANG, T., KOU, X. & GE, J. (2011) Population viability of the Siberian Tiger in a changing landscape: Going, going and gone? *Ecological Modelling*, 222, 3166–3180. Elsevier B.V.
- TIGAS, L.A., VAN VUREN, D.H. & SAUVAJOT, R.M. (2002) Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation*, 108, 299–306.

- TRISURAT, Y., BHUMPAKPHAN, N., REED, D.H. & KANCHANASAKA, B. (2012) Using species distribution modeling to set management priorities for mammals in northern Thailand. *Journal for Nature Conservation*, 20, 264–273.
- TUCKER, S.A., CLARK, W.R. & GOSSELINK, T.E. (2008) Space use and habitat selection by bobcats in the fragmented landscape of South-Central Iowa. *Journal of Wildlife Management*, 72, 1114–1124.
- VELÁZQUEZ, A., ROMERO, F., RANGEL-CORDERO, H. & HEIL, G.W. (2001) Effects of landscape changes on mammalian assemblages at Izta-Popo Volcanoes, Mexico. *Biodiversity and Conservation*, 10, 1059–1075.
- VIRGÓS, E. (2001) Relative value of riparian woodlands in landscapes with different forest cover for medium-sized Iberian carnivores. *Biodiversity and Conservation*, 10, 1039–1049.
- VIRGÓS, E., TELLERÍA, J.L. & SANTOS, T. (2002) A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain. *Biodiversity and Conservation*, 11, 1063–1079.
- VYNNE, C., SKALSKI, J., MACHADO, R.B., GROOM, M.J., JÁCOMO, A.T.A., MARINHO-FILHO, J., ET AL. (2011) Effectiveness of scat-detection dogs in determining species presence in a tropical savanna landscape. *Conservation Biology*, 25, 154–162.
- WHITEMAN, C.W., MATUSHIMA, E.R., CAVALCANTI CONFALONIERI, U.E., PALHA, M. DAS D.C., DA SILVA, A. DO S.L. & MONTEIRO, V.C. (2007) Human and domestic animal populations as a potential threat to wild carnivore conservation in a fragmented landscape from the Eastern Brazilian Amazon. *Biological Conservation*, 138, 290–296.
- WIBISONO, H.T. & PUSPARINI, W. (2010) Sumatran tiger (*Panthera tigris sumatrae*): a review of conservation status. *Integrative zoology*, 5, 313–323.

- WIKRAMANAYAKE, E.D., DINERSTEIN, E., ROBINSON, J.G., KARANTH, U., RABINOWITZ, A., OLSON, D., ET AL. (1998) An ecology-based method for defining priorities for large mammal conservation: the tiger as case study. *Conservation Biology*, 12, 865–878.
- XIAOFENG, L., YI, Q., DIQIANG, L., SHIRONG, L., XIULEI, W., BO, W. & CHUNQUAN, Z. (2011) Habitat evaluation of wild Amur tiger (*Panthera tigris altaica*) and conservation priority setting in north-eastern China. *Journal of Environmental Management*, 92, 31–42.
- ZIMMERMANN, F., BREITENMOSER-WÜRSTEN, C. & BREITENMOSER, U. (2007) Importance of dispersal for the expansion of a Eurasian lynx *Lynx lynx* population in a fragmented landscape. *Oryx*, 41, 358–368.

Appendix B – Species specific results about effect of habitat loss and fragmentation

Table S.B1 - Current threat status of felines and knowledge on HLF (N= 162 scientific publications). Species vulnerability was expressed considering threat status according to the IUCN Red List (IUCN 2011). Complete list of publications in Appendices A.

Species	IUCN	Summary of main results
<i>Acinonyx jubatus</i> *	VU ¹⁺	NA
<i>Caracal aurata</i> *	NT ¹⁺	NA
<i>Caracal caracal</i> *	LC ¹	NA
<i>Felis chaus</i> *	LC ¹	NA
<i>Felis margarita</i> *	NT ¹⁺	NA
<i>Felis nigripes</i> *	VU ¹⁺	<ul style="list-style-type: none"> • Negatively affected by increase of shrub cover.
<i>Felis silvestres</i>	LC ^{1,2}	<ul style="list-style-type: none"> • Stable populations in the most part of its distribution; • Negatively affected by human activities and settlement, construction of dams, and roads.
<i>Leopardus colocolo</i> *	NT ¹⁺	<ul style="list-style-type: none"> • In Goiás state (Brazil) is not found fragments larger than 10 times its home range; • Infection by domestic animals parasites.
<i>Leopardus geoffroyi</i>	NT ¹⁺	<ul style="list-style-type: none"> • Grassland are unsuitable, but can use areas of eucalypt plantation; • Habitat loss in rain station; • Infection by domestic animals parasites.
<i>Leopardus guigna</i> *	VU ¹⁺	<ul style="list-style-type: none"> • High habitat requirement: large patches of dense shrub cover and distant of roads;

Species	IUCN	Summary of main results
		<ul style="list-style-type: none"> • Many metapopulation in Chile are threatened.
<i>Leopardus jacobita</i> *	EN ¹	<ul style="list-style-type: none"> • Infection by parasites
<i>Leopardus pardalis</i>	LC ¹	<ul style="list-style-type: none"> • Threats: local loss of genetic diversity, diseases from domestic animals, and road kill; • Use of eucalypt and sugar-cane matrix as corridors.
<i>Leopardus tigrinus</i> *	VU ^{1,2}	<ul style="list-style-type: none"> • It can use small patches since it has good environmental quality; • Infection by parasites.
<i>Leopardus wiedii</i> *	NT ^{1,2}	<ul style="list-style-type: none"> • Populations are declining; • It is observed more frequently in core areas of fragments.
<i>Leptailurus serval</i> *	LC ¹	NA
<i>Lynx canadensis</i>	LC ¹	<ul style="list-style-type: none"> • Avoid open areas and roads; • Peripheral populations have lower genetic diversity.
<i>Lynx lynx</i>	LC ¹	<ul style="list-style-type: none"> • Its distribution is largely fragmented, resulting in a population marginalized, demographically unviable, more susceptible to disease, with low and sub-structured genetic diversity; • Reconnection of unviable population is difficult due to small size of adjacent patches and human construction working as barrier.
<i>Lynx pardinus</i>	CR ¹⁺²	<ul style="list-style-type: none"> • It is restricted to two populations; • Threats: range contraction due to HLF; low genetic

Species	IUCN	Summary of main results
		<p>variability leading to inbreeding depression; increase of mortality rate due to road kills, trapping, and shooting; and contagion by domestic animals diseases;</p> <ul style="list-style-type: none"> • Populations cannot be reconnected due to urban areas and roads working as barrier.
<i>Lynx rufus</i>	LC ¹⁺	<ul style="list-style-type: none"> • It can cross highways, but it increases mortality rate; • It uses anthropogenic land covers, but as less suitable habitat; • It presents domestic animals diseases in transitional areas of natural and anthropogenic land cover. • It responds positively to increase in patch size and habitat interspersion, but negatively to irregular patch shapes and increase in edge habitats; • Its populations are genetically structured due to roads, but still have high diversity.
<i>Neofelis diardi</i> *	VU ¹	NA
<i>Neofelis nebulosa</i> *	VU ¹	<ul style="list-style-type: none"> • High habitat area requirement.
<i>Otocolobus manul</i> *	NT ¹	NA
<i>Panthera leo</i>	VU ¹	<ul style="list-style-type: none"> • Inbreeding depression and local extinction due to habitat loss; • High index of infection by parasites.
<i>Panthera onca</i>	NT ¹⁺	<ul style="list-style-type: none"> • Low tolerance to habitat loss, fragmentation, and anthropogenic land cover;

Species	IUCN	Summary of main results
		<ul style="list-style-type: none"> • Isolated populations in Atlantic Forest and Cerrado biome (Brazil); • Native vegetation is an important predictor of its occurrence.
<i>Panthera pardus</i> *	NT ¹⁺	<ul style="list-style-type: none"> • Its population is subdivided by fragmentation and roads.
<i>Panthera tigris</i>	EN ¹⁺	<ul style="list-style-type: none"> • Moderately tolerant to human disturbance, but its abundance can be reduced in anthropogenic areas due to its high ecological requirements; • Populations divided by anthropogenic pressure, such as roads, infrastructure, and agriculture; • Unviable populations.
<i>Panthera uncia</i> *	EN ¹	<ul style="list-style-type: none"> • Climatic changes can reduce about 30% of snow leopard habitat in the Himalaya.
<i>Pardofelis badia</i> *	EN ¹⁺	NA
<i>Pardofelis marmorata</i> *	VU ¹⁺	NA
<i>Pardofelis temminckii</i> *	NT ¹⁺	NA
<i>Prionailurus bengalensis</i> *	LC ¹⁺	<ul style="list-style-type: none"> • Moderately tolerant to degraded habitat; • Threats: Habitat loss, competition with introduced species, and road kill.
<i>Prionailurus planiceps</i> *	EN ¹⁺	NA
<i>Prionailurus rubiginosus</i> *	VU ¹⁺	NA
<i>Prionailurus viverrinus</i> *	EN ¹⁺	NA

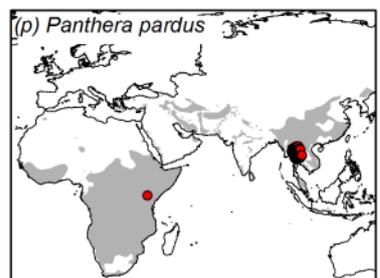
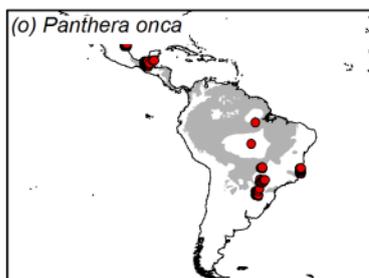
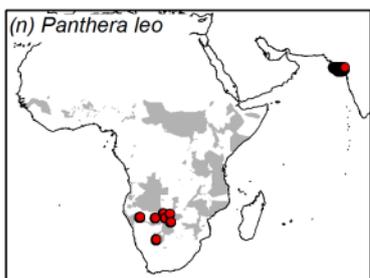
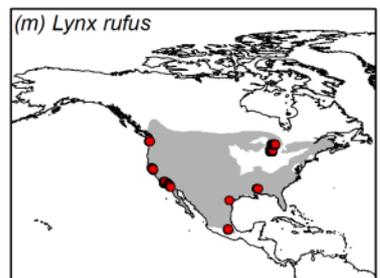
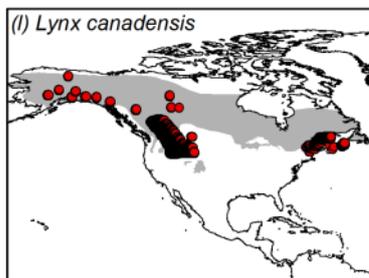
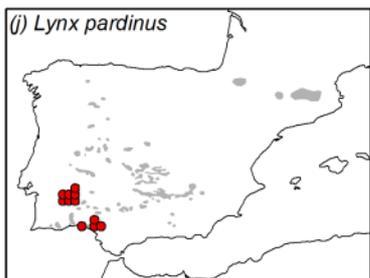
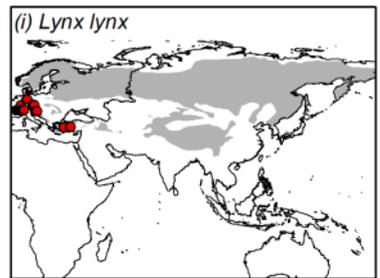
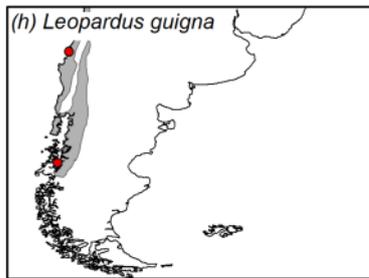
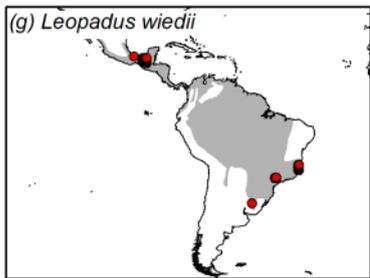
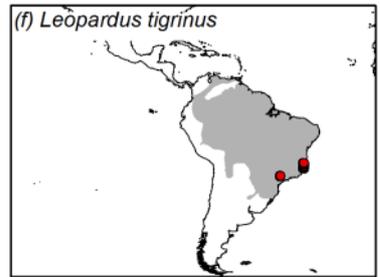
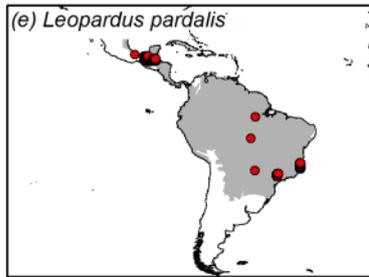
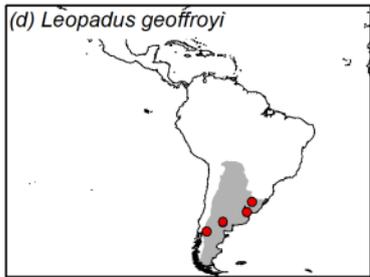
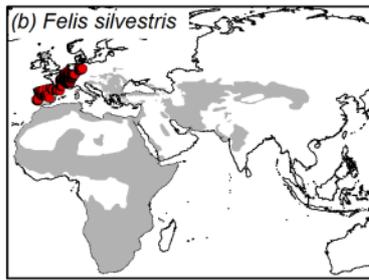
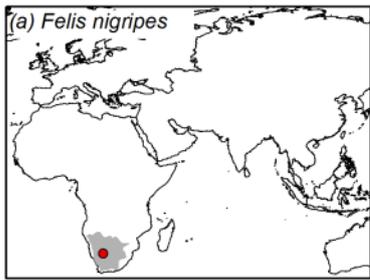
Species	IUCN	Summary of main results
<i>Puma concolor</i>	LC ^{1+,2}	<ul style="list-style-type: none"> • It has a high environmental plasticity that makes it capable to use landscapes with some level of anthropogenic influence and to cross areas with roads and bridges; • Threats: increase of mortality by road kill, sub-structuration of genetic variability among fragments, inbreeding depression, edge effects, and contagion by domestic animals diseases.
<i>Puma yagouaroundi</i> *	LC ¹⁺	<ul style="list-style-type: none"> • It is moderately tolerant to anthropogenic land cover and use edge fragments, but mainly habitat of better quality; • Infection by parasites.

* Poorly studied species

¹ HLF is considered a threat to species

² Road kill is considered a threat to species

⁺ The main threat to species



Continuation Figure S.B1

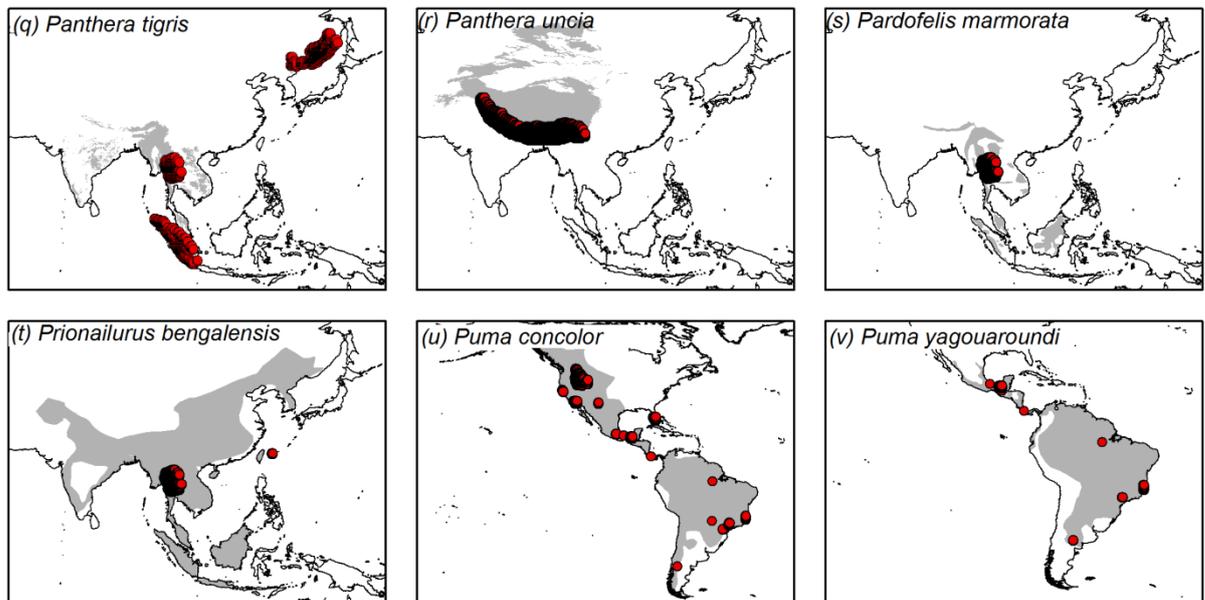


Figure S.B1 - Distribution of felines with at least one publication (in gray) and location where scientific studies about habitat loss and fragmentation have been conducted (red point).

CAPÍTULO 2

Esse capítulo foi submetido para a revista *Journal of Nature Conservation*, portanto, segue as normas de formatação da mesma. Atualmente, o artigo está avaliado como *Major Review* (Anexo 2).

1 **The jaguar's patches: the decline of jaguar populations**

2

3 **Marina Zanin***Departamento de Ecologia, Universidade Federal de Goiás, Caixa Postal 131,
4 CEP 74001-970, Goiania, Goiás, Brazil. E-mail: marinazaning@gmail.com

5

6 **Francisco Palomares** Department of Conservation Biology, Estación Biológica de Doñana
7 CSIC; Avenida Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla, Spain. E-mail:
8 ffpaloma@ebd.csic.es

9

10 **Daniel Brito** Departamento de Ecologia, Universidade Federal de Goiás, Caixa Postal 131,
11 CEP 74001-970, Goiania, Goiás, Brazil. E-mail: brito.dan@gmail.com

12

13 * Corresponding author.

14 **The jaguar's patches: the effects of fragmentation on jaguar populations**

15

16 **1. Abstract**

17 Habitat loss and fragmentation have serious consequences for population extinction risk, so
18 we investigated the effects of these processes on jaguar (*Panthera onca*) populations across
19 the species' distribution range. We employed theoretical simulations of population dynamics,
20 making use of real and hypothetical landscapes, which permitted us to measure the effects of
21 landscape configuration on persistence probability and to disentangle the effects of habitat
22 loss and fragmentation on jaguar populations. Jaguar persistence probability was related to
23 habitat configuration in real landscapes. However, habitat configuration was correlated with
24 the amount of total habitat, rendering it difficult to differentiate the processes of habitat loss
25 and fragmentation. The hypothetical landscapes helped us to understand the different effects
26 of these two processes. Our findings show that fragmentation affects jaguar long-term
27 persistence more than habitat loss, because jaguars had a higher persistence probability in
28 landscapes comprised of a continuous habitat patch than in landscapes with the greater
29 quantity of habitat but composed of several separate patches. Given the increase in habitat
30 fragmentation and the current threat status of the jaguar, conservation initiatives need to take
31 account of the results presented in this study for the development of jaguar conservation
32 strategies.

33

34 **Keywords**

35 Critical threshold, habitat loss, habitat fragmentation, *Panthera onca*, population viability
36 analyses

37 2. Introduction

38 The effects of habitat loss and fragmentation on species persistence are a central
39 topic in conservation biology (Lenore Fahrig, 1997, 2003). Habitat loss and fragmentation
40 reduce and subdivide the available habitat (Andr n, 1994; Lenore Fahrig, 2003), thereby
41 altering the colonization rates of patches (Belisle, Desrochers, & Fortin, 2001). Even though
42 habitat loss and fragmentation occur simultaneously in real landscapes, they are two different
43 processes, both of which affect wildlife populations. The majority of studies on this theme
44 have frequently investigated the integrated effects of both processes because they are
45 inevitably correlated in real landscapes (Smith, Koper, Francis, & Fahrig, 2009). Despite
46 inherent difficulties, it is critical to differentiate the effects of each process in order to better
47 guide wildlife management strategies, permitting a more efficient use of limited conservation
48 resources (Lindenmayer & Fischer, 2007; Smith et al., 2009).

49 Estimates of persistence probability provide useful insights for wildlife managers
50 planning species conservation in a world where habitat destruction and degradation rates are
51 soaring (Caughley, 1994). Habitat alteration may be perceived differently by species
52 (Lindenmayer & Fischer, 2007), and so a species-specific approach is essential for measuring
53 the effects of habitat loss and fragmentation. Population viability analysis (PVA) has become
54 a useful tool for investigating the effects of habitat loss and fragmentation on species, given
55 that it may evaluate persistence probability in relation to a variety of environmental threat
56 scenarios according to species-specific parameters (Brook, Tonkyn, O'Grady, & Frankham,
57 2002).

58 Our research focused on the effects of habitat loss and fragmentation on the long-
59 term persistence of jaguar (*Panthera onca*, Linnaeus 1758) in landscapes distributed
60 throughout its range. Historically, this species was distributed from the southern United States
61 to Argentina, but its geographic range has been reduced to less than 60% of its original extent

62 due to human pressures (Morrison, Sechrest, Dinerstein, Wilcove, & Lamoreux, 2007). The
63 jaguar is ranked 15th among the large-bodied mammals with greatest geographic range
64 contraction in the last 500 years due to anthropogenic effects (Morrison et al., 2007). Today,
65 the jaguar is listed as Near Threatened (IUCN, 2013), but this status may soon be revised to
66 reflect further declining populations (IUCN, 2013).

67 The current habitat configuration of landscapes is a result of past habitat loss and
68 fragmentation (Villard & Metzger, 2013); thus, present-day habitat configuration can be
69 considered as a pattern generated by the synergistic effects of both processes (habitat loss and
70 habitat fragmentation). Therefore, we mapped known jaguar populations across its
71 distribution range and then investigated how the current landscape configuration could
72 determine jaguar persistence probability. To better understand the consequences of habitat
73 loss and fragmentation for jaguars, we created hypothetical landscapes to investigate the non-
74 linear relationship of habitat configuration and species persistence based on the simplest
75 landscapes features, i.e. the total habitat area and the number of patches. For that, we modeled
76 jaguar population dynamics in landscape scenarios for (i) a controlled number of patches
77 while reducing the total habitat area, and (ii) a controlled total habitat area while increasing
78 the number of patches. This approach allowed us to disentangle the effects of habitat loss and
79 fragmentation on jaguar populations.

80 Habitat loss and fragmentation are the main threats to jaguar populations (IUCN,
81 2013). On this perspective, we measured the viability of jaguar populations at a landscape
82 level, generating a map of threatened populations. We also evaluated the amount of habitat
83 necessary to maintain a viable population and the extent of habitat fragmentation a jaguar
84 population can support while maintaining a high persistence probability. This gave us a
85 general insight into the importance of increasing total habitat area and connecting isolated
86 fragments to ensure the long-term persistence of jaguar populations in the landscapes.

87 **3. Methods**

88

89 **3.1. Study Area**

90 To conduct jaguar PVAs (see below) we selected 28 study areas for which jaguar
91 density estimates were available and had been measured in a similar way. We used as a
92 reference the review of Maffei et al. (2011), where authors reported jaguar densities for 49
93 study areas distributed across 14 countries. However, the studies considered in that review
94 used different density estimation methods and sampling designs, so we selected sites where
95 density was estimated by capture-recapture methods, using two camera-traps at each sampling
96 station as the census technique. The 28 study areas used in our investigation were located
97 throughout nine countries, with density estimations varying from 1.12 to 11.56 jaguars/100
98 km² (Supplementary Material A).

99

100 **3.2. Landscape scenarios**

101 PVAs were performed in real landscapes to evaluate the effect of landscape
102 configuration on jaguar persistence probability, but also in a set of hypothetical landscapes to
103 disentangle the effects of habitat loss and fragmentation. The real landscapes were delimited
104 by establishing a 10,000 km² buffer around the central point where the density studies were
105 conducted. A landcover map (Bontemps, Defourny, Bogaert, Kalogirou, & Perez, 2011) was
106 created using a binary classification; we categorized native vegetation cover as suitable for
107 jaguars and anthropogenic landcover as unsuitable. This level of generalization was adopted
108 because jaguars present significant environmental plasticity in terms of their use of vegetation
109 types (Colchero et al., 2011), making this a good generalization of jaguar habitat use at a
110 broad environmental grain. It is known that jaguars occupy anthropogenic vegetation
111 (Colchero et al., 2011; Figel, Durán, & Bray, 2011), but it is unclear from studies on habitat

112 suitability if jaguars use these areas or simply traverse them. Additionally, jaguar mortality
113 probably increases in anthropogenic vegetation, justifying our classification of it as unsuitable
114 for jaguars. The number and size of habitat patches were estimated for each landscape in the
115 jaguar habitat map. Patches larger than 100km² were included in our PVA because we
116 considered that these patches adequately function as stepping stones and since it is a
117 reasonable size for a jaguar home range (Cavalcanti & Gese, 2010; Cullen Jr., 2006).

118 The hypothetical landscapes were designed with a controlled structure to measure the
119 effects of habitat area and subdivision. The simulations started considering a landscape with
120 the maximum of structural integrity, i.e. a patch of 10,000 km². In order to model the effects
121 of habitat loss, the total area was reduced gradually, by blocks of 1,000 km², until only 1,000
122 km² remained, and then to 500 km² and finally to 100 km². In order to model the effects of
123 habitat fragmentation, the total area of habitat was kept constant (i.e. the same amount of
124 habitat used in the habitat loss simulations), but it was divided into a number of scenarios
125 where we gradually increased the number of patches. The first scenario had two patches, the
126 second had four patches of equal size, continuing progressively by steps of four up to 28
127 patches. The patches were of equal area without reducing the total area, and so each patch had
128 equivalent relevance to population persistence.

129

130 **3.3. Population Viability Analysis**

131 The software VORTEX version 9.99 (Lacy, 2012) was used to simulated the
132 population dynamics of jaguars and estimate persistence probability for 200 years. VORTEX
133 is a Monte Carlo simulation that considers a set of factors affecting a population, including:
134 deterministic forces (e.g. trends in carrying capacity); demographic, environmental and
135 genetic stochasticity; and catastrophes (Lacy, 2000). We chose VORTEX due to its spatially-
136 implicit approach, which was necessary for our study because the literature concerning the

137 jaguar lacks information about dispersal rates and mortality in different landcover types and
138 areas.

139 Most of the life history data were obtained from the ‘Brazilian Action Plan for
140 Jaguars’ because it compiles the most up-to-date biological data on the species (de Paula,
141 Desbiez, & Cavalcanti, 2010) (Table 1). These data represent an actual, but non-specified,
142 jaguar population (de Paula et al., 2010), so the population might be derived from anywhere
143 within the species distribution. The differences among the populations modeled in our study
144 only concerned the landscapes where they are located, so the differences among PVAs in this
145 study related only to landscape features. We designed the (meta)population structure based on
146 the simplest landscape features, i.e. patch number and area. The number of patches in the
147 landscape determined whether the dynamics were best modeled by a population or a
148 metapopulation. The total area of the patches determined initial population size, which was
149 calculated as a product of area and jaguar density. Due to the spatially-implicit approach, the
150 total habitat area and the number of patches were integrated into the PVA indirectly; the
151 number of patches was used as a surrogate for the number of populations and the total amount
152 of suitable habitat was a surrogate for population size.

153 We assumed that carrying capacity was equal to the initial population size, which
154 was a conservative approach because there is no information about the temporal change in
155 carrying capacities of these studies areas. There is also no information about jaguar dispersal
156 rates or mortality in the different landcover types. Therefore, we chose a generalized
157 approach, whereby the movement of migrants between fragments was considered symmetric,
158 i.e. individuals could move in either direction between patches at the same rate. The total
159 number of migrants was estimated as a function of the number of subadults in the population
160 because, typically, at this life-history stage, felines are looking to establish a territory
161 (Funston, Mills, Richardson, & van Jaarsveld, 2003). The proportion of subadults was

162 determined as a proportion of the dynamic sites (*sensu* Gotelli, 1991) that can be occupied in
163 the metapopulation. Since a subadult competitively excludes another individual from its *site*,
164 the excluded jaguar (which can be an adult or another subadult) can compete for another *site*
165 in the metapopulation. Therefore, the number of subadults defined the proportion of
166 dispersers, but the dispersers could be any jaguar in the population.

167 Of the estimated life-history parameters for jaguars, the percentage of males in the
168 breeding pool and mortality were those having the greatest degree of uncertainty. The
169 percentage of males in the breeding pool is difficult to estimate. An accurate estimate would
170 require long-term demographic study, using expensive techniques, such as genetic analysis
171 and GPS monitoring. Mortality too is a complex parameter that varies according to sex, age
172 and location (Ferrerias et al., 2004), as well as anthropogenic factors (Inskip & Zimmermann,
173 2009). We modeled PVAs based on the best preserved landscape in our study area (jaguar
174 density of 11.56 jaguars/100 km² and 10,000 km² of available habitat), with different values
175 for the percentage of males in the breeding pool and jaguar mortality to take into account the
176 uncertainty of these parameters. The proportions of males in the breeding pool used in the
177 models were 100%, 80% and 70% while, for mortality rates, we used 10%, 30% and 50% (for
178 both sexes and every age class). These values were attributed randomly into the 500 PVA
179 models.

180

181 **3.4. Statistical Analysis**

182 To investigate the synergistic effects of habitat loss and fragmentation on jaguar
183 population viability, we used landscape metrics as a measure of landscape configuration. We
184 calculated landscape metrics using the Fragstats software program (McGarigal & Marks,
185 1994) on a landcover map (Bontemps et al., 2011), with our classification of
186 suitable/unsuitable habitat for jaguars. The selected metrics included: the proportion of native

187 cover in the landscape (PLand); largest patch index (LPI); landscape shape index (LSI); patch
188 number (PN); cohesion; mean size of patches (Area-MN); and the standard deviation of patch
189 area (Area-SD) (Table2). These various landscape metrics might capture the same process,
190 resulting in over-parameterization of the statistical analysis. Thus, we conducted a principal
191 components analysis (PCA) to remove redundant parameters (Legendre & Legendre, 1998),
192 and the associated principal component scores were used to represent the landscape
193 configuration.

194 The real landscapes studied could be spatially structured throughout the jaguars'
195 distribution and may depict spatial autocorrelation, so we adopted the use of spatial filters as a
196 covariable to address this problem. Spatial filters consist of synthetic variables added into
197 analyses with the objective of expressing the geographic relationships among landscapes
198 (Dray, 2011; Patuelli, Griffith, Tiefelsdorf, & Nijkamp, 2010). They capture orthogonal
199 variation in spatial structure at different scales without inserting redundant parameters (Diniz-
200 Filho & Bini, 2005). Spatial filters are eigenvectors from a principal coordinates analysis of
201 neighbor matrices (Borcard & Legendre, 2002), calculated through the truncated distance
202 matrix W

$$W = (w_{ij}) = \begin{cases} 0 \rightarrow i = j \\ 0 \rightarrow d_{ij} > t \\ [1 - (d_{ij} / 4t)^2] \rightarrow d_{ij} \leq t \end{cases}$$

203

204 where w_{ij} is each one of the elements and t is the truncation distance. The spatial filters were
205 generated by the Spatial Analysis Macroecology software (SAM) (Rangel, Diniz-Filho, &
206 Bini, 2010) based on the geographical distance between landscape centroids.

207 Model selection was performed to evaluate the best model explaining the relationship
208 between persistence probability, landscape configuration and spatial filters. This was
209 accomplished through the use of the Akaike Information Criterion corrected for small sample

210 size (AICc) (Burnham & Anderson, 2004), which permits a hierarchical ordination of models
211 according to their descriptive power and complexity (Burnham & Anderson, 2004). We
212 expected to generate a non-linear pattern of species responses to habitat loss and
213 fragmentation (Swift & Hannon, 2010), so we used a logistic adjustment for our models to be
214 more consistent with theory. We also included a model composed only of a linear coefficient
215 to evaluate if a random solution explained the persistence probability better than the proposed
216 variables. We considered models with AICc values lower than two as complementary
217 explanations of pattern (Burnham & Anderson, 2004), since the null model was not among
218 the best solutions.

219 To measure the amount of habitat necessary to maintain a viable population of
220 jaguars, and the extent of fragmentation a jaguar population can support while maintaining its
221 viability, we performed a piecewise linear regression with the hypothetical landscape data.
222 Piecewise analysis estimates the tipping point at which system alteration generates qualitative
223 changes in population persistence probability, i.e. from viable to unviable. This tipping point
224 is known as the critical threshold and it is defined as an abrupt and non-linear alteration in a
225 given variable occasioned by small changes in the original system (Leonore Fahrig, 2001;
226 Scheffer et al., 2009). Mathematically, piecewise analyses adjust more than one regression
227 line through data variation, and the “breakpoint” (or the place where the lines converge) is
228 considered the critical threshold (Toms & Lesperance, 2003). We calculated the critical
229 threshold using the *SiZer* package (Sonderegger, 2011) in R software (R Core Team, 2013).

230 The sensitivity of our base population viability model was investigated using a
231 regression tree (Cutler et al., 2007; Harper, Stella, & Fremier, 2011), which permits the
232 evaluation of multiple uncertain parameters and their nonlinear interaction (Harper et al.,
233 2011). The regression tree structures data through hierarchical and binary partitions (splits) to
234 create groups (nodes) of higher homogeneity, reflecting parameter importance, up to an

235 undivided group of populations (leaves) (Rejwan, Collins, Brunner, Shuter, & Ridgway,
236 1999). The evaluation of node numbers in the regression tree was accomplished by a cross-
237 validation procedure, which calculates the true prediction error in the addition of nodes
238 (Breiman, 2001). A random forest was performed to evaluate the relative importance of each
239 parameter in the PVA estimations (Cutler et al., 2007), which indicated the variable that
240 needed to be more accurately estimated (Harper et al., 2011). The random forest analysis was
241 carried out using 1000 random trees through bootstrap sampling (Breiman, 2001). We used
242 the *rpart* (Therneau, Atkinson, Ripley, & Ripley, 2011) and *randomForest* (Liaw & Wiener,
243 2002) packages to conduct the regression tree and random forest analyses in R software (R
244 Core Team, 2013).

245

246 **4. Results**

247 The landscape metrics used to calculate the configuration of real landscapes were
248 correlated (Figure 2), so we selected only the first principal component of the PCA, according
249 to a broke-stick method, which described 58% of the landscape metrics variation. The
250 variables PLand, LPI, Area-MN, Area-SD and cohesion were positively correlated with the
251 principal component, while PN and LSI were negatively correlated.

252 Two out of the 64 competitive models were considered the best (i.e. $AICc < 2$) in
253 explaining the persistence probability of jaguars in the landscape, the null model not being
254 amongst them (Table 3 and Supplementary Material B). The principal component condensing
255 the landscape configuration appeared in both models (Table 3), evidencing the homogenous
256 effect of landscape configuration, which could be observed due to the low variance in the
257 coefficient value and the low standard error of the competitive models (Figure 3). Spatial
258 filters three and five also appeared in the best models, but had large standard errors associated
259 with them, obscuring their importance in predicting persistence probability (Table 3).

260 Therefore, we considered only the principal component summarizing landscape configuration
261 as an efficient predictor of jaguar persistence probability.

262 The habitat loss critical thresholds varied widely among jaguar populations, attaining
263 values ranging from 230 km² to 5,841 km² (Figure 1A). These values were strongly correlated
264 with jaguar density (Figure 4 A) due to the direct effects of initial population size on
265 persistence probability. Variation in the order of decimal degrees generated changes of more
266 than 100 km² in the critical threshold. However, the fragmentation critical threshold was more
267 sensitive to changes in the landscape than the habitat loss critical threshold. The tolerance of
268 jaguar populations to fragmentation was not sufficient to determine fragmentation critical
269 thresholds; the piecewise linear regression calculated the critical thresholds when the
270 metapopulation had a persistence probability close to zero (tipping points have a negative
271 slope –Supplementary Material C). In only a few cases did the populations have a high
272 persistence probability after the first subdivision, even in landscapes with 10,000 km² of
273 suitable habitat (Figure 5 and Supplementary Material C).

274 As a complementary result, we calculated a habitat critical threshold with a 97.5%
275 confidence interval, to have a conservative estimate of ensuring long-term jaguar persistence.
276 When populations had a density greater than 4.13 jaguars/100 km², jaguar population viability
277 suffered an abrupt and stable change following a small reduction of habitat, which resulted in
278 almost uniform residuals and an inadequate fit of the piecewise-regression to bootstrap
279 samples. This mathematical artifact generated a relationship between density and the critical
280 threshold similar to a parabola, in which the estimated density decreases to 4.13 jaguars/100
281 km² and thereafter starts to increase (Figure 4 B). Of course, there is no biological sense to
282 this pattern since the area needed to maintain a jaguar population must decrease with higher
283 density. Thus we considered it acceptable, from a conservation perspective, to consider the
284 threshold estimated at 4.13 jaguars/100 km² for populations with greater densities. Based on

285 that, the jaguar habitat critical threshold varied from 3,000 km² to 7,000 km² (Supplementary
286 Material A).

287 The real landscapes evaluated were able to support a jaguar population only in two
288 out of the 28 sites investigated (Figure 1B; Supplementary Material A), based on 95%
289 persistence probability after 200 years (Table 1). Both of these viable populations are located
290 in Guatemala and exhibit high jaguar density and a landscape with almost 100% native
291 vegetation. Many other high density populations were unviable (Figure 1B and
292 Supplementary Material A). These landscapes frequently had a total area that was larger than
293 the habitat loss critical threshold, but the area was divided into a number of patches that were
294 also larger than the fragmentation critical threshold, which resulted in unviable populations.
295 Therefore, the main threat to the long-term persistence of the jaguar populations studied
296 seemed to be habitat fragmentation.

297 The sensitivity analysis showed that 82% of the predictors' variance could be
298 explained by random forest. The regression tree was composed of six nodes, all defined by
299 female mortality (Figure 6). Therefore, the PVA model was sensitive to poorly-estimated
300 parameters, especially adult female mortality (Figure 7). The final node showed the
301 populations with higher persistence probability, which were those with a female mortality rate
302 lower than 20% from birth to sexual maturity (i.e. three years of age) (Figure 6). Thus, low
303 mortality in female jaguars may be seen as a surrogate of population persistence probability.

304

305 **5. Discussion**

306 Our study investigated the effects of habitat loss and fragmentation on the
307 persistence probability of jaguar populations. To do that, it is first necessary to perceive
308 habitat loss and fragmentation as processes that have a known spatial pattern on landscape
309 configuration. We observed a strong correlation between the selected landscape metrics used

310 to measure the spatial configuration of our real landscapes. This finding is a product of the
311 large amount of jaguar suitable habitat in the landscapes (Average P_{Land} = 77.7%), which
312 homogenized the landscape configuration as predicted by percolation theory (landscapes
313 composed of an amount of suitable habitat greater than 65% are structurally connected)
314 (Bascompte & Sole, 1996; K. A. With, 1997).

315 As expected, persistence probability was related to the proportion of jaguar suitable
316 habitat in the landscapes (Table 3). According to percolation theory predictions, we expected
317 that the landscapes composed of habitat aggregated into one single patch had a larger
318 proportion of suitable habitat than landscapes with two or more patches. The landscapes
319 analyzed in the current study supported this general prediction (\bar{X} P_{Land_{metapopulation}}=65%; \bar{X}
320 P_{Land_{population}}=87%; t-value = 2.18; DF = 26; p = 0.04). Therefore, the relationship we found
321 between total habitat available and persistence probability expresses more than a simple
322 metric for the predictability of an ecological process. The increase in availability of suitable
323 habitat acts directly on landscape connectivity, thereby altering population structure
324 (Bascompte & Solé, 1996).

325 There are several empirical examples of habitat configuration affecting species
326 persistence in the landscape (see review of Villard & Metzger, 2013). The general findings
327 indicate that habitat configuration abruptly reduces species richness at the landscape scale
328 when the amount of suitable habitat is around 10–30% (Andrén, 1994; Estavillo, Pardini, &
329 da Rocha, 2013; Lenore Fahrig, 2003), which is the threshold for conversion from a
330 fragmented to a relictual landscape (McIntyre & Hobbs, 1999). However, the amount of
331 suitable habitat and its configuration establishes a complex relationship, whereby habitat
332 configuration could potentially reduce the effects of habitat loss, which is species-dependent
333 since habitat perception is a species-specific attribute (Villard & Metzger, 2013).

334 The hypothetical landscapes used in our study helped us to understand the complex
335 relationship between landscape configuration and species persistence based on the simplest
336 landscapes features, i.e. total habitat area and number of patches. We observed that an
337 increase in patch number generated a stronger reduction in jaguar persistence probability than
338 a decrease in the amount of suitable habitat. Therefore, we can confirm that fragmentation is
339 more detrimental than habitat loss for jaguar populations. Other theoretical studies have given
340 similar predictions (Lenore Fahrig, 2003; K. With, Cadaret, & Davis, 1999), but our results
341 differ from those of empirical studies (Mortelliti et al., 2011, 2012; Tian et al., 2011; Villard
342 & Metzger, 2013).

343 The low persistence probability of jaguar populations in fragmented landscapes is
344 probably linked to an increase in overall mortality, arising by impediments to dispersal. We
345 established a stable proportion of migrants and survivors between patches in our models, so
346 total mortality increased with an increase in the number of patches. The effects of mortality
347 were reinforced by our sensitivity analysis, especially for female mortality, since the PVA
348 estimates were sensitive to this parameter. Jaguar mortality can vary widely among
349 populations because it is strongly influenced by extrinsic factors (Azevedo, 2008; Polisar et
350 al., 2003). However, it seems reasonable that female mortality at the reproductive stage is
351 important because a relationship between the total number of females in the reproductive pool
352 and growth rate is expected for a polygenic species. Even though this parameter is quite
353 relevant for jaguar ecological studies, there is no information about the variability and
354 intensity of jaguar mortality in terms of sex, age or matrix type. This resulted in persistence
355 probabilities that were sensitive to poorly-estimated parameters. However, an increase in
356 mortality during dispersal in a fragmented landscape can be expected, as we assumed in our
357 models even with the different rates we used. Thus, while our results might vary in intensity
358 with better model parameterization, the overall findings would not change.

359 *Conservation implications*

360 Our approach permitted us not only to summarize the effects of habitat loss and
361 fragmentation on jaguar persistence probability, but also to generate a diagnostic of jaguar
362 conservation status because all the results discussed here have strong applicability from a
363 conservation perspective. According to our results, we can confirm that jaguar conservation is
364 in a precarious situation, given that only two of the 28 evaluated populations had a high
365 probability of persistence. Over recent years, the species has become more dependent on
366 protected areas (Riley, 2006), but currently few such areas can support demographically-
367 viable jaguar populations (Sollmann, Torres, & Silveira, 2008). Thus, our results provide an
368 important contribution to jaguar conservation because the habitat loss critical thresholds can
369 be used to predict the necessary size of protected areas (L. Traill, Bradshaw, & Brook, 2007;
370 L. W. Traill, Brook, Frankham, & Bradshaw, 2010).

371 Even with our growing dependence on protected areas for species conservation,
372 many are not fulfilling their conservation function because they do not support long-term
373 viable populations (Sollmann et al., 2008). We can highlight Iguazu National Park (INP) and
374 its surrounding areas as a significant example because it supports one of the few remaining
375 southern jaguar populations located in an area with large suitable habitat fragments
376 (Altrichter, Boaglio, & Perovic, 2006; Mazzolli, 2009). However, the jaguar population in this
377 landscape is highly vulnerable to extinction (Persistence Probability < 0.01, Mean time to
378 extinction = 58.7 years), even though the landscape comprises 9,200 km² of native vegetation
379 cover in a practically single and large patch. The unviability of this population might be due
380 to the low number of individuals it harbors, since it had the lowest density of all the locations
381 evaluated in this study. Due to the time lag of species' responses to environmental alterations,
382 especially those species of significant longevity (Krauss et al., 2010) such as jaguars, the
383 mean time to extinction can be higher than those estimated. Nevertheless, INP still has one of

384 the most threatened jaguar populations. The areas surrounding INP suffer from severe hunting
385 pressures (Azevedo, 2008), which decrease jaguar population density both directly by
386 poaching and indirectly by prey reduction.

387 Currently, the implementation of dispersal corridors is the main strategy
388 recommended by researchers and conservation managers to bolster threatened jaguar
389 populations and to connect protected areas (Rabinowitz & Zeller, 2010; Rodríguez-Soto,
390 Monroy-Vilchis, & Zarco-González, 2013). Our study provides theoretical evidence of low
391 jaguar persistence probability under metapopulation dynamics (Figure 5). Thus, the
392 establishment of dispersal corridors needs to be carefully planned, given that the negative
393 consequences of metapopulation dynamics can be worse than those for populations that
394 remain isolated (Brito & Fernandez, 2002). A corridor can force species to cross less-suitable
395 habitats (Franklin & Lindenmayer, 2009). For top-predators such as jaguars, this can
396 exacerbate retaliatory hunting in response to the intensification of jaguar predation on
397 domestic animals (Inskip & Zimmermann, 2009), which would probably occur in these
398 contexts.

399 Therefore, our results raise the question of how to manage jaguar populations in
400 fragmented landscapes. Perhaps jaguar conservation planning should emphasize strategies
401 that increase population size by decreasing human-wildlife conflicts and increasing habitat
402 quality. Decreasing human-wildlife conflict will depend on multiple factors because it has an
403 ecological, social and probable regional context (Zanin et al. unpublished data). Increasing
404 habitat quality is also a complex task because it will involve landscape management - though
405 the field of restoration ecology is rapidly advancing, which will be of assistance in this area.
406 Of course, jaguar conservation is far more complex than the connectivity between two areas,
407 as has been suggested by researchers (Rabinowitz & Zeller, 2010; Rodríguez-Soto et al.,
408 2013), but it seems to be of fundamental significance for long-term jaguar conservation.

409 **6. References**

- 410 Altrichter, M., Boaglio, G., & Perovic, P. (2006). The decline of jaguars *Panthera onca* in the
411 Argentine Chaco. *Oryx*, *40*(3), 302–309. doi:10.1017/S0030605306000731
- 412 Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with
413 different proportions of suitable habitat: A review. *Oikos*, *71*(3), 355–366.
- 414 Azevedo, F. C. C. (2008). Food habits and livestock depredation of sympatric jaguars and
415 pumas in the Iguaçu National Park Area, South Brazil. *Biotropica*, *40*(4), 494–500.
416 doi:10.1111/j.1744-7429.2008.00404.x
- 417 Bascompte, J., & Sole, R. V. (1996). Habitat fragmentation and extinction thresholds in
418 spatially explicit models. *The Journal of Animal Ecology*, *65*(4), 465–473.
419 doi:10.2307/5781
- 420 Bascompte, J., & Solé, R. V. (1996). Habitat fragmentation and extinction thresholds in
421 spatially explicit models. *Journal of Animal Ecology*, *65*, 465–473.
- 422 Belisle, M., Desrochers, A., & Fortin, M.-J. (2001). Influence of forest cover on the
423 movements of forest birds: a homing experiment. *Ecology*, *82*(7), 1893.
424 doi:10.2307/2680055
- 425 Bontemps, S., Defourny, P., Bogaert, E. Van, Kalogirou, V., & Perez, J. R. (2011).
426 GLOBCOVER 2009. UCLouvain & ESA Team.
- 427 Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of
428 principal coordinates of neighbour matrices. *Ecological Modelling*, *153*(1-2), 51–68.
429 doi:10.1016/S0304-3800(01)00501-4
- 430 Breiman, L. (2001). Random forest. Berkeley, California: University of California.
- 431 Brito, D., & Fernandez, F. A. S. (2002). Patch relative importance to metapopulation
432 viability: the neotropical marsupial *Micoureus demerarae* as a case study. *Animal*
433 *Conservation*, *5*, 45–51.

434 Brook, B. W., Tonkyn, D. W., O'Grady, J. J., & Frankham, R. (2002). Contribution of
435 inbreeding to extinction risk in threatened species. *Conservation Ecology*, 6(1).

436 Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and
437 BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304.
438 doi:10.1177/0049124104268644

439 Caughley, G. (1994). Directions in conservation biology. *Journal of Animal Ecology*, 63(2),
440 215–244.

441 Cavalcanti, S. M. C., & Gese, E. M. (2010). Kill rates and predation patterns of jaguars
442 (*Panthera onca*) in the southern Pantanal, Brazil. *Journal of Mammalogy*, 91(3), 722–
443 736. doi:10.1644/09-MAMM-A-171.1.Key

444 Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A., & Ceballos, G. (2011).
445 Jaguars on the move: modeling movement to mitigate fragmentation from road
446 expansion in the Mayan Forest. *Animal Conservation*, 14(2), 158–166.
447 doi:10.1111/j.1469-1795.2010.00406.x

448 Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J.
449 (2007). Random forests for classification in ecology. *Ecology*, 88(11), 2783–2792.

450 De Paula, R. C., Desbiez, A. L. J., & Cavalcanti, S. M. C. (2010). *Plano de ação para a*
451 *conservação da onça-pintada (Panthera onca)*. Brasília.

452 Diniz-Filho, J. A. F., & Bini, L. M. (2005). Modelling geographical patterns in species
453 richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*,
454 14(2), 177–185. doi:10.1111/j.1466-822X.2005.00147.x

455 Dray, S. (2011). A new perspective about Moran's coefficient: spatial autocorrelation as a
456 linear regression problem. *Geographical Analysis*, 43, 127–141.

457 Estavillo, C., Pardini, R., & da Rocha, P. L. B. (2013). Forest loss and the biodiversity
458 threshold: an evaluation considering species habitat requirements and the use of matrix
459 habitats. *PloS One*, 8(12), e82369. doi:10.1371/journal.pone.0082369

460 Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction.
461 *The Journal of Wildlife Management*, 61(3), 603–610. doi:10.2307/3802168

462 Fahrig, L. (2001). How much habitat is enough? *Biological Conservation*, 100(1), 65–74.
463 doi:10.1016/S0006-3207(00)00208-1

464 Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology,*
465 *Evolution, and Systematics*, 34(1), 487–515.
466 doi:10.1146/annurev.ecolsys.34.011802.132419

467 Ferreras, P., Delibes, M., Palomares, F., Fedriani, J. M., Calzada, J., & Revilla, E. (2004).
468 Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behavioral*
469 *Ecology*, 15(1), 31–40. doi:10.1093/beheco/arg097

470 Figel, J. J., Durán, E., & Bray, D. B. (2011). Conservation of the jaguar *Panthera onca* in a
471 community-dominated landscape in montane forests in Oaxaca, Mexico. *Oryx*, 45(4),
472 554–560. doi:10.1017/S0030605310001353

473 Franklin, J. F., & Lindenmayer, D. B. (2009). Importance of matrix habitats in maintaining
474 biological diversity. *Proceedings of the National Academy of Sciences of the United*
475 *States of America*, 106(2), 349–350. doi:10.1073/pnas.0812016105

476 Funston, P. J., Mills, M. G. L., Richardson, P. R. K., & van Jaarsveld, A. S. (2003). Reduced
477 dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of*
478 *Zoology*, 259(2), 131–142. doi:10.1017/S0952836902003126

479 Gotelli, N. J. (1991). Metapopulation models: the rescue effect, the propagule rain, and the
480 core-satellite hypothesis. *The American Naturalist*, 138(3), 768–776.

481 Harper, E. B., Stella, J. C., & Fremier, A. K. (2011). Global sensitivity analysis for complex
482 ecological models: a case study of riparian cottonwood population dynamics. *Ecological*
483 *Applications*, 21(4), 1225–1240.

484 Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: a review of patterns and
485 priorities worldwide. *Oryx*, 43(01), 18–34. doi:10.1017/S003060530899030X

486 IUCN. (2013). The IUCN red list of threatened Species. Retrieved December 01, 2013, from
487 <http://www.iucnredlist.org/>

488 Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., ...
489 Steffan-Dewenter, I. (2010). Habitat fragmentation causes immediate and time-delayed
490 biodiversity loss at different trophic levels. *Ecology Letters*, 13(5), 597–605.
491 doi:10.1111/j.1461-0248.2010.01457.x

492 Lacy, R. (2000). Structure of VORTEX simulation model for population viability analysis.
493 *Ecological Bulletins*, 48, 191–203.

494 Lacy, R. (2012). VORTEX: Population Viability Analysis Software. Chicago Zoological
495 Society and Conservation Breeding Specialist Group.

496 Legendre, P., & Legendre, L. (1998). *Numerical ecology* (Second ed., p. 870). Amsterdam:
497 Elsevier Science.

498 Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, 2(3),
499 18–22.

500 Lindenmayer, D. B., & Fischer, J. (2007). Tackling the habitat fragmentation panchreston.
501 *Trends in Ecology & Evolution*, 22(3), 127–32. doi:10.1016/j.tree.2006.11.006

502 Maffei, L., Noss, A. J., Silver, S. C., & Kelly, M. J. (2011). Abundance/density case study:
503 jaguars in the Americas. In A. F. O’Connell, J. D. Nichols, & K. U. Karanth (Eds.),
504 *Camera traps in animal ecology: Methods and analyses* (pp. 134–159). Tokyo: Springer
505 Japan. doi:10.1007/978-4-431-99495-4

506 Mazzolli, M. (2009). Loss of historical range of jaguars in southern Brazil. *Biodiversity and*
507 *Conservation*, 18(6), 1715–1717. doi:10.1007/s10531-008-9552-8

508 McGarigal, K., & Marks, B. J. (1994). *Fragstats: spatial pattern analysis program for*
509 *quantifying landscape structure* (Vol. 97331, p. 144). Colorado.

510 McIntyre, S., & Hobbs, R. (1999). A framework for conceptualizing human effects on
511 landscapes and its relevance to management and research models. *Conservation Biology*,
512 13(6), 1282–1292. doi:10.1046/j.1523-1739.1999.97509.x

513 Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S., & Lamoreux, J. F. (2007).
514 Persistence of large mammal faunas as indicators of global human impacts. *Journal of*
515 *Mammalogy*, 88(6), 1363–1380. doi:10.1644/06-MAMM-A-124R2.1

516 Mortelliti, A., Amori, G., Capizzi, D., Cervone, C., Fagiani, S., Pollini, B., & Boitani, L.
517 (2011). Independent effects of habitat loss, habitat fragmentation and structural
518 connectivity on the distribution of two arboreal rodents. *Journal of Applied Ecology*,
519 48(1), 153–162. doi:10.1111/j.1365-2664.2010.01918.x

520 Mortelliti, A., Sozio, G., Boccacci, F., Ranchelli, E., Cecere, J. G., Battisti, C., & Boitani, L.
521 (2012). Effect of habitat amount, configuration and quality in fragmented landscapes.
522 *Acta Oecologica*, 45, 1–7. doi:10.1016/j.actao.2012.08.001

523 Patuelli, R., Griffith, D. a., Tiefelsdorf, M., & Nijkamp, P. (2010). Spatial filtering and
524 eigenvector stability: space-time models for German unemployment data. *International*
525 *Regional Science Review*, 34(2), 253–280. doi:10.1177/0160017610386482

526 Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunkuist, M. E., & Eisenberg, J. F. (2003).
527 Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a
528 management problem. *Biological Conservation*, 109(2), 297–310. doi:10.1016/S0006-
529 3207(02)00157-X

530 R Core Team. (2013). R: A language and environment for statistical computing. Vienna,
531 Austria: R Foundation for Statistical Computing.

532 Rabinowitz, A., & Zeller, K. a. (2010). A range-wide model of landscape connectivity and
533 conservation for the jaguar, *Panthera onca*. *Biological Conservation*, *143*(4), 939–945.
534 doi:10.1016/j.biocon.2010.01.002

535 Rangel, T. F., Diniz-Filho, J. A. F., & Bini, L. M. (2010). SAM: a comprehensive application
536 for Spatial Analysis in Macroecology. *Ecography*, *33*(1), 46–50. doi:10.1111/j.1600-
537 0587.2009.06299.x

538 Rejwan, C., Collins, N. C., Brunner, L. J., Shuter, B. J., & Ridgway, M. S. (1999). Tree
539 regression analysis on the nesting habitat of smallmouth bass. *Ecology*, *80*(1), 341–348.
540 doi:10.1890/0012-9658(1999)080[0341:TRAOTN]2.0.CO;2

541 Riley, S. P. D. (2006). Spatial ecology of bobcats and gray foxes in urban and rural zones of a
542 national park. *Journal of Wildlife Management*, *70*(5), 1425–1435. doi:10.2193/0022-
543 541X(2006)70[1425:SEOBAG]2.0.CO;2

544 Rodríguez-Soto, C., Monroy-Vilchis, O., & Zarco-González, M. M. (2013). Corridors for
545 jaguar (*Panthera onca*) in Mexico: conservation strategies. *Journal for Nature
546 Conservation*, *21*(6), 438–443. doi:10.1016/j.jnc.2013.07.002

547 Scheffer, M., Bascompte, J., Brock, W. a, Brovkin, V., Carpenter, S. R., Dakos, V., ...
548 Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, *461*(7260),
549 53–59. doi:10.1038/nature08227

550 Smith, A. C., Koper, N., Francis, C. M., & Fahrig, L. (2009). Confronting collinearity:
551 comparing methods for disentangling the effects of habitat loss and fragmentation.
552 *Landscape Ecology*, *24*(10), 1271–1285. doi:10.1007/s10980-009-9383-3

553 Sollmann, R., Torres, N. M., & Silveira, L. (2008). Jaguar conservation in Brasil: the role of
554 protected areas. *Cat News*, (Spetial Issue 4), 22–31.

555 Sonderegger, D. (2011). SiZer: Significant zero crossings. CRAN.

556 Swift, T. L., & Hannon, S. J. (2010). Critical thresholds associated with habitat loss: a review
557 of the concepts, evidence, and applications. *Biological Reviews*, 85(1), 35–53.
558 doi:10.1111/j.1469-185X.2009.00093.x

559 Therneau, A. T. M., Atkinson, B., Ripley, B., & Ripley, M. B. (2011). Package “rpart.”

560 Tian, Y., Wu, J., Smith, A. T., Wang, T., Kou, X., & Ge, J. (2011). Population viability of the
561 Siberian Tiger in a changing landscape: going, going and gone? *Ecological Modelling*,
562 222(17), 3166–3180. doi:10.1016/j.ecolmodel.2011.06.003

563 Toms, J. D., & Lesperance, M. L. (2003). Piecewise regression: a tool for identifying
564 ecological thresholds. *Ecology*, 84(8), 2034–2041. doi:10.2307/3450028

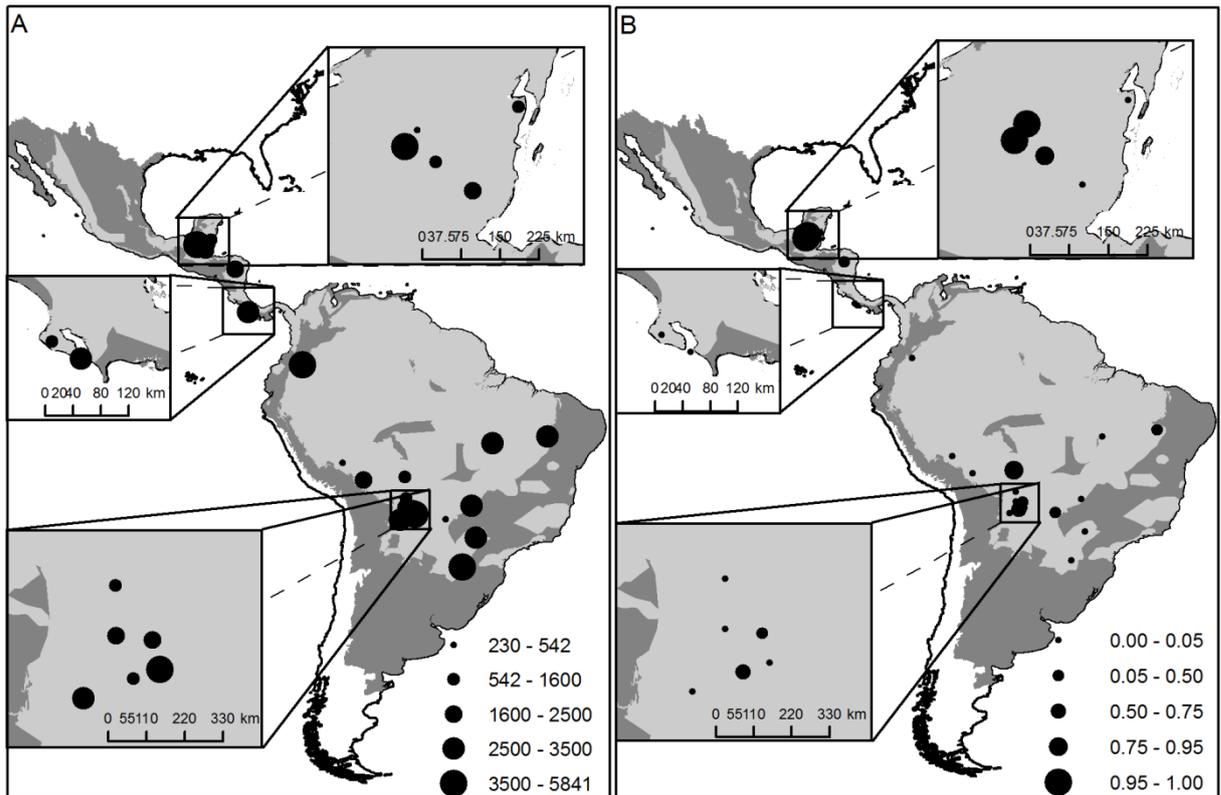
565 Traill, L., Bradshaw, C., & Brook, B. (2007). Minimum viable population size: a meta-
566 analysis of 30 years of published estimates. *Biological Conservation*, 139(1-2), 159–166.
567 doi:10.1016/j.biocon.2007.06.011

568 Traill, L. W., Brook, B. W., Frankham, R. R., & Bradshaw, C. J. a. A. (2010). Pragmatic
569 population viability targets in a rapidly changing world. *Biological Conservation*,
570 143(1), 28–34. doi:10.1016/j.biocon.2009.09.001

571 Villard, M.-A., & Metzger, J. P. (2013). Beyond the fragmentation debate: a conceptual
572 model to predict when habitat configuration really matters. *Journal of Applied Ecology*,
573 online version. doi:10.1111/1365-2664.12190

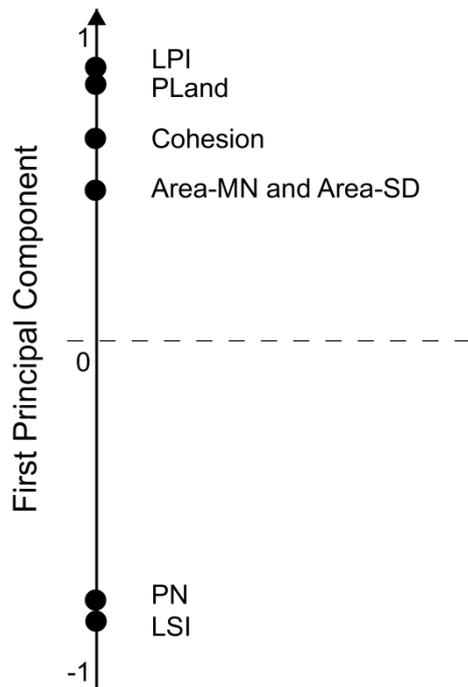
574 With, K. A. (1997). The application of neutral landscape models in conservation biology.
575 *Conservation Biology*, 11(5), 1069–1080.

576 With, K., Cadaret, S., & Davis, C. (1999). Movement responses to patch structure in
577 experimental fractal landscapes. *Ecology*, 80(4), 1340–1353.



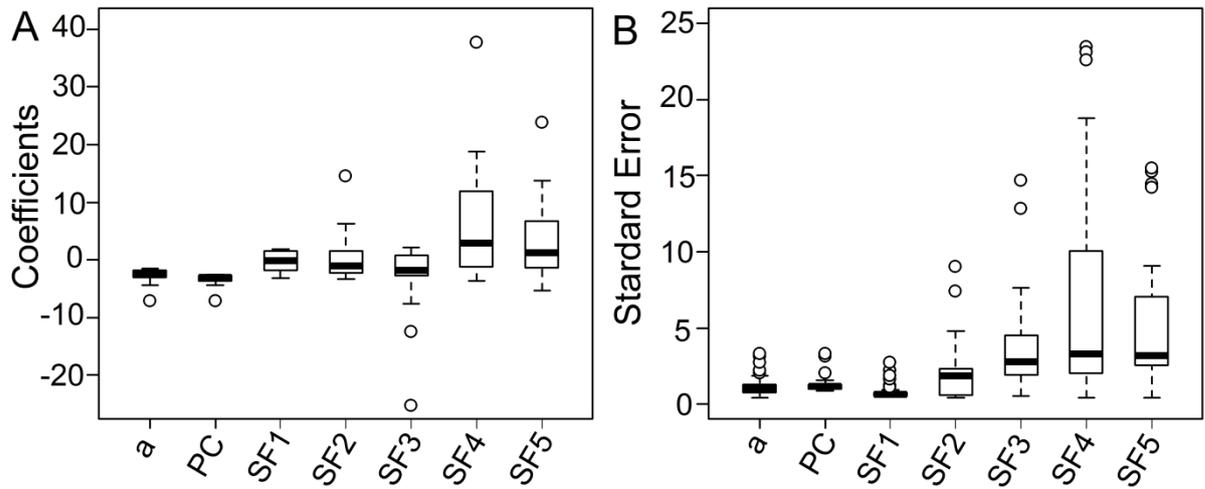
578

579 Figure 1. Maps of the jaguar populations used in our study according to (A) the
 580 requirement (in km²) needed to maintain viable populations (also called the habitat loss
 581 critical threshold) and (B) their persistence probabilities in 200 years based on actual
 582 landscape configurations. Dark gray indicates original jaguar distribution range and light gray
 583 the current distribution.



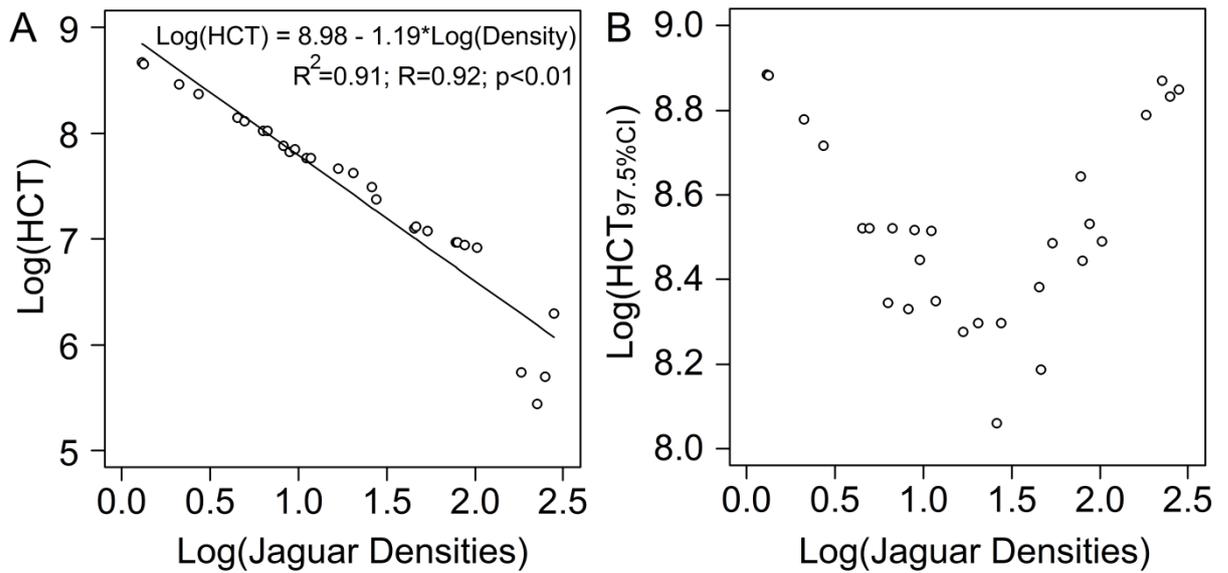
584

585 Figure 2. Principal components selected by the broken-stick method in a principal
 586 components analysis, which shows the correlation between landscape metrics. LPI – large
 587 patch index, PLand – proportion of native vegetation in the landscapes, Area-MN – size of
 588 patch, Area-SD – standard deviation of patch area, PN – patch number, and LSI – landscape
 589 shape index.



590

591 Figure 3. Variation in coefficients (A) and standard error (B) of the explanatory variables
 592 employed to describe jaguar persistence probability: a = coefficient of non-linear regression;
 593 PC = first principal component condensing landscape configuration; SF (1-5) = spatial filters
 594 capturing differing spatial structures of selected landscapes.



595

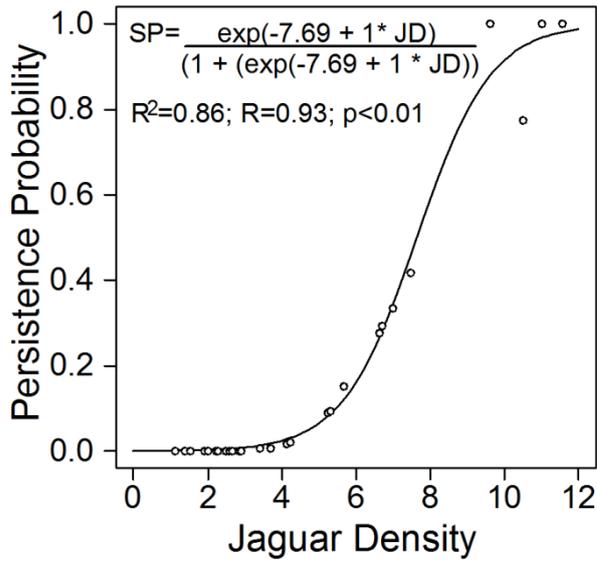
596 Figure 4. Relationship between jaguar density and the habitat loss critical threshold (HCT).

597 (A) Habitat critical threshold estimated to maintain a jaguar population with a high

598 persistence probability. (B) Habitat critical threshold with a 97.5% confidence interval (97.5%

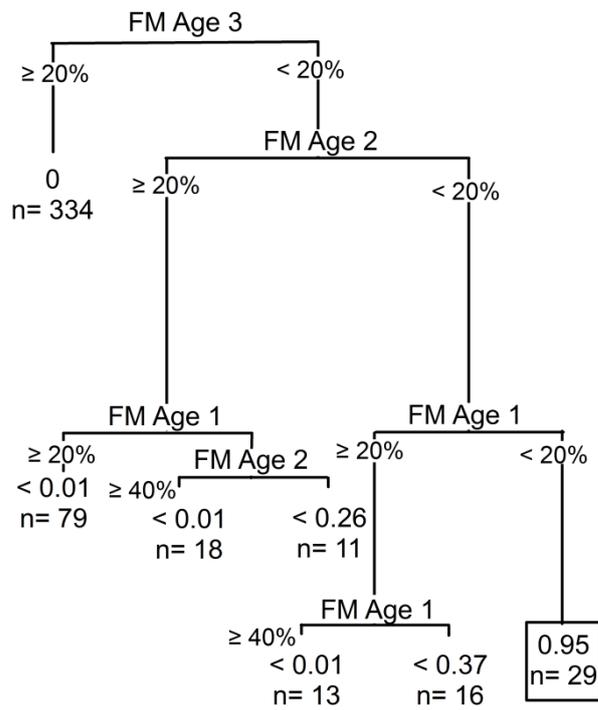
599 CI). The log transformed HCT ranged from 5.3 to 8.9, which is equivalent to a range of 230 to

600 5,841 km².



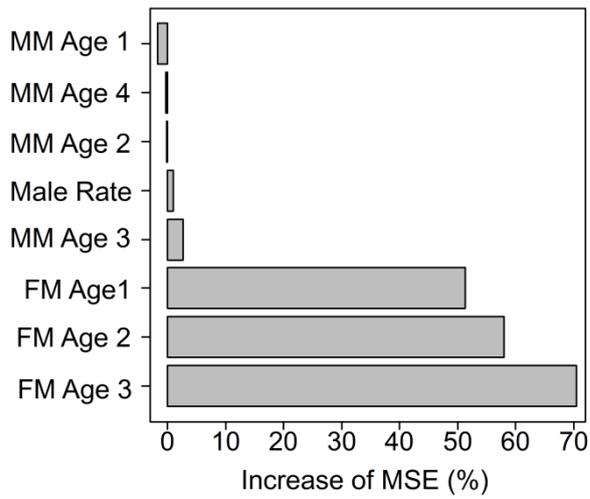
601

602 Figure 5. Persistence probability (SP) of metapopulations relative to jaguar density (JD) in
 603 landscapes composed of two patches, each of 5,000 km².



604

605 Figure 6. Illustration of the regression tree and the relationships between parameters used to
 606 estimate jaguar persistence probability. The final node indicates the probability values along
 607 with the number of observations (“n”). FM is female mortality. There is only one pathway
 608 (delimited by the square) that leads to viable populations (high persistence probability).



609

610 Figure 7. Sensitivity of jaguar persistence probability estimates for each variable in the global

611 sensitivity analysis. Mean standard error (MSE) was evaluated by random forest.

612 Table 1. Biological and statistical parameters used in the jaguar population viability analysis.

613 EV - environmental variation; SD - standard deviation.

Parameter	Value
Number of interactions	1000
Number of years	200
Extinction	Only 1 sex remains
Inbreeding	Yes (Default)
EV concordance in persistence and reproduction	Yes (Default)
Reproductive system	Polygynous
Age of first offspring for females	3
Age of first offspring for males	4
Maximum age of reproduction	10
Maximum number of progeny per year	4
Sex ratio at birth (% males)	50
Alle parameter, A	0.5
Steepness parameter, B	2
% adult females breeding	$(P0((P0-PK)*((N/K)^2)))*(N/(A+K))$
EV in % breeding	12.5
EV in % breeding	Specific
Adult females producing	
1 young	5%
2 young	40%
3 young	30%

Parameter	Value
4 young	25%
Mortality rates in females	
Age 0-1	34 ± 10
Age 1-2	17 ± 8
Age 2-3 (Subadult)	19 ± 5
Age 3-4 (Adult)	20 ± 5
Mortality rates in males	
Age 0-1	34 ± 10
Age 1-2	17 ± 8
Age 2-3 (Subadult)	35 ± 5
Age 3-4 (Subadult)	30 ± 5
Age 4-5 (Adult)	30 ± 5
Males in breeding pool	90%
Age distribution	Stable
SD carrying capacity	5% of N(0)
Migration rate	20%
Dispersers surviving	90%

615 Table 2. Fragmentation metrics used in this study. Abbreviations used in the fragmentation
 616 metrics formulae: N - patch number (unit); a_{ij} - area of ij patch (m^2); A - total area in the
 617 landscape (m^2); $\max a_{ij}$ - patch with the largest area (m^2); p_{ij} - perimeter of patch ij (unit of
 618 cells); $\min p_{ij}$ - minimum perimeter if patch was maximally aggregated (unit of cells); Z -
 619 total number of cells in the landscape.

Metric	Formula
Proportion of landscape with natural vegetation	$\frac{\sum_{j=1}^N a_{ij}}{A} \cdot 100$
Largest patch index	$\frac{\max(a_{ij})}{A} \cdot 100$
Landscape shape index	$\frac{p_{ij}}{\min p_{ij}}$
Patch number	N
Cohesion	$\left[1 - \frac{\sum_{j=1}^N p_{ij}}{\sum_{j=1}^n p_{ij} \sqrt{a_{ij}}} \right] \cdot \left[1 - \frac{1}{\sqrt{Z}} \right]^{-1} \cdot 100$
Mean size of patch	$\frac{\sum_{j=1}^N a_{ij}}{N}$
Standard deviation of patch area	$\sqrt{\frac{\sum_{j=1}^N \left[a_{ij} - \left(\frac{\sum_{j=1}^N a_{ij}}{N} \right) \right]^2}{N}}$

620 Table 3. Models with AICc values lower than four describing jaguar persistence probability
 621 based on landscape configuration and spatial structure (complete list in Supplementary
 622 Material B). PC - first principal component condensing landscape configuration; SF (1-5) -
 623 spatial filters capturing the different spatial structures of selected landscapes.

Variables in the model	Δ AICc	AICc Weighted	Residual Standard Error	Degrees of freedom
PC, SF3	0.00	0.24	0.25	25
PC, SF3, SF5	1.93	0.09	0.25	24
PC, SF2, SF3	2.17	0.08	0.25	24
PC	2.53	0.07	0.27	26
PC, SF3, SF4	2.80	0.06	0.25	24
PC, SF1, SF3	2.94	0.05	0.25	24
PC, SF2, SF5	3.08	0.05	0.26	24
PC, SF5	3.26	0.05	0.26	25

Supplementary Material A

Jaguar populations studied on the basis of the effects of habitat loss and fragmentation on population dynamics. Locations were selected based on density studies with similar sampling designs (for a review of density studies, see Leonardo Maffei et al. 2011). N – number of jaguars estimated in the landscape through multiplying total habitat area and jaguar density; SP – persistence probability; MTE – mean time of extinction (in years); N pop – number of population in the landscape; CT – habitat loss critical threshold; and CT_{97.5%} – habitat loss critical threshold calculated with a confidence interval of 97.5% by a bootstrapping method.

Study site	Reference	N	SP	MTE	N Pop	CT	CT _{97.5%}
Iguazú, Argentina	Paviolo, De Angelo, Di Blanco, & Di Bitetti (2008)	99	0.00 0.01	59	1	5841	7221
Palmar (Ravelo) - Kaa-Iya, Bolivia	Montaño, Maffei, & Noss, 2007; Romero-Muñoz (2008)	63	0.00	25	2	5743	7203
Yasuní-Waorani, Ecuador	Espinosa, S (unpublished data)	63	0.00	21	3	4721	6497
La Gloria-Lechugal, Guatemala	Moreira et al. (2007)	132	0.01	67	1	4341	6100
Ravelo, Kaa-Iya, Bolivia	Cuéllar, Dosapei, Peña, & Noss (2003)	105	0.00	30	2	3460	5025

Study site	Reference	N	SP	MTE	N Pop	CT	CT _{97.5%}
Emas National Park, Brazil	Silveira (2004)	18	0.00	13	4	3334	5016
Golfo Dulce/Golfito, Costa Rica	Ho (2008)	29	0.00	14	5	3334	5016
Morro do Diabolo, Brazil	Cullen Jr. (2006)	8	0.00	11	1	3055	4211
Guanacos - Kaa-Iya, Bolivia	Cuéllar, Segundo, Castro, & Noss (2004)	105	0.00	28	3	3046	5022
Fazenda Santa Fé, Brazil	Jaguar Conservation Fund (unpublished data)	52	0.00	19	5	2504	5001
Serra da Capivara National Park, Brazil	Silveira et al. (2009)	251	0.20	83	1	2553	4654
Rios Tuichi & Hondo – Madidi, Bolivia	Silver et al. (2004)	188	0.00	35	4	2349	4985
Estación Isoso - Kaa-Iya, Bolivia	Romero-Muñoz, Maffei, Cuéllar, & Noss (2010)	222	0.00	37	4	2352	4228
Tucavaca - Kaa-Iya, Bolivia	L Maffei, Julio, Paredes, Posiño, & Noss (2004)	309	0.31	86	1	2140	3929

Study site	Reference	N	SP	MTE	N Pop	CT	CT _{97.5%}
Bosawas, Nicaragua	Polisar (2006)	282	0.26	84	1	2051	4014
Mountain Pine Ridge	Kelly (2003)	340	0.00	42	4	1797	3167
San Miguelito, Bolivia	Arispe, Rumiz, & Venegas (2005)	205	0.00	36	4	1599	3167
Cerro Cortado - Kaa-Iya, Bolivia	L. Maffei, Barrientos, Mendoza, Ity, & Noss (2003)	394	0.53	90	1	1218	3167
Fireburn, Belize	Miller (2006)	191	0.00	39	2	1234	3167
El Encanto, Bolivia	Arispe, Rumiz, & Venegas (2007)	543	0.81	93	1	1185	3167
Tikal, Guatemala	García et al. (2006)	617	0.89	93	1	1061	3167
San Cristovan, Costa Rica	Amit (2007)	98	0.00	25	5	1060	3167
Corcovado, Costa Rica	Salom-Pérez, Carrillo, Sáenz, & Mora (2007)	103	0.00	26	5	1033	3167
Chiquibul, Belize	Silver et al. (2004)	606	0.00	49	4	1015	3167
Los Amigos, Peru	Carrillo-Percastegui, S; Tobler M.; and Powell, G. (unpublished data)	920	0.00	64	2	310	3167
Rio Azul, Guatemala	Miller and Miller (unpublished report)	1037	0.99	94	1	230	3167

Study site	Reference	N	SP	MTE	N Pop	CT	CT _{97.5%}
FazendaSete, Brazil	Soisalo & Cavalcanti (2006)	321	0.39	88	1	298	3167
Carmelita-AFISAP, Guatemala	McNab et al. (2008)	993	0.99	96	1	542	3167

References

- Amit, R. R. (2007). *Densidad de jaguares (Panthera onca), en el Sector San Cristóbal del Área de Conservación Guanacaste, Costa Rica*. Universidade Nacional.
- Arispe, R., Rumiz, D. I., & Venegas, C. (2005). *Segundo censo de jaguares (Panthera onca) y otros mamíferos con trampas cámara en la Estancia San Miguelito*. Santa Cruz, Bolivia.
- Arispe, R., Rumiz, D. I., & Venegas, C. (2007). *Censo de jaguares (Panthera onca) y otros mamíferos con trampas-cámara en la Concesión Forestal El Encanto (23 de septiembre–20 de noviembre)*. Santa Cruz, Bolivia.
- Cuéllar, E., Dosapei, T., Peña, R., & Noss, A. J. (2003). *Jaguar and other mammal camera trap survey Ravelo II, Ravelo field camp (19° 17' 44"S, 60° 37' 10"W), Kaa-Iya del Gran Chaco National Park, 18 September–18 November 2003*. Santa Cruz, Bolivia.
- Cuéllar, E., Segundo, J., Castro, G., & Noss, A. J. (2004). *Jaguar and other mammal camera trap survey Ravelo II, Ravelo field camp (19° 17' 44"S, 60° 37' 10"W), Kaa-Iya del Gran Chaco National Park, 18 August–18 October 2004*. Santa Cruz, Bolivia.
- Cullen Jr., L. (2006). *Jaguars as landscape detectives for the conservation of Atlantic Forests in Brazil*. University of Kent, UK.
- García, R., McNab, R. B., Shownder, J. S., Radachowsky, J., Moreira, J., Estrada, C., ... Tabla. (2006). *Los jaguares del corazón del Parque Nacional Tikal, Petén, Guatemala* (pp. 1–12).
- Ho, A. B. (2008). *Densidade y uso de hábitat por los felinos en la parte sureste del área de mortiguamiento del Parque Nacional Corcovado, Península de Osa, Costa Rica*. Universidade Nacional.
- Kelly, M. J. (2003). Jaguar monitoring in the Chiquibul Forest, Belize. *Caribbean Geography*, 13(1), 19–32.

- Maffei, L., Barrientos, J., Mendoza, F., Ity, E., & Noss, A. J. (2003). *Jaguar and other mammal camera trap survey Cerro II, Cerro Cortado field camp (19° 31' 36"S, 61° 18' 36"W), Kaa-Iya del Gran Chaco National Park, 28 November 2002–28 January 2003*. Santa Cruz, Bolivia.
- Maffei, L., Julio, B., Paredes, R., Posiño, A., & Noss, A. J. (2004). *Estudios con trampas-cámara en el campamento Tucavaca III (18° 30' 97"S, 60° 48' 62"W), Parque Nacional Kaa-Iya del Gran Chaco, 28 de marzo-28 de mayo de 2004*. Santa Cruz, Bolivia.
- Maffei, L., Noss, A. J., Silver, S. C., & Kelly, M. J. (2011). Abundance/density case study: jaguars in the Americas. In A. F. O'Connell, J. D. Nichols, & K. U. Karanth (Eds.), *Camera traps in animal ecology: Methods and analyses* (pp. 134–159). Tokyo: Springer Japan. doi:10.1007/978-4-431-99495-4
- McNab, R. B., Moreira, J., García, R., Ponce, G., Méndez, V., Córdova, M., ... Monzón, R. (2008). *Densidad de jaguares en la Concesión Comunitaria de Carmelita y Asociación Forestal Integral San Andrés Petén, Reserva de la Biosfera Maya*. Flores, Guatemala.
- Miller, C. M. (2006). *Jaguar density in Fireburn, Belize* (p. 11).
- Montaño, R. R., Maffei, L., & Noss, A. J. (2007). *Segundo muestreo con trampas cámaras de jaguares y otros mamíferos en el Campamento Palmar de las Islas y Ravelo*. Santa Cruz, Bolivia.
- Moreira, J., McNab, R. B., Thornton, D., García, R., Méndez, V., Vanegas, A., ... Córdova, M. (2007). *The comparative abundance of jaguars in La Gloria-El Lechugal, Multiple Use Zone, Maya Biosphere Reserve, Guatemala*. Flores, Guatemala.
- Paviolo, A., De Angelo, C. D., Di Blanco, Y. E., & Di Bitetti, M. S. (2008). Jaguar *Panthera onca* population decline in the Upper Paraná Atlantic Forest of Argentina and Brazil. *Oryx*, 42(04), 554. doi:10.1017/S0030605308000641

- Polisar, J. (2006). *Jaguares, presas y gente en Territorios Indígenas Mayangna Sauni Bu, Reserva Biosfera Bosawas*. Managua, Nicaragua.
- Romero-Muñoz, A. (2008). *Densidad, patrones de actividad y comportamiento espacial de felinos en dos sitios del Gran Chaco con diferente presión de ganadería*. Universidade Mayor de San Simon.
- Romero-Muñoz, A., Maffei, L., Cuéllar, E., & Noss, A. J. (2010). Temporal separation between jaguar and puma in the dry forests of southern Bolivia. *Journal of Tropical Ecology*, 26(03), 303. doi:10.1017/S0266467410000052
- Salom-Pérez, R., Carrillo, E., Sáenz, J. C., & Mora, J. M. (2007). Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. *Oryx*, 41(01), 51. doi:10.1017/S0030605307001615
- Silveira, L. (2004). *Ecologia comparada e conservação da onça-pintada (Panthera onca) e onça-parda (Puma concolor) no Cerrado e Pantanal*. Universidade de Brasília.
- Silveira, L., Jácomo, A. T. a., Astete, S., Sollmann, R., Tôrres, N. M., Furtado, M. M., & Marinho-Filho, J. (2009). Density of the Near Threatened jaguar *Panthera onca* in the caatinga of north-eastern Brazil. *Oryx*, 44(01), 104–109. doi:10.1017/S0030605309990433
- Silver, S. C., Ostro, L. E. T., Marsh, L. K., Maffei, L., Noss, A. J., Kelly, M. J., ... Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, 38(2), 1–7. doi:10.1017/S0030605303000000
- Soisalo, M. K., & Cavalcanti, S. M. C. C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129(4), 487–496. doi:10.1016/j.biocon.2005.11.023

Supplementary Material B

Models used to test the predictive power of landscape configuration and spatial structure for jaguar population persistence probability. The models were ordinated according to their descriptive power and complexity. PC is the first principal component from the principal component analysis condensing landscape configuration. SFs (1-5) are spatial filters capturing the different spatial structures of the selected landscapes.

Variables	AICc	Δ AICc	AICc Weighted	Cumulative Weight
PC, SF3	8.33	0.00	0.24	0.24
PC, SF3, SF5	10.26	1.93	0.09	0.33
PC, SF2, SF3	10.49	2.17	0.08	0.41
PC	10.86	2.53	0.07	0.48
PC, SF3, SF4	11.12	2.80	0.06	0.53
PC, SF1, SF3	11.27	2.94	0.05	0.59
PC, SF2, SF5	11.41	3.08	0.05	0.64
PC, SF5	11.58	3.26	0.05	0.69
PC, SF4	12.50	4.17	0.03	0.72
PC, SF1	12.69	4.36	0.03	0.74
PC, SF2	12.80	4.48	0.03	0.77
PC, SF2, SF3, SF5	13.02	4.69	0.02	0.79
PC, SF2, SF3, SF4	13.12	4.79	0.02	0.81
PC, SF4, SF5	13.33	5.01	0.02	0.83
PC, SF1, SF3, SF5	13.40	5.07	0.02	0.85
PC, SF3, SF4, SF5	13.51	5.18	0.02	0.87

Variables	AICc	Δ AICc	AICc Weighted	Cumulative Weight
PC, SF1, SF5	13.53	5.21	0.02	0.89
PC, SF1, SF2, SF3	13.76	5.44	0.02	0.90
PC, SF2, SF4, SF5	14.27	5.94	0.01	0.91
PC, SF1, SF4	14.34	6.02	0.01	0.92
PC, SF1, SF3, SF4	14.40	6.07	0.01	0.94
PC, SF1, SF2, SF5	14.45	6.13	0.01	0.95
PC, SF1, SF2, SF3, SF4	14.91	6.58	0.01	0.96
PC, SF2, SF4	15.00	6.68	0.01	0.96
PC, SF1, SF4, SF5	15.13	6.81	0.01	0.97
PC, SF1, SF2	15.35	7.02	0.01	0.98
PC, SF2, SF3, SF4, SF5	16.45	8.12	0.00	0.98
PC, SF1, SF2, SF3, SF5	16.59	8.26	0.00	0.99
PC, SF1, SF3, SF4, SF5	16.96	8.63	0.00	0.99
PC, SF1, SF2, SF4	17.49	9.16	0.00	0.99
PC, SF1, SF2, SF3, SF4, SF5	17.51	9.19	0.00	1.00
PC, SF1, SF2, SF4, SF5	17.62	9.29	0.00	1.00
SF3	21.17	12.85	0.00	1.00
Null Model	21.54	13.22	0.00	1.00
SF3, SF4	22.09	13.76	0.00	1.00
SF1, SF3	22.27	13.95	0.00	1.00
SF1	22.98	14.65	0.00	1.00
SF4	23.56	15.24	0.00	1.00

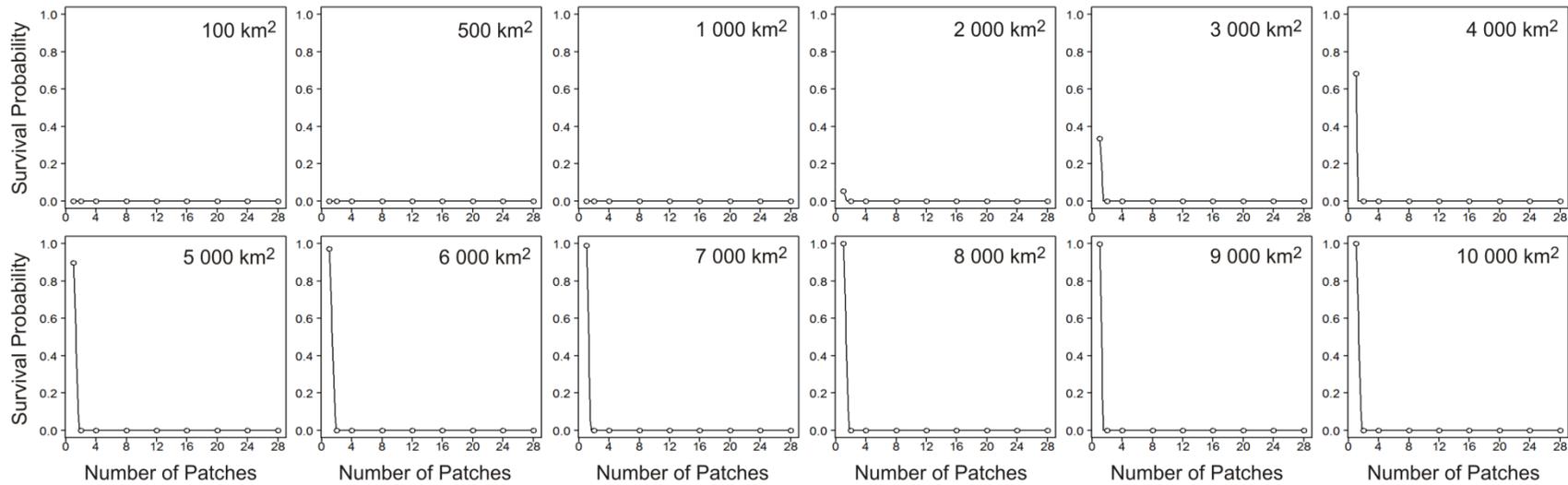
Variables	AICc	Δ AICc	AICc Weighted	Cumulative Weight
SF3, SF5	23.58	15.26	0.00	1.00
SF2, SF3, SF4	23.89	15.56	0.00	1.00
SF2, SF3	23.91	15.58	0.00	1.00
SF5	24.00	15.67	0.00	1.00
SF2	24.03	15.70	0.00	1.00
SF1, SF3, SF4	24.48	16.15	0.00	1.00
SF3, SF4, SF5	24.62	16.29	0.00	1.00
SF1, SF4	24.62	16.30	0.00	1.00
SF1, SF3, SF5	24.98	16.65	0.00	1.00
SF1, SF2, SF3	25.22	16.89	0.00	1.00
SF1, SF5	25.51	17.18	0.00	1.00
SF1, SF2	25.58	17.26	0.00	1.00
SF4, SF5	26.24	17.91	0.00	1.00
SF2, SF4	26.25	17.92	0.00	1.00
SF2, SF3, SF5	26.38	18.05	0.00	1.00
SF2, SF5	26.70	18.38	0.00	1.00
SF1, SF2, SF3, SF4	27.10	18.78	0.00	1.00
SF2, SF3, SF4, SF5	27.16	18.83	0.00	1.00
SF1, SF3, SF4, SF5	27.55	19.22	0.00	1.00
SF1, SF2, SF4	27.55	19.23	0.00	1.00
SF1, SF4, SF5	27.57	19.24	0.00	1.00
SF1, SF2, SF3, SF5	27.95	19.63	0.00	1.00

Variables	AICc	Δ AICc	AICc Weighted	Cumulative Weight
SF1, SF2, SF5	28.43	20.10	0.00	1.00
SF2, SF4, SF5	29.18	20.85	0.00	1.00
SF1, SF2, SF3, SF4, SF5	30.63	22.31	0.00	1.00
SF1, SF2, SF4, SF5	30.80	22.47	0.00	1.00

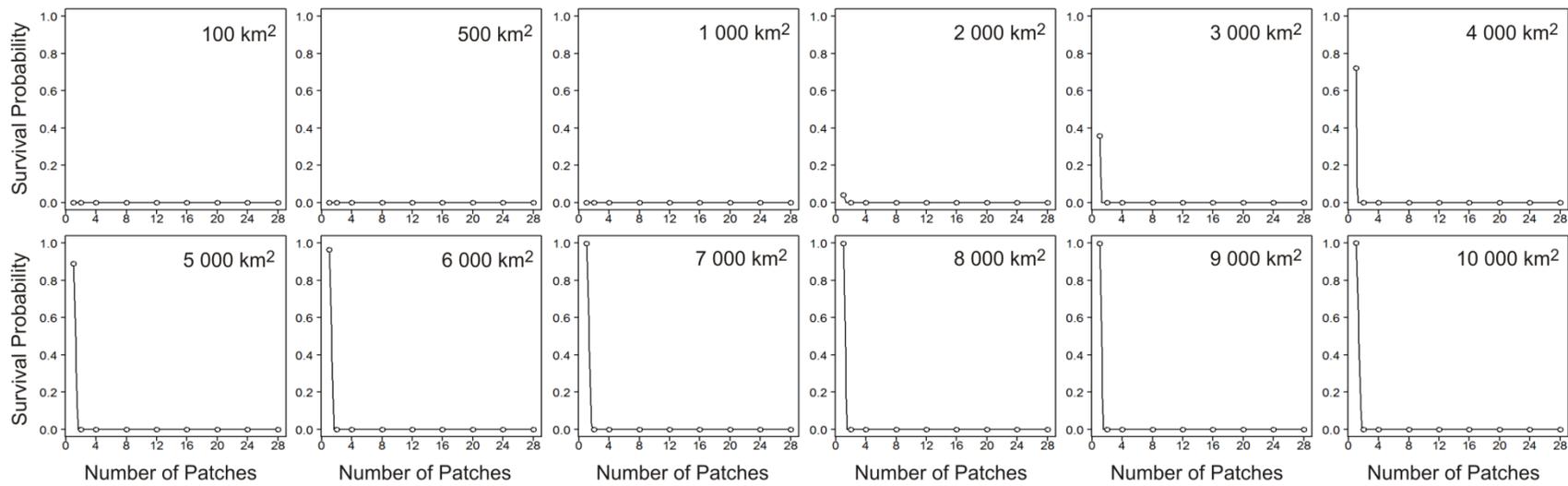
Supplementary Material C

Graphs generated by the piecewise linear regression and used to calculate the fragmentation critical thresholds. All scenarios failed to maintain viable jaguar metapopulations, so the analysis outcome presents a negative slope. Consequently, the critical thresholds indicated when metapopulation persistence probability became zero, which was not the focus of our study. The values within the graphs are the landscape total area for each simulation.

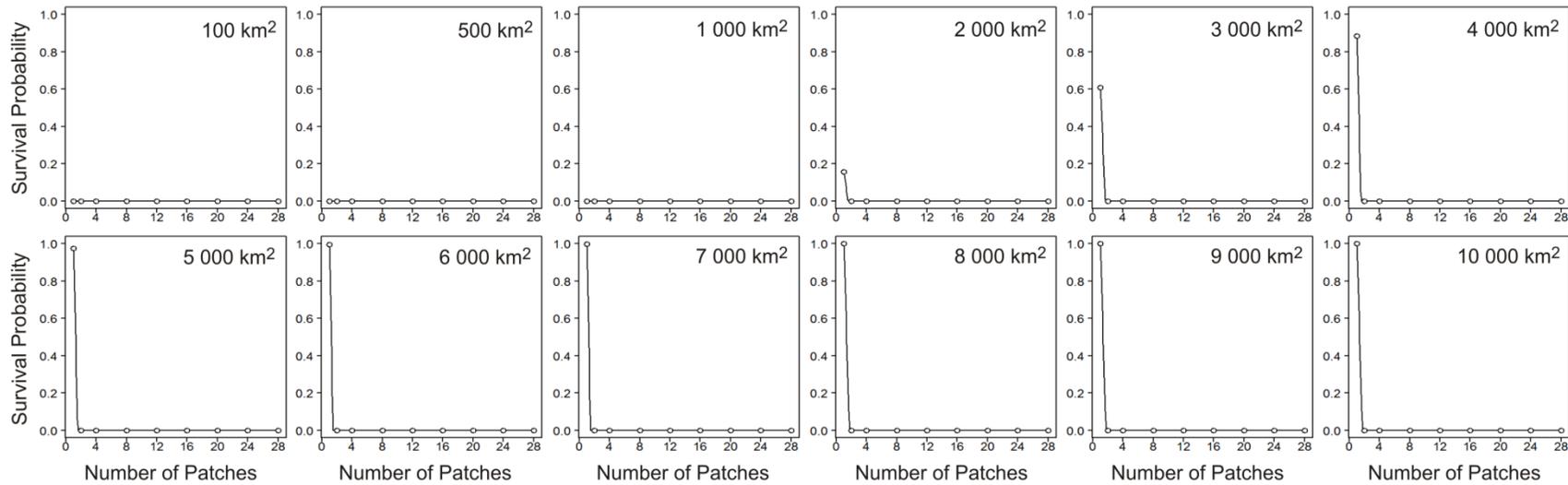
Scenarios to jaguar density = 1.12 (100 km²)



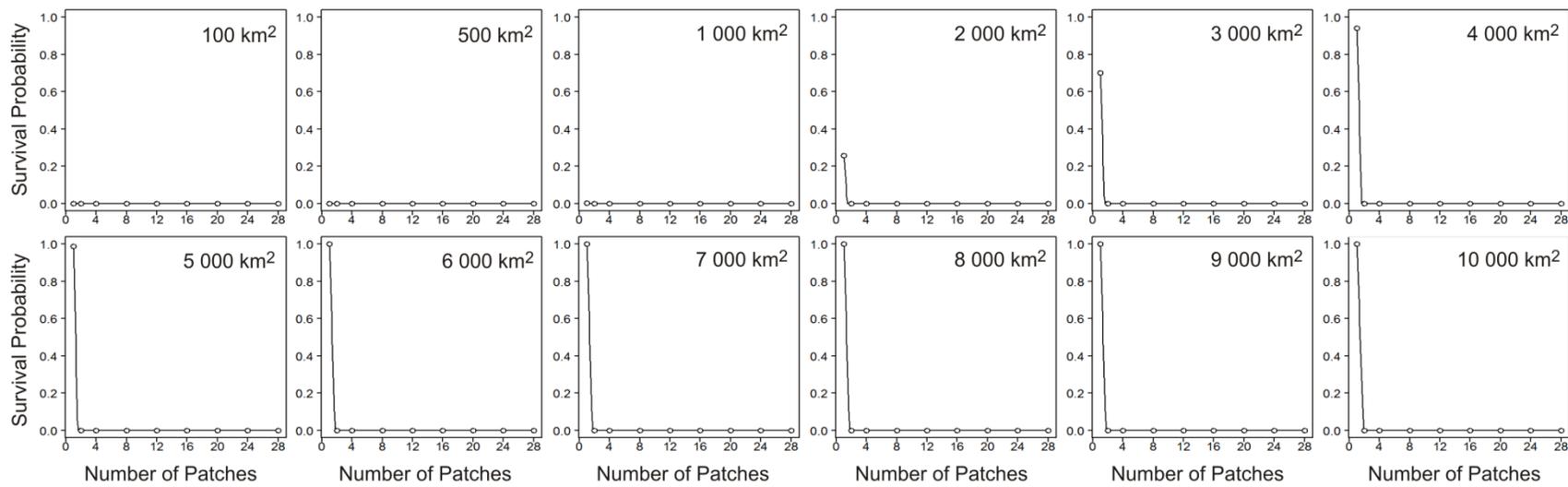
Scenarios to jaguar density = 1.13 (100 km²)



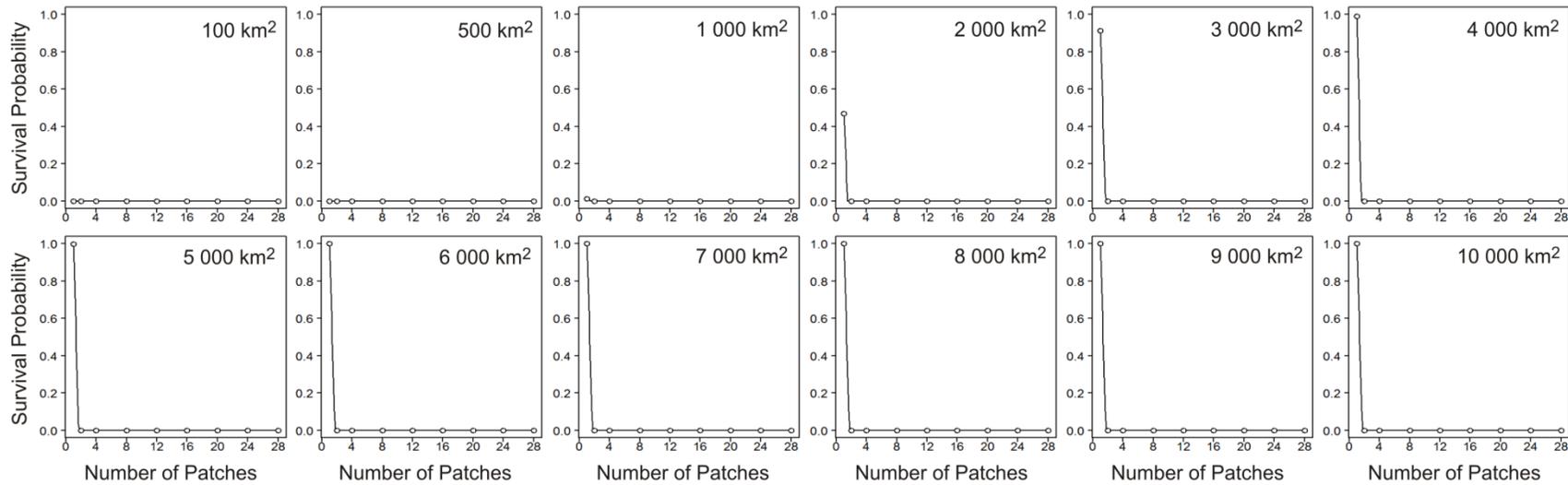
Scenarios to jaguar density = 1.38 (100 km²)



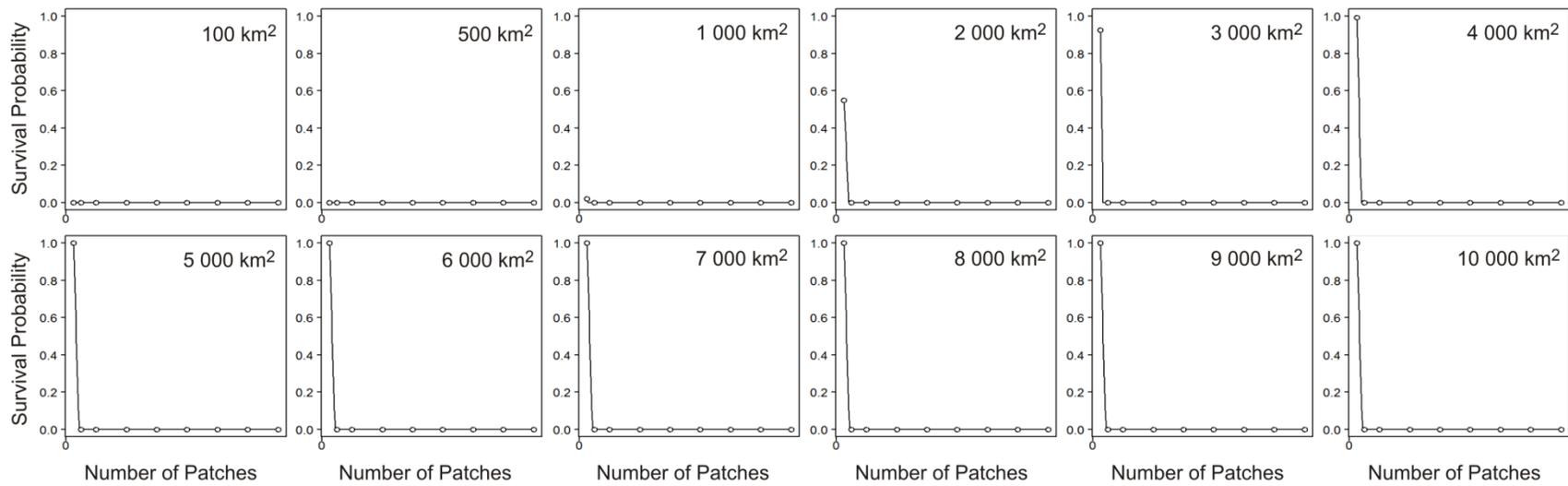
Scenarios to jaguar density = 1.54 (100 km²)



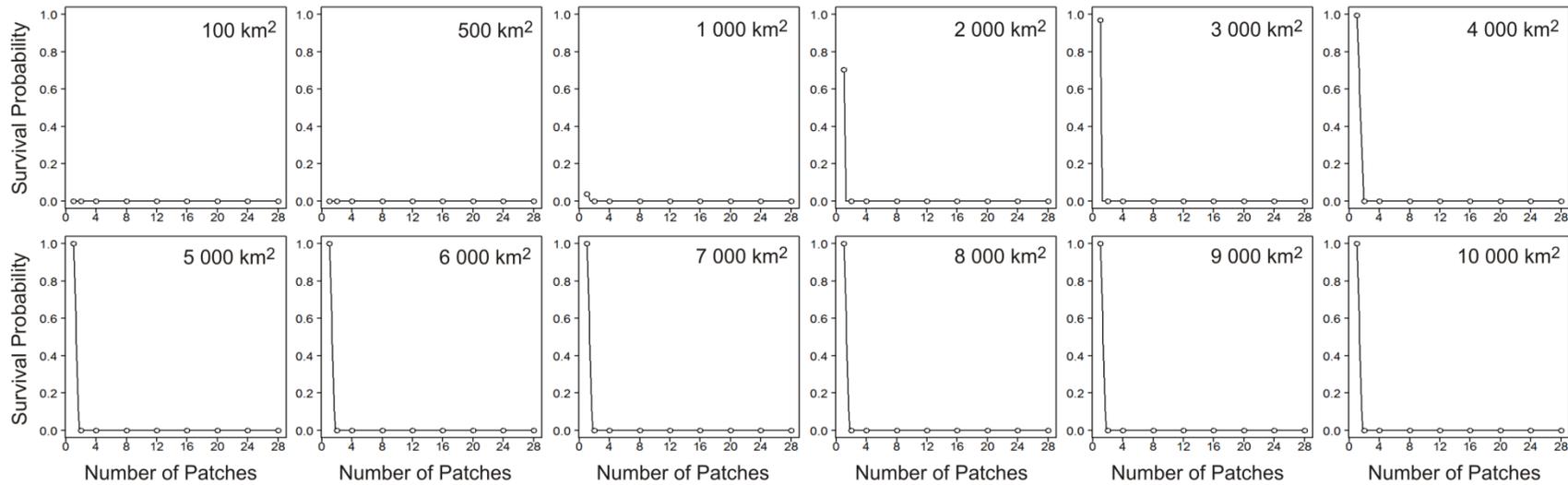
Scenarios to jaguar density = 1.92 (100 km²)



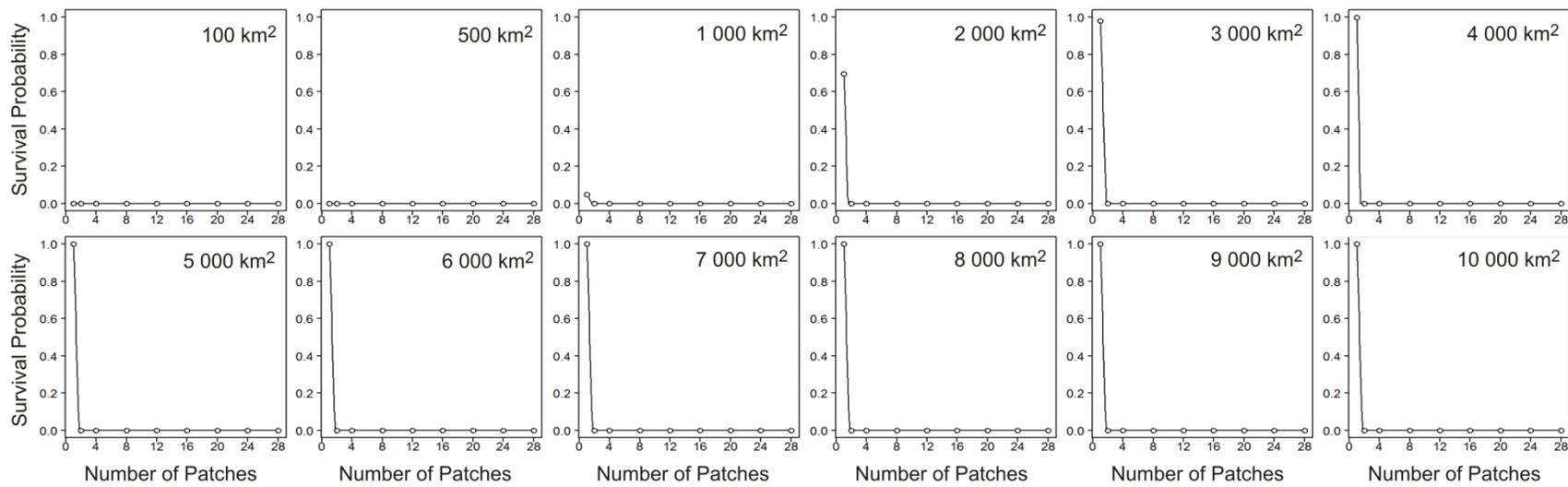
Scenarios to jaguar density = 2.00 (100 km²)



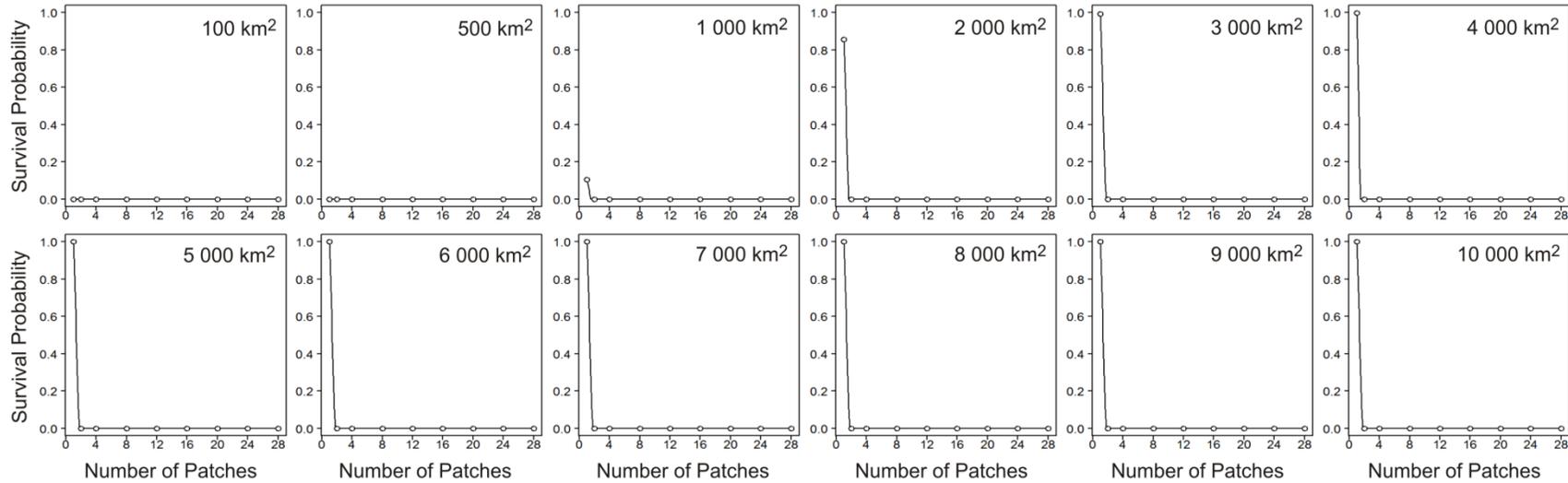
Scenarios to jaguar density = 2.22 (100 km²)



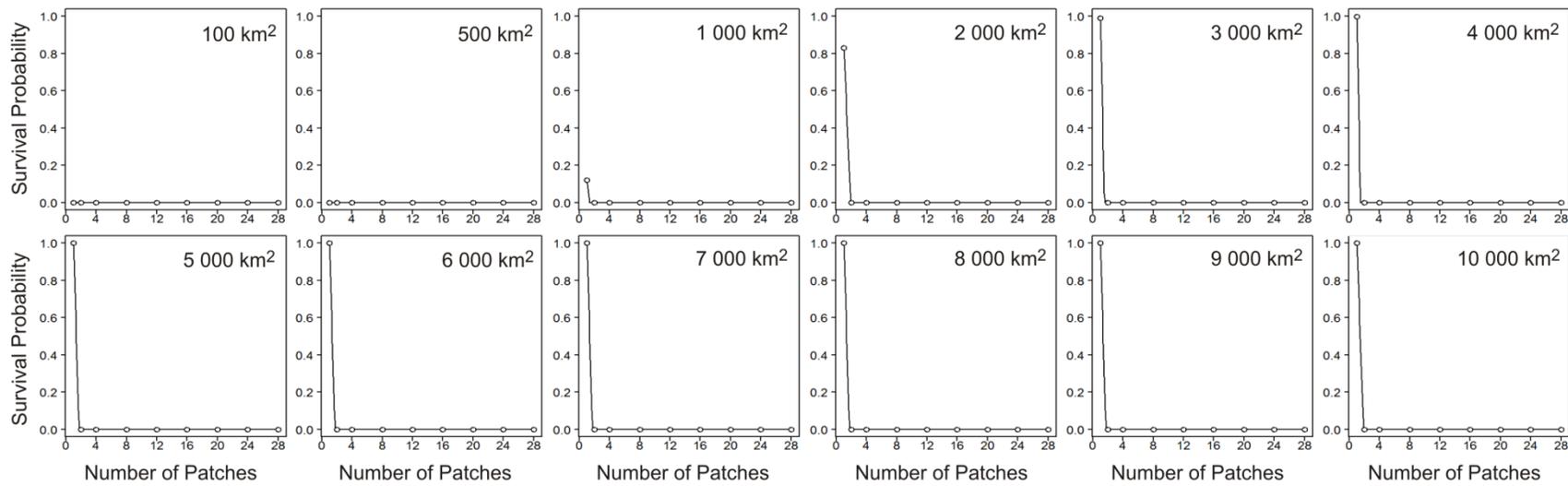
Scenarios to jaguar density = 2.28 (100 km²)



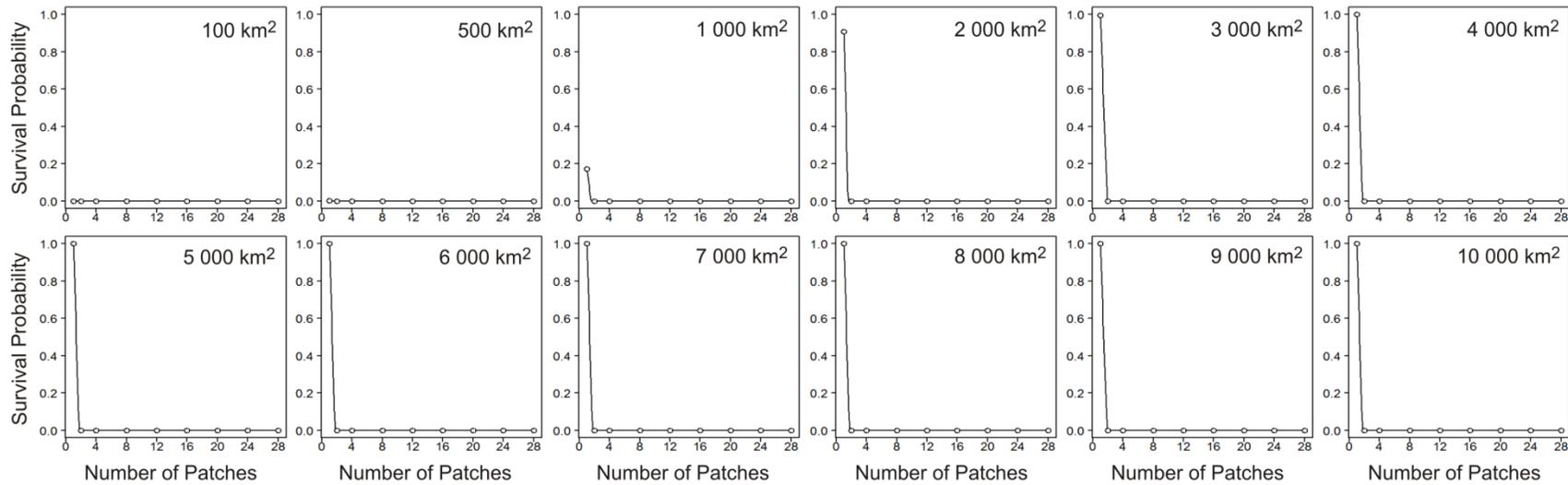
Scenarios to jaguar density = 2.59 (100 km²)



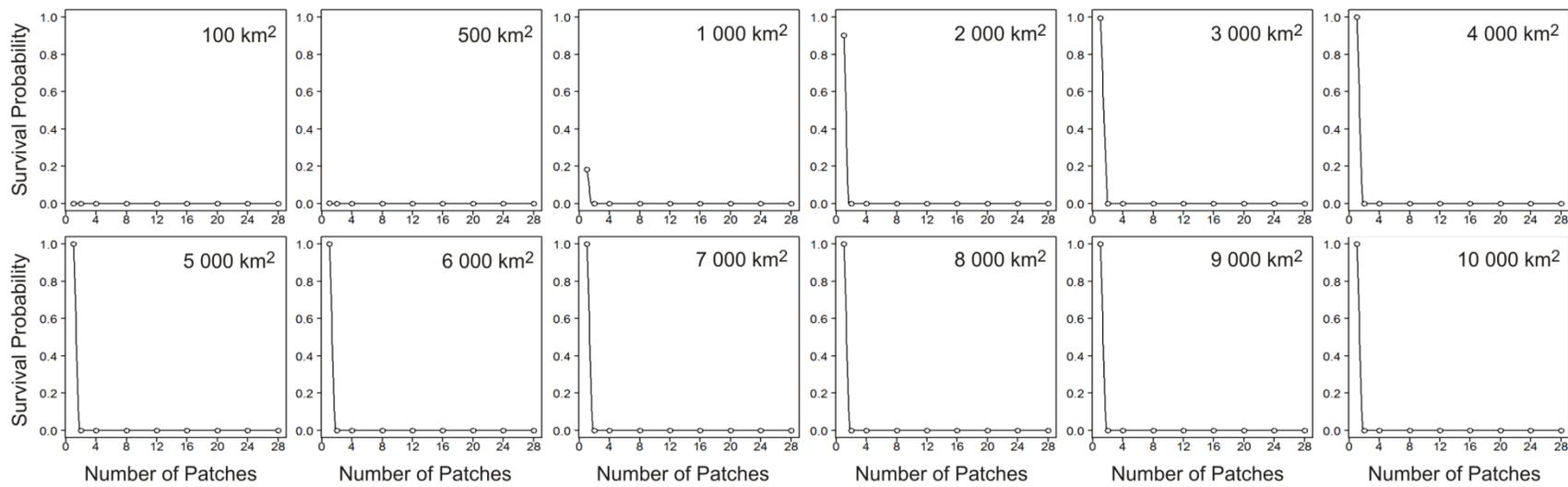
Scenarios to jaguar density = 2.67 (100 km²)



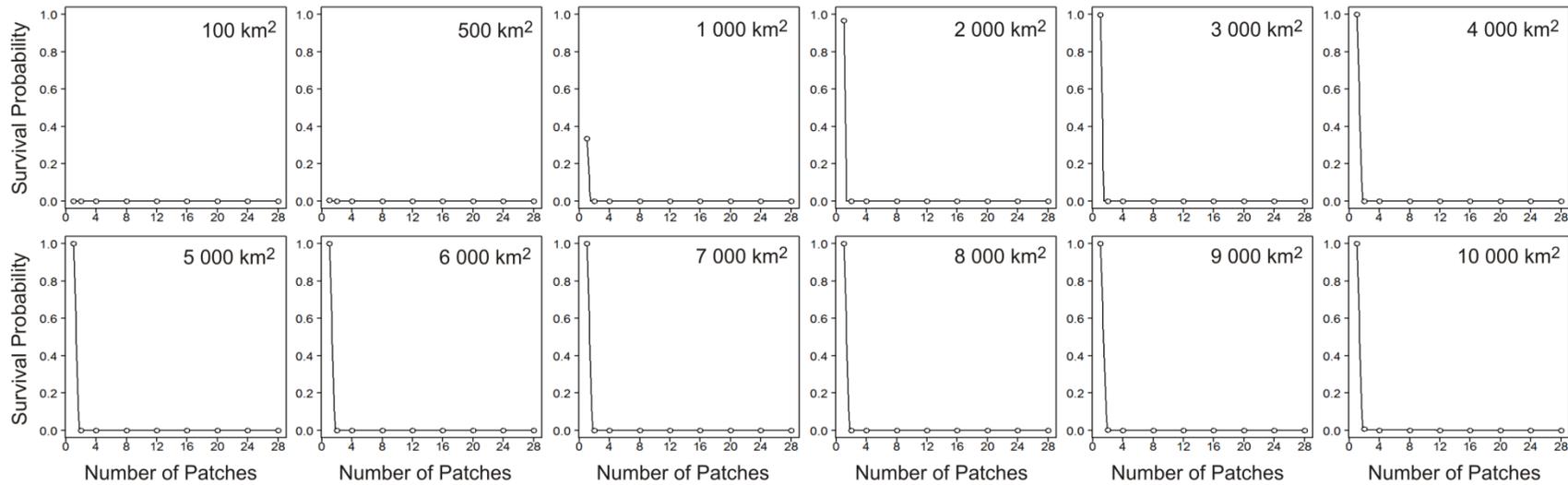
Scenarios to jaguar density = 2.84 (100 km²)



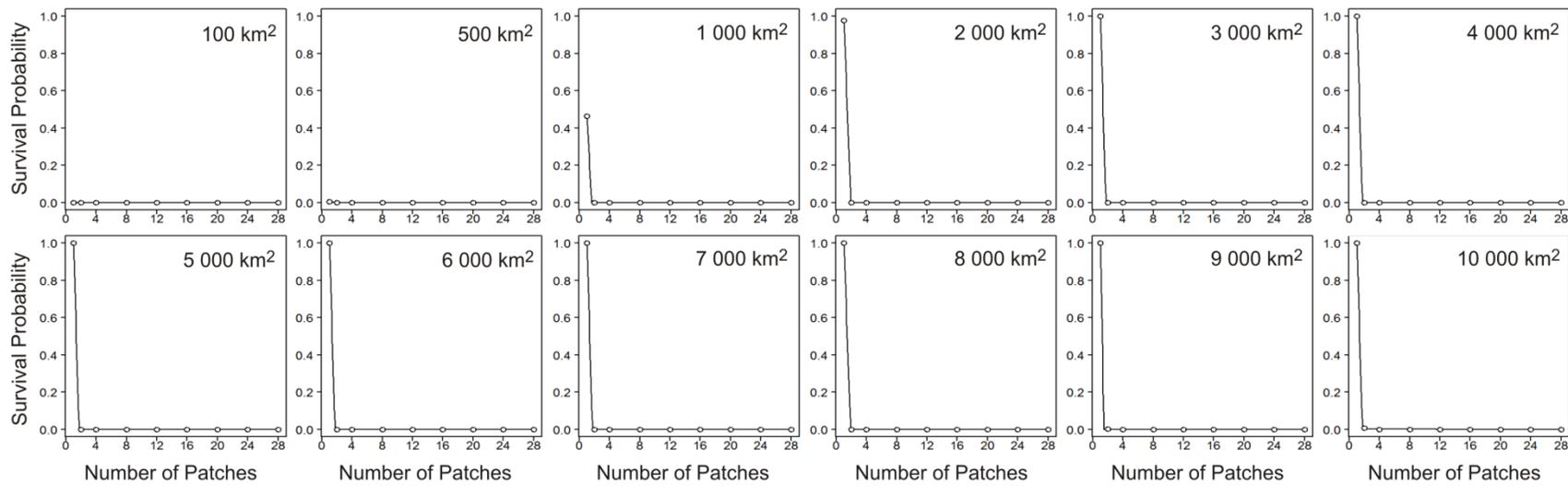
Scenarios to jaguar density = 2.91 (100 km²)



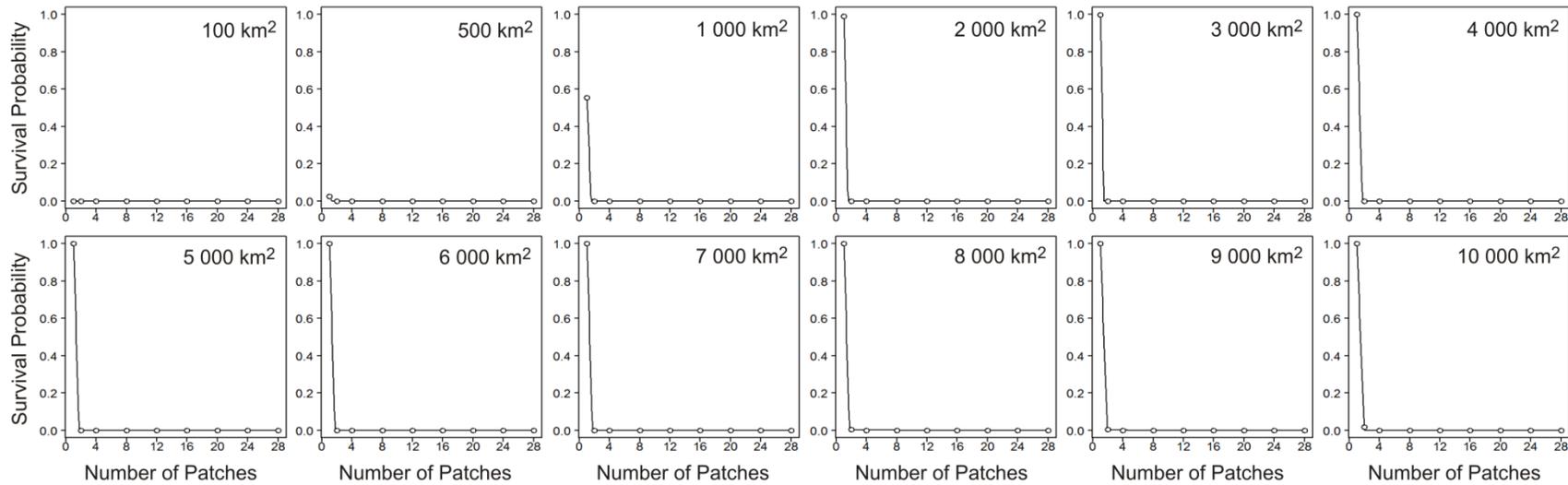
Scenarios to jaguar density = 3.14 (100 km²)



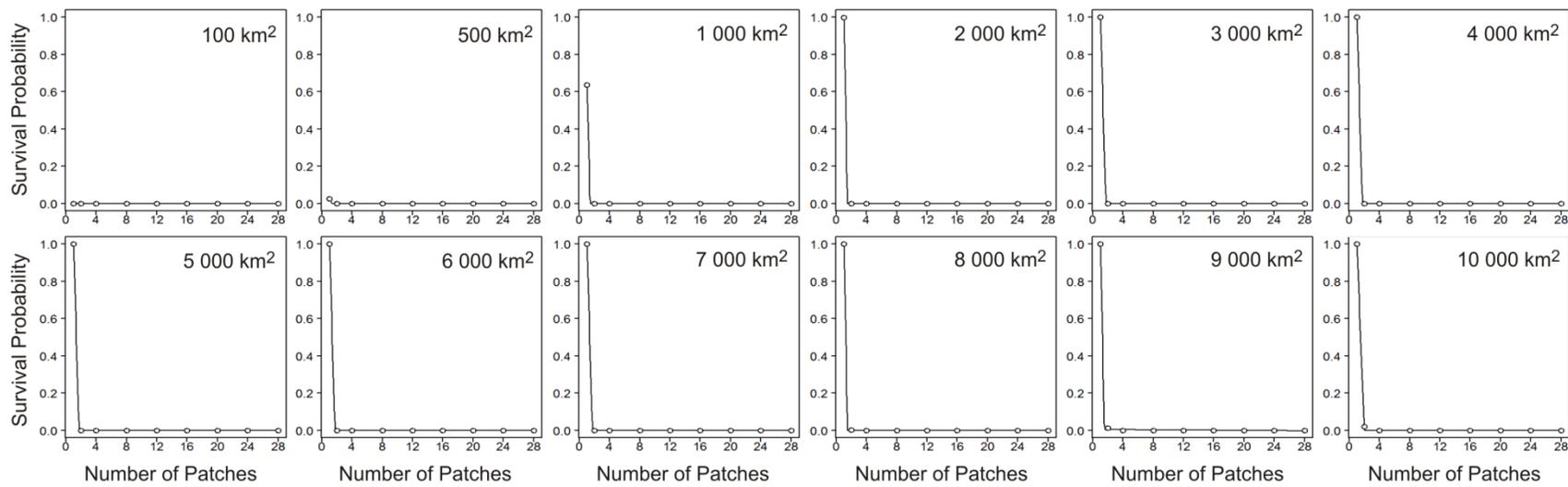
Scenarios to jaguar density = 3.70 (100 km²)



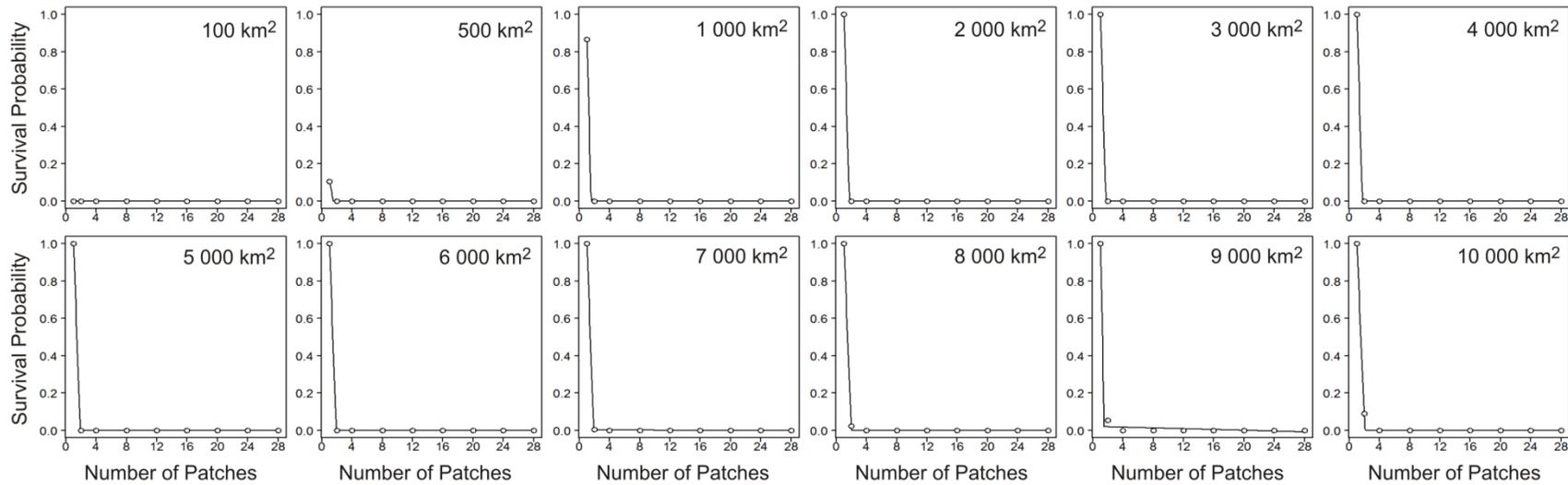
Scenarios to jaguar density = 4.13 (100 km²)



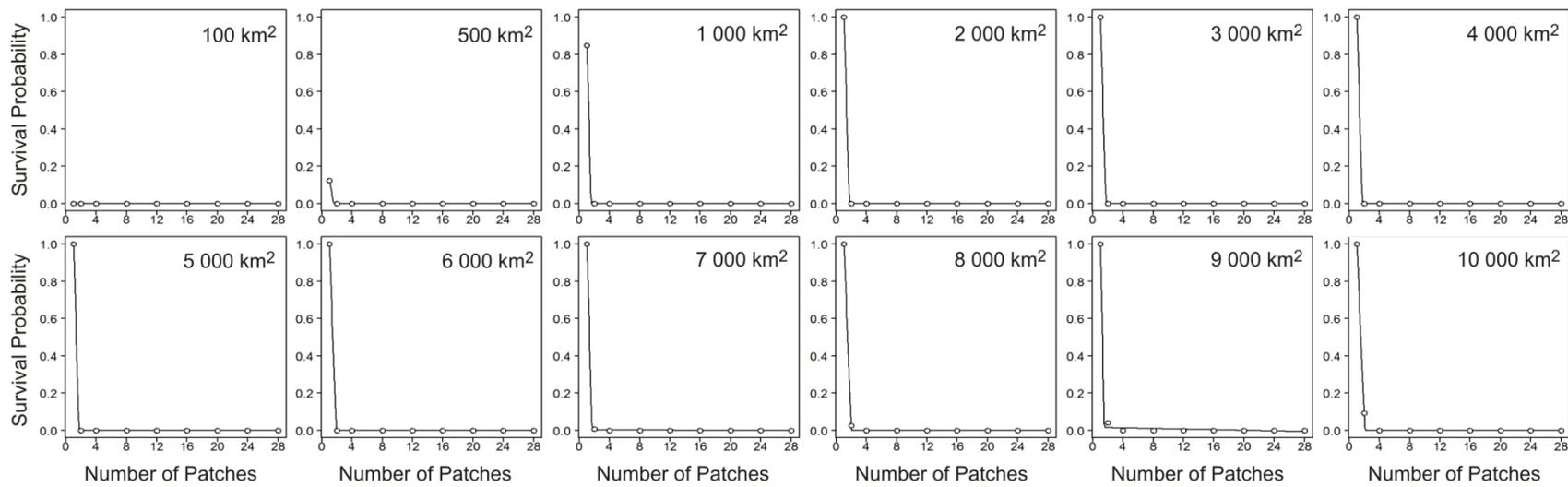
Scenarios to jaguar density = 4.23 (100 km²)



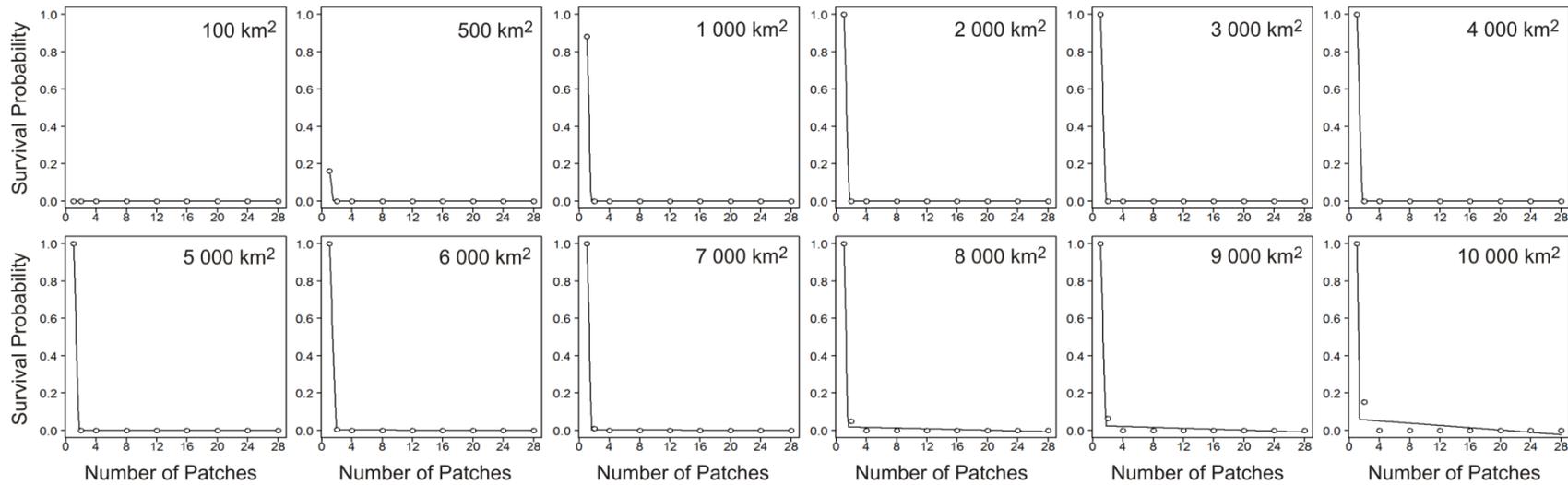
Scenarios to jaguar density = 5.24 (100 km²)



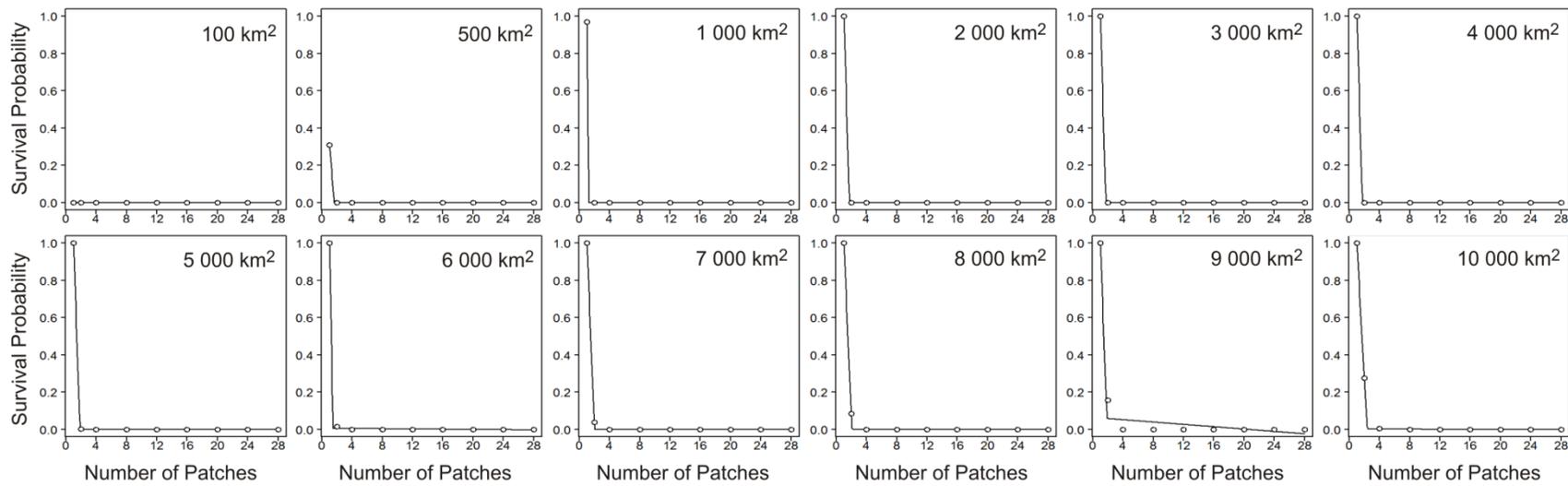
Scenarios to jaguar density = 5.30 (100 km²)



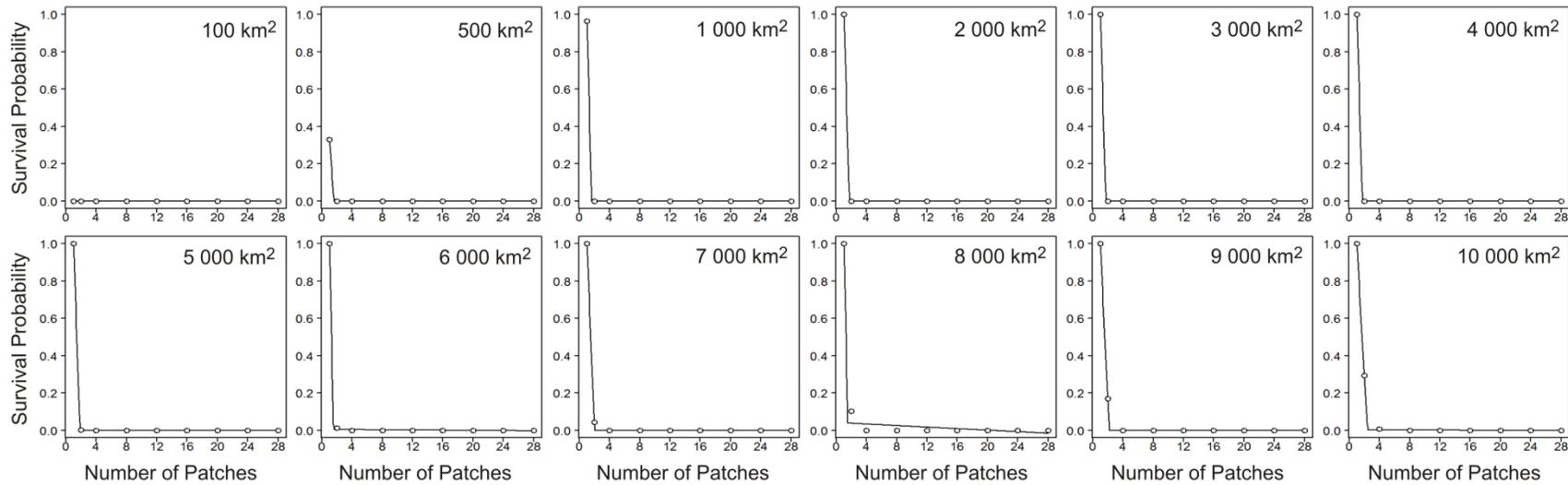
Scenarios to jaguar density = 5.66 (100 km²)



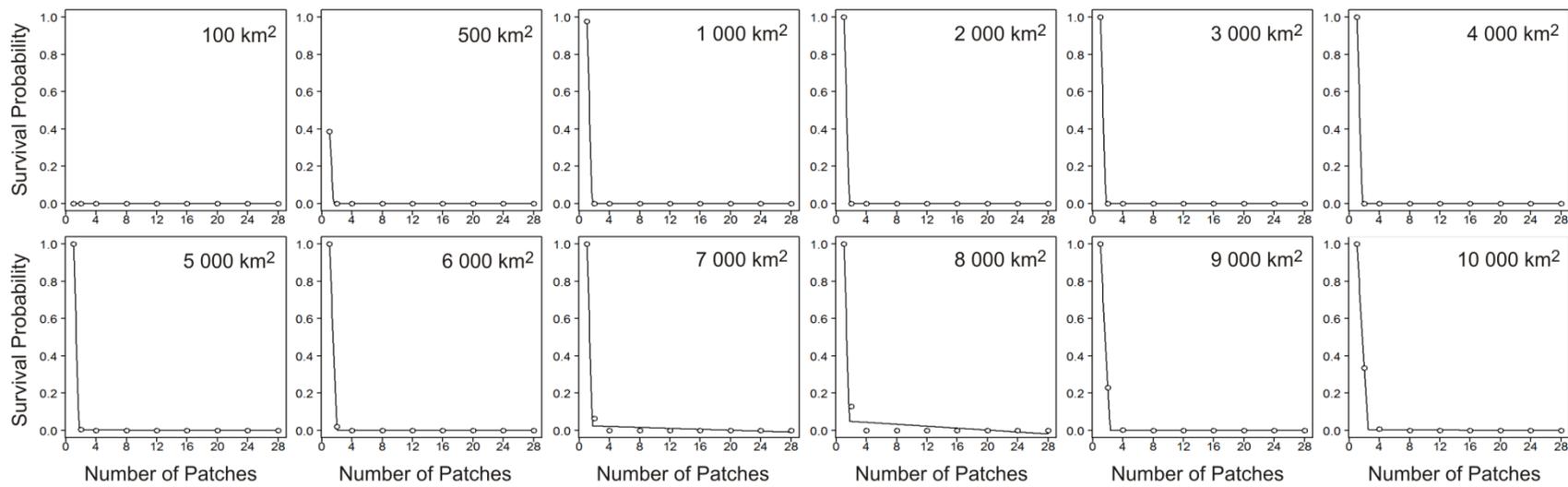
Scenarios to jaguar density = 6.63 (100 km²)



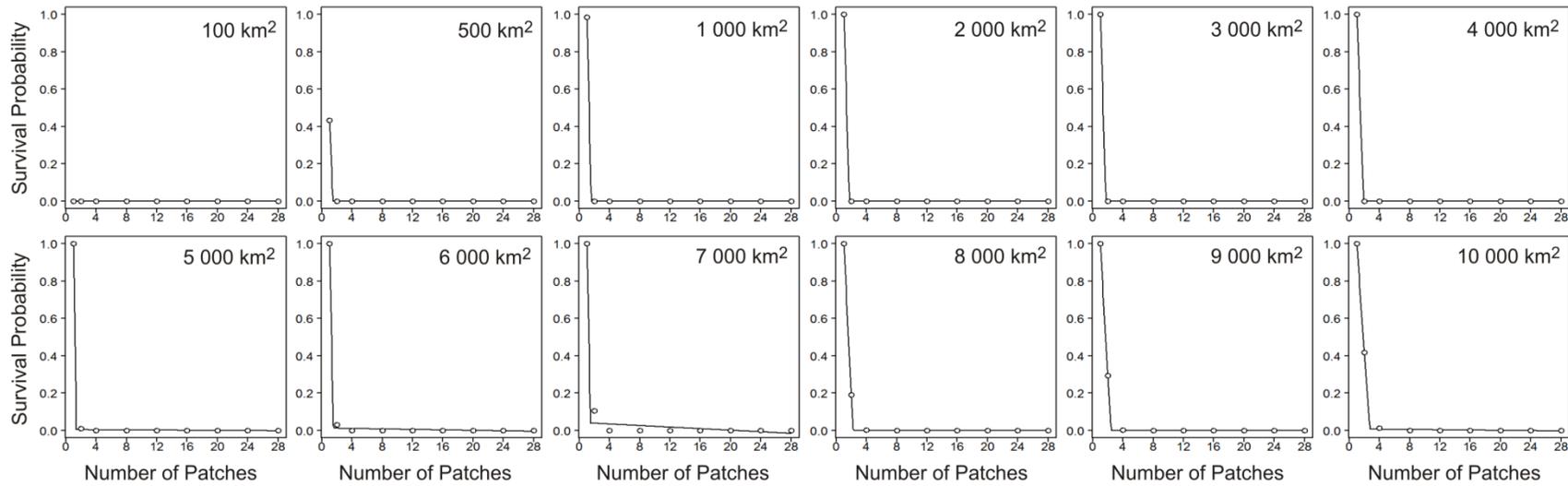
Scenarios to jaguar density = 6.70 (100 km²)



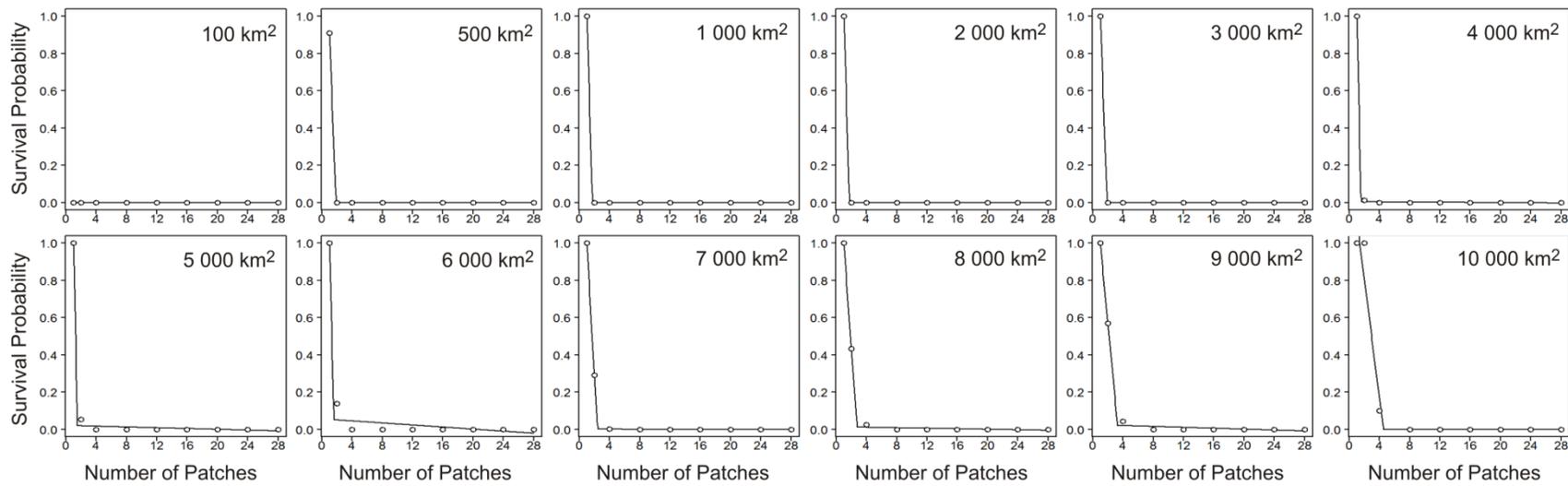
Scenarios to jaguar density = 6.98 (100 km²)



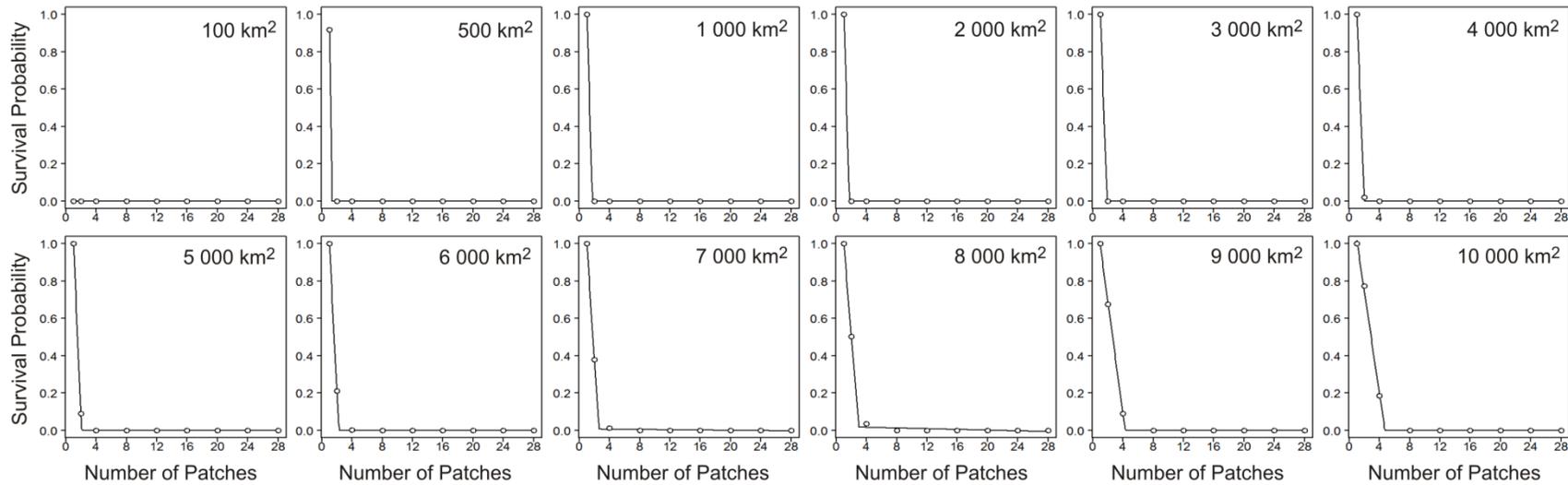
Scenarios to jaguar density = 7.48 (100 km²)



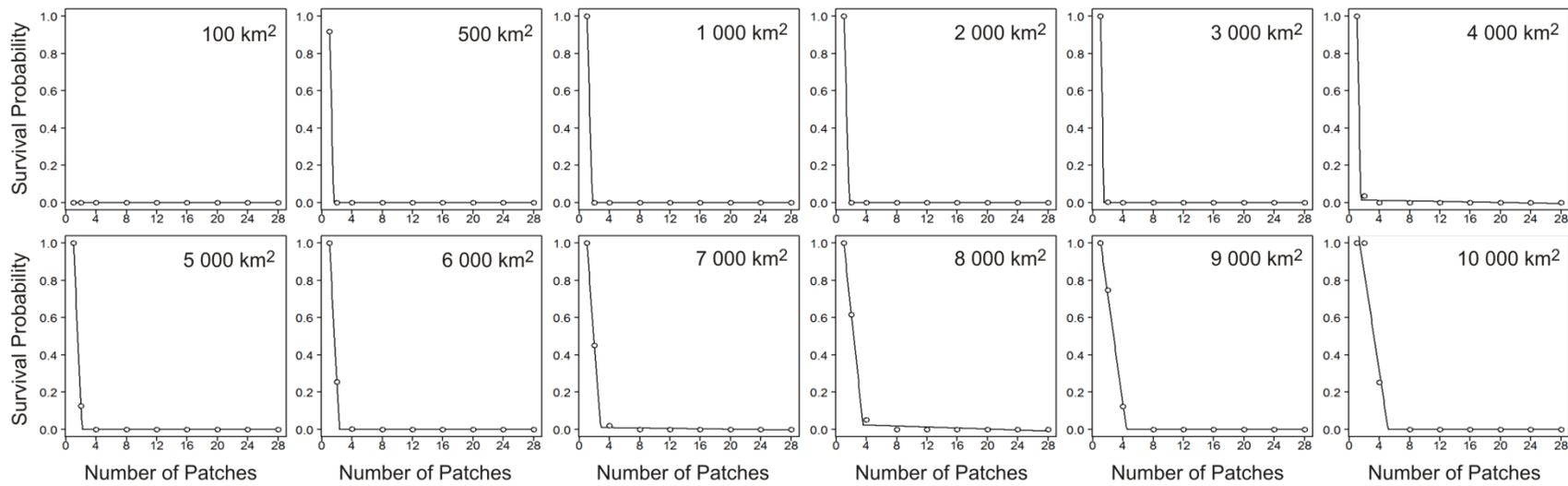
Scenarios to jaguar density = 9.60 (100 km²)



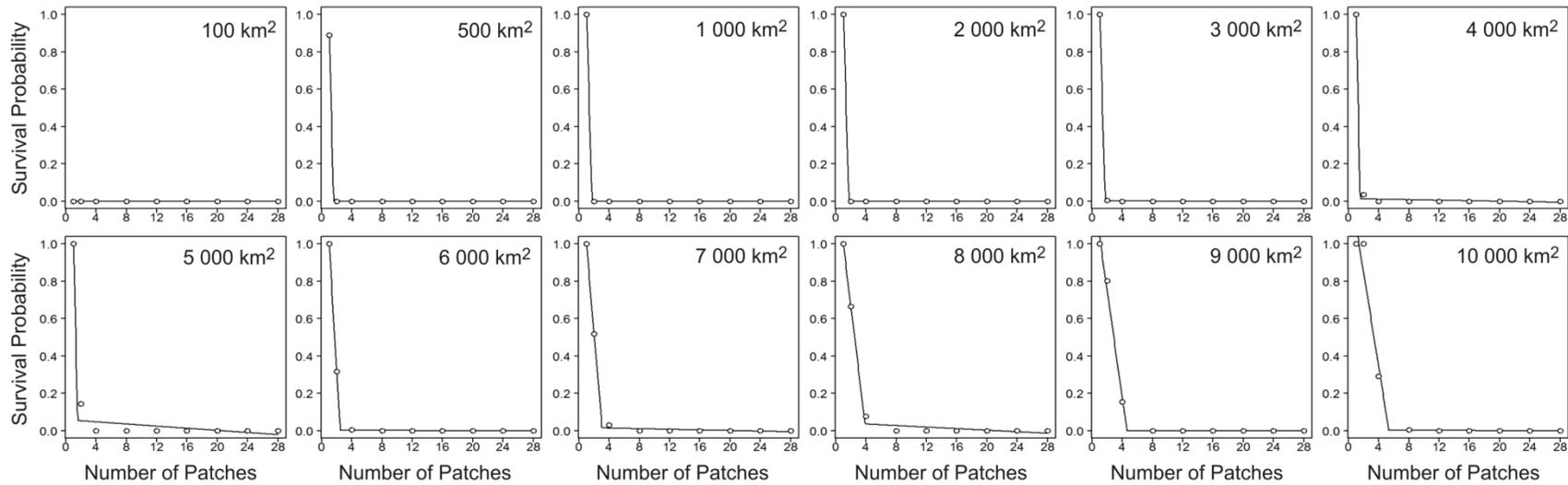
Scenarios to jaguar density = 10.50 (100 km²)



Scenarios to jaguar density = 11.00 (100 km²)



Scenarios to jaguar density = 11.56 (100 km²)



CAPÍTULO 3

Esse capítulo segue as normas de formatação da revista *Molecular Ecology*.

1 **Landscape genetics of American felids: from regional to local scales**

2

3 Zanin, M.^{1*}; Adrados, B.²; Roques, S.²; Brito, D.¹; González, N.²; Chavez, C.³; Rubio,

4 Y⁴; Palomares, F.²

5

6 ¹ Departamento de Ecología, Universidade Federal de Goiás, Caixa Postal 131, CEP

7 74001-970, Goiania, Goiás, Brazil.

8

9 ² Department of Conservation Biology, Estación Biológica de Doñana CSIC; Avenida

10 Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla, Spain.

11

12 ³ Universidad Autónoma Metropolitana-Unidad Lerma, Lerma de Villada, México,

13 México.

14

15 ⁴ Universidad de Sinaloa, Ciudad Universitaria SN, Ciudad Universitaria, 80040

16 Culiacán Rosales, Sinaloa, México.

17

18 * Corresponding author: marinazaning@gmail.com

19 **Landscape genetics of American felids: from regional to local scales**

20

21 **1. Abstract**

22 Human induced changes in landscapes can modify environmental permeability, which
23 affects gene flow and the genetic structure of species. We investigated such changes in
24 the genetic structure of puma and jaguar populations, from the regional to the local
25 scale. In order to address this issue, we first tested the hypotheses of isolation by
26 distance, isolation by effective distance, and isolation by resistance. We used
27 individuals pairwise distance analyses to calculate landscape isolation and correlated
28 these measures with genetic distances. Then, we evaluated the genetic structure through
29 cluster analysis, delineating species populations and subpopulations. We found that
30 jaguars and pumas are not a uniform and panmictic population. At the regional scale,
31 spatial trends in allele frequencies for both species generated clinal patterns. However,
32 their genetic structures differed at the local scales, both in terms of the numbers of
33 subpopulations and their limits. Therefore, we observed two levels of genetic
34 structuring (clines and clusters), occurring simultaneously, but at different scales. These
35 patterns were generated according to isolation by distance because the landscape could
36 be considered pristine, due to its low complexity. Lower genetic structuring was
37 expected for jaguar because they have greater movement ability in pristine areas.
38 However, it is known that pumas have greater movement ability plasticity in
39 anthropogenic vegetation, so we suggest new studies comparing the genetic structure
40 for both jaguars and pumas in areas with a higher degree of habitat loss and
41 fragmentation.

42

- 43 **Key words:** clinal pattern; isolation by distance; spatial principal component analysis;
- 44 discriminant analysis of principal components; *Panthera onca*; *Puma concolor*.

45 **2. Introduction**

46 Gene flow is a mechanism that ensures gene movement among populations,
47 which homogenizes allele frequencies (Slatkin 1985). Gene flow is of critical
48 importance for a wide array of demographic and evolutionary processes, such as the
49 regulation of local adaptation, polymorphism, effective population size, genetic drift,
50 selection and speciation (Lenormand 2002; Bolnick & Otto 2013). Species dispersal
51 abilities play an important role on a given population's genetic structure, as it is a
52 mechanism for gene transfer among populations and subpopulations (Lenormand 2002;
53 François & Durand 2010). Since landscape permeability affects dispersal success, it has
54 a major impact on gene flow (Baguette & Van Dyck 2007; Pérez-Espona *et al.* 2012).

55 Human-induced landscape changes can produce discontinuities in the
56 environment and modify its permeability due to alterations of the composition and
57 configuration of the landscape (Ewers & Didham 2006; Fischer & Lindenmayer 2007).
58 Such changes may modify the genetic structure of species because they inhibit natural
59 patterns of gene flow and alter the distribution of genetic variation, thereby restricting
60 dispersal and isolating populations (Guillot *et al.* 2005; Vandergast *et al.* 2007; Walker
61 *et al.* 2008). Susceptibility to human-induced landscape changes is related to species
62 ecological plasticity (Davidson *et al.* 2009; Thornton *et al.* 2011), so it is expected that
63 species with high ecological plasticity are less affected (or sometimes even favored) by
64 landscape changes than species with strict environmental requirements (Ryall & Fahrig
65 2006; Villard & Metzger 2013). Therefore, comprehending how landscape alterations
66 affect species' spatial genetic structure is fundamental to their conservation and should
67 guide the design of management strategies (Eizirik *et al.* 2001; Schmidt *et al.* 2011;
68 Loxterman 2011).

69 Here, we investigated the genetic structure of the largest felids of the Americas,
70 the puma (*Puma concolor*, Linnaeus, 1771) and the jaguar (*Panthera onca*, Linnaeus
71 1758). Pumas and jaguars have a continental distribution (IUCN 2013), suggesting both
72 species exhibit high environmental plasticity. However, their historical distribution has
73 largely been reduced by human-induced landcover changes (Morrison *et al.* 2007).
74 Currently, pumas and jaguars are not listed as globally threatened, but both species
75 display a general trend of population declines (IUCN 2013). Studies at smaller scales
76 have diagnosed habitat loss and fragmentation as a threat to both species, generating
77 isolated (Haag *et al.* 2010; Andreassen *et al.* 2012) and unviable populations (Reed 2004;
78 Hostetler *et al.* 2012; Galetti *et al.* 2013). These effects seem to be more severe in
79 jaguars than in pumas (IUCN 2013) because jaguars are less tolerant of anthropogenic
80 alterations in their environment (De Angelo *et al.* 2011).

81 Due to their large distributional range and the wide scale of potential genetic
82 responses, our study tested how dispersal capacity influences the local and regional
83 genetic structure of pumas and jaguars. We investigated the spatial genetic structure at
84 the regional scale by searching for a clinal pattern for both species. To do this, we
85 measured the strength of the signal of isolation by distance in the structuring of genetic
86 variation *sensu* (Wright 1943). We also estimated the relative importance of landscape
87 and environmental variables on gene flow, testing both the hypotheses of isolation by
88 effective distance *sensu* (Adriaensen *et al.* 2003) and isolation by resistance *sensu*
89 (McRae 2006).

90 Afterwards, we examined genetic structuring at a smaller scale, looking for
91 genetic clusters and delineating populations and subpopulations. Here, we examined the
92 difference in genetic structure (here measured as the number of clusters) between both
93 species. Current theory predicts that dispersal capacity is positively correlated with

94 body size (Whitmee & Orme 2013), so we expected jaguars to be able to disperse over
95 longer distances than pumas. As a consequence, genetic structuring should be lower in
96 jaguars. However, pumas have greater environmental plasticity, making them more
97 efficient at moving across human-modified landscapes (Dickson *et al.* 2005; De Angelo
98 *et al.* 2011). Consequently, pumas might have greater dispersal capacity in
99 anthropogenic landscapes than jaguars. Therefore, we have two predictions according to
100 the level of anthropogenic influence on the landscape: (i) we expect a larger number of
101 clusters for jaguars in anthropogenic landscapes; and (ii) a larger number of clusters for
102 pumas in pristine landscapes.

103

104 **3. Methods**

105

106 **3.1. Sample collection and laboratory procedures**

107 Our study area is located in Mexico between longitudes 107° 52' 12"W and 86°
108 31' 48" W and latitudes 24° 27' N and 14° 28' 48" N (Figure 1), covering more than 50%
109 of the country and comprising 27 states. The study area still contains a large proportion
110 of pristine habitat, composed of grasslands, scrublands, temperate forests, and lowland,
111 medium and montane forests (Bontemps *et al.* 2011). The study area also contains
112 anthropogenic landcover, especially agriculture and urban areas (Bontemps *et al.* 2011).
113 Fecal samples were collected from nine opportunistically-selected locations within the
114 study area (Figure 1). As a result, the sampling locations were not equidistant from each
115 other, varying from 60 km to 1900 km apart.

116 The genomic data was obtained from fecal DNA extracted from feces collected
117 between 2005 and 2012. Fecal DNA is a non-invasive technique that has been
118 successfully used in feline monitoring (Palomares *et al.* 2002; Bhagavatula & Singh

119 2006; Perez *et al.* 2006; Mondol *et al.* 2009; Borthakur *et al.* 2010). The samples were
120 collected through actively searching along dirt roads and trails. The location of each
121 fecal sample was georeferenced using a GPS and it was stored in silica gel until genetic
122 analyses were conducted.

123 The DNA was extracted using a GuSCN/silica method (Boom *et al.* 1990; Frantz
124 *et al.* 2003), and then purified and concentrated by ultra-filtration using Microcon-30
125 (Millipore). Species identification was performed according to Roques *et al.* 2011.
126 Individual genotyping was conducted using an optimized set of different microsatellite
127 markers for each species. For jaguars, we used 11 domestic cat microsatellite markers
128 (Fca024, Fca126, F115a, Fca176, Fca026, Fca082b, Fca077, Fca090, Fca043, Fca547b,
129 and Fca566b; Menotti-Raymond *et al.* 1999); whereas, for pumas, we used 12
130 microsatellite markers, eight of which were originally described for pumas (Kurushima
131 *et al.* 2006) and four for cats (PcoA208, PcoA216, PcoA339, PcoB003, PcoB010,
132 PcoB210, PcoC108, PcoC112, Fca077, Fca82b, Fca126, and Fca547b). For a detailed
133 description of these methods, see Roques *et al.* (2014) and Villela *et al.* (unpublished
134 data).

135

136 **3.2. Distance models**

137 We adopted individual-based analyses to measure the degree of isolation in
138 terms of puma and jaguar genetic structuring. We constructed a distance matrix from all
139 possible pairwise combinations of individuals. This approach organized the data
140 according to the similarity of the genetic profile of each individual to those of all other
141 individuals tested. For individuals having more than one record, we randomly selected
142 one of its locations to be used in the pairwise distance analyses.

143 We calculated the classical Euclidian distance to test the hypothesis of isolation
144 by distance, which consisted of the shortest distance between pairs of individuals. We
145 developed cost and resistance models to test both of our hypotheses. The cost models
146 adopted least-cost route analysis, which estimates efficient movement routes and costs
147 in landscapes (Adriaensen *et al.* 2003). The resistance models were a random walk
148 prediction of species movements generated from a connectivity measure based on
149 circuit theory (McRae 2006).

150 We selected a set of variables to express landscape components that could affect
151 jaguar and puma movement and, consequently, gene flow. Variable selection was based
152 on studies of habitat suitability and animal movement for both jaguars and pumas,
153 trying to select studies conducted in areas as similar as possible to our study area. For
154 jaguars, we constructed the cost and resistance models based on the studies of Conde *et*
155 *al.* (2010) and Colchero *et al.* (2011), which highlighted the effects of distance to roads,
156 human population density and landcover. For pumas, the variables selected for the cost
157 and resistance models were road density, landcover, and elevation (Dickson *et al.* 2005;
158 Burdett *et al.* 2010 - more details of the variables and models are given in the
159 Supplementary Material, Appendix A).

160 We used Geographic Information System data of landcover (Bontemps *et al.*
161 2011), roads, human population density and elevation (Diva-GIS, 2014) to construct the
162 cost and resistance models for each species. The continuous variables (distance to roads,
163 population density and elevation) were transformed into permeability maps through the
164 model function that described the species relationship to the variable (Supplementary
165 Material, Appendix A). The landcover map is a categorical expression of the landscape,
166 so we linearized the angular coefficients of the species suitability models and attributed
167 the transformed values according to the cover type. Previous jaguar studies had

168 observed differences in the movements of males and females (Conde *et al.* 2010;
169 Colchero *et al.* 2011), so we constructed different GIS raster maps to express the
170 differing permeability of the landscape for each sex.

171 Despite having information about species movements in the landscape from
172 previous studies, it was not clear which landscape features might affect gene flow.
173 Therefore, we applied a multifactorial approach, assuming that all combinations of
174 variables could potentially explain gene flow patterns, with each combination of
175 variables representing a hypothesis of landscape permeability. For jaguars, which
176 exhibit sex-biased permeability, the multifactorial approach was conducted with five
177 sets of variables: (i) average sex permeability for each variable, i.e. we assumed that
178 gene flow was symmetric of both sexes; (ii) female- and (iii) male-specific permeability
179 rasters, i.e. we supposed an asymmetric sex-biased effect whereby only one gender was
180 responsible for gene flow; (iv) minimum permeability based on the barrier principle, so
181 the lower permeability for one sex was sufficient to restrict gene flow; and the
182 alternative (v) maximum permeability, whereby the higher permeability of one sex was
183 sufficient to permit gene flow. These cost and resistance models were analyzed in R
184 software (R Core Team 2013) using the *gdistance* package (van Etten 2012); the final
185 output of these analyses being pairwise estimates of effective distance and resistance
186 between individuals.

187

188 **3.3. Isolation pattern among individuals**

189 We used Spatial Principal Component Analyses (sPCA) to summarize the
190 genetic diversity and, at the same time, to reveal spatial structure. As for classical
191 Principal Component Analysis (PCA), sPCA is an ordination method for variable
192 reduction, but it has the advantage of optimizing the data variance for principal

193 components scores as well as encompassing spatial structure (Jombart *et al.* 2008).
194 Therefore, when applied to allelic frequency data, the genetic variability among
195 individuals is summarized into a few uncorrelated components, which maximizes the
196 genotypic variance, and spatial information is also taken into account (Jombart *et al.*
197 2008). Moreover, the use of sPCA to explore genetic data does not require populations
198 to be in Hardy–Weinberg equilibrium or linkage equilibrium, since it is not based on a
199 genetic model (Jombart *et al.* 2008).

200 This approach requires the generation of a connection network to define the
201 neighboring sites, transforming the PCA into a spatially explicit method. We used a
202 distance-based neighborhood graph with 100 km as a threshold of maximal distance
203 between connected individuals (a reasonable average of species home-ranges) (Cullen
204 Jr. 2006; Cavalcanti & Gese 2009). This type of connection network is recommended
205 for data with an aggregated distribution (Jombart *et al.* 2008), such as our records.
206 Spatial structure was detected by conducting Moran’s I test (Moran 1948, 1950), which
207 may assume positive or negative values. Therefore, the sPCA eigenvalues can reveal
208 two types of spatial pattern: positive Moran’s I (global structure) and negative Moran’s
209 I (local structure) (*sensu* Thioulouse *et al.* 1995). A pattern of global spatial structure
210 occurs when the allelic frequencies among neighbors are more similar than that of a
211 random distribution, whereas a local spatial structure occurs when the allelic
212 frequencies among neighbors are more dissimilar than for a random distribution
213 (Jombart *et al.* 2008).

214 The selection of principal components was done graphically, balancing the
215 genetic variability and spatial structure summarized in the principal components. The
216 criterion of percentage variability explained by eigenvalues that is common in a
217 classical PCA cannot be applied in a sPCA because the principal components also

218 express the product of spatial autocorrelation. Therefore, we considered the abrupt
219 decrease in information contained in the eigenvalues as a threshold to select principal
220 components (Legendre & Legendre 1998). Due to the subjectivity of our criterion, the
221 global and local tests (Jombart *et al.* 2008) were applied to confirm the presence of a
222 spatial pattern in the axes. These analyses were done in R software (R Core Team 2013)
223 using the *adegenet* package (Jombart & Ahmed 2011).

224 The principal components selected were used to calculate the pairwise genetic
225 dissimilarity between individuals, which consisted of a Euclidian distance of
226 individuals' score. Genetic dissimilarity was correlated with landscape distances to
227 evaluate the pattern of gene flow, following a causal modeling framework (Cushman
228 2006). The causal modeling framework is an efficient method to identify paths of gene
229 flow in complex landscapes, allowing landscape permeability hypothesis to be tested
230 (Cushman & Landguth 2010; Cushman *et al.* 2013). Correlations were carried out by
231 means of a Mantel test in the *vegan* package (Oksanen 2012) in R (R Core Team 2013).

232

233 **3.4. Genetic clustering analysis**

234 Bayesian cluster analyses were performed to investigate population structure in
235 the data set, i.e. to assign individuals into clusters. It has been recommended to confirm
236 genetic structure patterns using both non-spatial and spatial approaches (Chen *et al.*
237 2007; Frantz *et al.* 2009), so we employed both the STRUCTURE (non-spatial;
238 Pritchard *et al.* 2000; Falush *et al.* 2003) and TESS (spatial; Chen *et al.* 2007; Durand *et*
239 *al.* 2009) software packages to identify populations. Both of these software packages
240 use Markov Chain Monte Carlo algorithms to identify *k* populations without *a priori*
241 group definition. They also have the option of applying an admixture model, which
242 permits efficient classification of individuals into a population even if the source

243 population has not been sampled (Durand *et al.* 2009). The main difference between the
244 two algorithms applied by these packages is that TESS assumes geographical continuity
245 of allele frequencies, which would make neighboring sites more similar than distant
246 sites (François *et al.* 2006). This feature allows TESS to detect clines and/or clusters,
247 making it the most efficient Bayes algorithm to be applied to scenarios with data on the
248 effects of isolation by distance (François & Durand 2010).

249 We ran admixture models in STRUCTURE and TESS, using 10,000 iterations
250 after a burn-in period of 100,000 iterations, for $k = 2 - 9$, with 10 independent runs for
251 each k . For the non-spatial model, the logarithm of the probability of the data ($\text{LnP}(D)$;
252 Pritchard *et al.* 2000) and Δk (Evanno *et al.* 2005) were plotted against k to identify the
253 plateau of the curve and, consequently, to estimate the number of clusters (François &
254 Durand 2010); for the spatial model, this relationship was determined using the
255 deviance information criterion (DIC; Spiegelhalter *et al.* 2002). The CLUMPP software
256 (Jakobsson & Rosenberg 2007) was used to average the admixture proportions of
257 individuals over the 10 replicates of the most likely k .

258 These Bayesian methods are efficient for assigning individuals into populations,
259 but they may fail to identify subdivisions within populations (Jombart & Ahmed 2011).
260 Thus, a classical statistical analysis may detect fine-scale changes in genetic
261 configuration more efficiently because it is not based on models of population genetics.
262 We performed a Discriminant Analysis of Principal Components (DAPC) to investigate
263 if the two species showed a finer substructure than that of population. Discriminant
264 Analysis (DA) is a method that sorts individuals into pre-defined clusters, focusing on
265 increasing between-group variability while reducing within-group variation (Legendre
266 & Legendre 1998). It has limited use in genetic studies because DA demands a higher
267 number of sampling units than variables (Legendre & Legendre 1998), which is rarely

268 the case in genetic data. DAPC uses PCA as a prior step to DA, condensing the data and
269 thereby satisfying the DA requirements (Jombart & Ahmed 2011). We used the
270 sampling areas as *a priori* individual clusters and made a graphical interpretation of
271 individuals' ordination and assignment to define the final subpopulations. DAPC was
272 performed using the *adegenet* package (Jombart & Ahmed 2011) in R software (R Core
273 Team 2013).

274

275 **3.5. Descriptive statistics of genetic clusters**

276 To measure the genetic diversity of the identified groups (populations and
277 subpopulations), we calculated the allele richness and rarefied allele richness (using the
278 Hp-Rare software - Kalinowski 2005), and the observed (H_o) and expected
279 heterozygosity (H_e) under Hardy-Weinberg assumptions (using the FSTAT software -
280 Goudet 2002). The significance of Hardy-Weinberg equilibrium was evaluated through
281 a Bonferroni correction of P-values (Rice 1989). We estimated inbreeding for each
282 subpopulation to measure the degree of substructure, which may be driving the
283 subpopulations into more divergent groups. Therefore, we calculated F_{IS} over
284 subpopulations and loci using the FSTAT software (Goudet 2002) with 10,000
285 permutations. The degree of population differentiation was measured by F_{ST} and R_{ST}
286 using the SPAGeDi software (Hardy & Vekemans 2013).

287

288 **4. Results**

289 We could identify a total of 205 samples for each species. For pumas, a total of
290 158 samples belonging to 67 individuals were genotyped. For jaguars, a total of 151
291 samples belonging to 34 individuals were genotyped (Table S4). For both species, the
292 cost and resistance models produced landscape distances strongly correlated with

293 Euclidian distances (average Pearson correlation between landscape distance and
294 Euclidian distance; Puma - $r = 0.98$, $p < 0.01$; Jaguar - $r = 0.99$, $p < 0.01$). Therefore, the
295 least-cost and resistance distances were not informative about landscape permeability
296 and species movement. Thus, we assumed that the environment was pristine for both
297 species because we did not detect high contrast of suitability on the landscape.
298 Consequently, we only used Euclidian distances in the subsequent analyses to test the
299 isolation-by-distance hypothesis.

300 We only selected the first eigenvalue from each sPCA because there was a
301 strong decrease in eigenvalues thereafter (Figure 2a and b), they summarized a
302 significant amount of the genetic variance (Variance ≈ 0.4) and captured the spatial
303 structure (Figure 2 c and d). The global test confirmed the evidence of a global spatial
304 pattern indicated by a positive eigenvalue score (Global Test; Puma = 0.06, $p < 0.01$;
305 Jaguar = 0.09, $p < 0.01$), whereas there was no support for a local spatial pattern (Local
306 Test; Puma = 0.03, $p = 0.18$; Jaguar = 0.05, $p = 0.62$). Therefore, we only used the first
307 principal component to calculate pairwise genetic distances between individuals. The
308 Mantel tests evidenced a correlation between genetic distance and the logarithm of
309 Euclidian distance (Figure 3), revealing a gradual and continuous change in genetic
310 composition according to spatial distance, which is characteristic of a clinal pattern at a
311 regional scale. Thus, we corroborated the hypothesis of isolation by distance for both
312 pumas and jaguars.

313 We observed differing numbers of clusters according to the curve plateau of the
314 Bayesian methods used. STRUCTURE inferred six populations for pumas and three for
315 jaguars when we interpreted the Δk scores (Figure 4a and b), while $\ln P(D)$ scores also
316 suggested six populations for pumas, but only two for jaguars (Figure 4c and d). The
317 DIC score estimated by TESS identified three and four as the most likely k for pumas

318 and jaguars, respectively (Figure 4e and f). However, STRUCTURE was inefficient in
319 assigning either puma or jaguar individuals into genetic clusters; plots of its assignment
320 proportion estimates showed a continuous and unbroken allele frequency distribution,
321 making it impossible to define subclusters (Figure 5a-f, top plots). In contrast, TESS
322 presented more consistent individual assignments (Figure 5a-f, bottom plots), allowing
323 us to distinguish boundaries between genetic clusters. We identified a clear
324 discontinuity in assignment proportions in the region of El Carmen, making this a clear
325 boundary between two populations for both species (Figure 5a-f, bottom plots). The F_{ST}
326 and R_{ST} values confirmed the significant genetic differentiation between puma
327 populations ($F_{ST}= 0.07$, $p < 0.01$; $R_{ST}= 0.13$, $p < 0.01$) and jaguar populations ($F_{ST}=$
328 0.15 , $p < 0.01$; $R_{ST}=0.17$, $p=0.01$). Thus, we could conclude that the number of clusters
329 suggested by these curve plateau approaches (i.e. Δk , $\ln P(D)$ and DIC score) are all
330 overestimated.

331 In the DAPC clustering method, we selected the principal components to
332 accumulate 80% of the total variation, which consisted of 21 eigenvalues for puma and
333 13 eigenvalues for jaguar. The final ordination was done with the first two discriminant
334 functions because we observed a strong reduction in explanatory power after the second
335 function (Figure 6). The assignment efficiency of DAPC was higher for pumas than for
336 jaguars (average assignment probability: Puma = 0.75 and Jaguar = 0.62). Therefore, we
337 did an additional analysis to evaluate if the higher efficiency for pumas could reveal a
338 biological pattern to be further explored, or if it was only a mathematical artifact due to
339 having sampled a higher number of individuals of this species and, thus,
340 disproportionately having greater statistical power. We evaluated the assignment
341 efficiency of DAPC by means of 10,000 random subsamples of 34 pumas, i.e. the same
342 sample size for jaguars in our study. The higher assignment efficiency for pumas was

343 observed even for the smaller dataset (Figure 7), giving us the first evidence of stronger
344 genetic structuring in pumas compared to jaguars.

345 We confirmed the structure of the populations, but the subpopulations
346 corresponded only partially to the *a priori* groups (Figure 8). In the DAPC, El Carmen
347 was considered a different cluster for both species, but jaguars from El Carmen were
348 more isolated than pumas (Figure 8). El Eden and Zapotal can be considered the same
349 subpopulation for both species (Figure 8). However, we note a transitioning of the
350 genetic configuration for pumas, akin to a gradient (best visualized in the assignment
351 proportions of Figure 8), revealing genetic structuring at a small spatial scale. This same
352 pattern is also observed for pumas from Petcacab, Cojolite, Calakmul and Caobá
353 (Figure 8a) and for jaguars from Petcacab, Caobá, Calakmul and Ocotones (Figure 8b);
354 these four areas respectively defining other subpopulations of pumas and jaguars. For
355 pumas, we also identified Selva de Ocone and Ocotones as subpopulations (Figure 8a).
356 Therefore, we assumed a total of five subpopulations for pumas and three for jaguars
357 (Table 2), which corroborates our hypothesis of stronger spatial structure for pumas in a
358 pristine environment (as suggested by permeability models).

359 We adopted the DAPC clusters to carry out diversity estimates. All loci were
360 polymorphic for both species; the numbers of alleles in subpopulations ranged from 20
361 to 76 for pumas and from 29 to 57 for jaguars (see Table S4 and S5 for estimates by
362 locus). Following a rarefaction procedure, the average allele richness over loci ranged
363 from 1.67 to 4.00 for pumas and from 2.57 to 2.79 for jaguars (Table 1). No locus
364 showed linkage disequilibrium after Bonferroni correction for multiple comparisons. In
365 addition, following Bonferroni correction, there was no evidence of inbreeding in
366 subpopulations for either species (Table 1). However, pumas exhibited higher variation

367 in genetic diversity (ranging from 0.56 to 0.76) compared to jaguars (ranging from 0.62
368 to 0.70) (Table 1).

369

370 **5. Discussion**

371 The overall genetic variation showed that the study area does not represent a
372 uniform and panmictic population for pumas and jaguars. At a regional scale, pumas
373 and jaguars exhibited similar patterns, showing a clinal trend in allele frequencies from
374 El Carmen to El Edén (François & Durand 2010). At the same time, their genetic
375 structures differed at the local scale because they showed differences in the number of
376 subpopulations. Therefore, we note that both levels of genetic structure investigated
377 (clines and clusters) acted simultaneously, but at different scales.

378 The study area exhibited low landscape heterogeneity and complexity, so our
379 results do not support the isolation by effective distance or resistance hypotheses. The
380 absence of landscape population structuring is probably due to two features of our study
381 area. The first is the low complexity of the landscape configuration; the study area
382 comprises a large and connected block of native vegetation extending from El Edén to
383 Los Ocotones. The second is the limited variability in permeability among the landscape
384 features. The detectability of landscape effects on genetic structure is correlated with the
385 extent to which landscape features limit animal movement and gene flow. It is also
386 correlated with animal perceptions of the boundaries between landscape elements
387 (Jaquiéry *et al.* 2011; Cushman *et al.* 2011, 2013). Therefore, genetic differentiation due
388 to landscape alteration is stronger for species with lower environmental plasticity
389 because the boundaries between landscapes elements will affect them more strongly
390 (Cushman *et al.* 2013).

391 Our results showed a clinal pattern for both species, indicating that vegetation
392 was not a genetic barrier. It is known that genetic processes act within different time
393 scales compared to landscape change (Wagner & Fortin 2013; Ewers *et al.* 2013), so it
394 is possible that the spatial genetic structure of puma and jaguar will change over
395 generations. The time it takes for a species to respond to landscape changes is called
396 ‘relaxation time’ in the ecological literature and it seems to be positively correlated with
397 longevity and dispersal ability (Hylander & Ehrlén 2013), suggesting a long relaxation
398 time for jaguars and pumas.

399 Both species could be divided into two populations, with the fragmented area
400 between Los Ocotones and El Carmen as a boundary. However, this fragmented area
401 also represents a sampling gap in our study, so this population division is probably
402 gradual as suggested by the clinal pattern found. Such clinal patterns can confuse the
403 determination of populations and their boundaries, even using software that adopt
404 spatial approaches, making it difficult to differentiate genuine clusters from sampling
405 artifacts (Dyer & Nason 2004; Frantz *et al.* 2009). However, assignment statistics can
406 be quite revealing in terms of uncovering patterns of isolation by distance.

407 Pumas are structured into a larger number of subpopulations than jaguar in our
408 study area, corroborating our hypothesis of a stronger influence of landscape effects on
409 isolation by distance in pumas due to low landscape complexity. Our prediction was
410 associated with the generalized theory of dispersal ability for species (Whitmee & Orme
411 2013), so we had expected that jaguar would have a greater movement potential in
412 pristine areas due to its larger body size. However, jaguars are known to have lower
413 ecological plasticity than pumas in anthropogenic habitats, so such habitats should
414 structure jaguar populations into more clusters due to a reduced dispersal success.
415 Therefore, we recommend that new studies be carried out comparing the genetic

416 structuring of jaguars and pumas in areas with a higher degree of habitat loss and
417 fragmentation.

418 In our study, we observed that the clusters and clinal patterns detected were
419 mainly generated due to isolation by distance. In landscapes with a low degree of
420 fragmentation, animal movements approach a random walk pattern, thereby structuring
421 the genetic configuration at a local scale (François & Durand 2010). This pattern can
422 extend across larger distances, generating isolation by distance pattern from regional- to
423 species-distribution scales (François & Durand 2010). Isolation by distance is one of the
424 most tested patterns in population genetics and evidence for it has been presented for
425 many species, including other carnivores with large dispersal ability (Paetkau *et al.*
426 1999; Castilho *et al.* 2011; Loxterman 2011).

427 In a conservation context, we observed that no subpopulation of either species
428 presented a signal of inbreeding depression and the genetic diversity indices are similar
429 to those of other feline populations (Loxterman 2011; Miotto *et al.* 2011; Andreasen *et*
430 *al.* 2012; Dutta *et al.* 2013). However, fragmentation of the habitat between these
431 populations represents a potential future risk for these species by driving loss of genetic
432 diversity due to a reduction in gene flux and population viability (Flather & Bevers
433 2002; Ovaskainen & Hanski 2003; Cushman *et al.* 2006, 2013). Species conservation is
434 not only related to maintenance of genetic diversity and avoiding inbreeding depression,
435 it is also necessary to secure evolutionary and demographic processes. Therefore, the
436 current scenario should not be viewed as a reason not to enact management strategies.
437 Instead, it should be seen as an opportune time to evaluate the future consequences of
438 recent human-induced changes and, if necessary, to design appropriate conservation
439 plans to avoid further genetic erosion.

440

441 **6. References**

- 442 Adriaensen F, Chardon JP, De Blust G *et al.* (2003) The application of “least-cost”
443 modelling as a functional landscape model. *Landscape and Urban Planning*, **64**,
444 233–247.
- 445 Andreasen AM, Stewart KM, Longland WS, Beckmann JP, Forister ML (2012)
446 Identification of source-sink dynamics in mountain lions of the Great Basin.
447 *Molecular Ecology*, **21**, 5689–5701.
- 448 De Angelo C, Paviolo A, Di Bitetti M, Angelo C De, Bitetti M Di (2011) Differential
449 impact of landscape transformation on pumas (*Puma concolor*) and jaguars
450 (*Panthera onca*) in the Upper Paraná Atlantic Forest. *Diversity and Distributions*,
451 **17**, 422–436.
- 452 Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior:
453 functional grain as a key determinant for dispersal. *Landscape Ecology*, **22**, 1117–
454 1129.
- 455 Bhagavatula J, Singh L (2006) Genotyping faecal samples of Bengal tiger *Panthera*
456 *tigris tigris* for population estimation: a pilot study. *BMC genetics*, **7**, 48.
- 457 Bolnick DI, Otto SP (2013) The magnitude of local adaptation under genotype-
458 dependent dispersal. *Ecology and Evolution*, **3**, 4722–35.
- 459 Bontemps S, Defourny P, Bogaert E Van, Kalogirou V, Perez JR (2011) GLOBCOVER
460 2009. p.10.
- 461 Boom R, Sol CJ, Salimans MM *et al.* (1990) Rapid and simple method for purification
462 of nucleic acids. *Journal of Clinical Microbiology*, **28**, 495–503.
- 463 Borthakur U, Barman RD, Das C *et al.* (2010) Noninvasive genetic monitoring of tiger
464 (*Panthera tigris tigris*) population of Orang National Park in the Brahmaputra
465 floodplain, Assam, India. *European Journal of Wildlife Research*, **57**, 603–613.

466 Burdett CL, Crooks KR, Theobald DM *et al.* (2010) Interfacing models of wildlife
467 habitat and human development to predict the future distribution of puma habitat.
468 *Ecosphere*, **1**, 1–21.

469 Castilho CS, Marins-Sa LG, Benedet RC, Freitas TO (2011) Landscape genetics of
470 mountain lions (*Puma concolor*) in southern Brazil. *Mammalian Biology*, **76**, 476–
471 483.

472 Cavalcanti SMC, Gese EM (2009) Spatial ecology and social interactions of jaguars
473 (*Panthera onca*) in the Southern Pantanal, Brazil. *Journal of Mammalogy*, **90**,
474 935–945.

475 Chen C, Durand E, Forbes F, François O (2007) Bayesian clustering algorithms
476 ascertaining spatial population structure: a new computer program and a
477 comparison study. *Molecular Ecology Notes*, **7**, 747–756.

478 Colchero F, Conde DA, Manterola C *et al.* (2011) Jaguars on the move: modeling
479 movement to mitigate fragmentation from road expansion in the Mayan Forest.
480 *Animal Conservation*, **14**, 158–166.

481 Conde DA, Colchero F, Zarza H *et al.* (2010) Sex matters: Modeling male and female
482 habitat differences for jaguar conservation. *Biological Conservation*, **143**, 1980–
483 1988.

484 Cullen Jr. L (2006) Jaguars as landscape detectives for the conservation of Atlantic
485 Forests in Brazil. University of Kent, UK.

486 Cushman S a. (2006) Effects of habitat loss and fragmentation on amphibians: a review
487 and prospectus. *Biological Conservation*, **128**, 231–240.

488 Cushman S a, Landguth EL (2010) Spurious correlations and inference in landscape
489 genetics. *Molecular ecology*, **19**, 3592–602.

490 Cushman S a, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex
491 landscapes: testing multiple hypotheses with causal modeling. *The American*
492 *Naturalist*, **168**, 486–99.

493 Cushman S a., Raphael MG, Ruggiero LF *et al.* (2011) Limiting factors and landscape
494 connectivity: the American marten in the Rocky Mountains. *Landscape Ecology*,
495 **26**, 1137–1149.

496 Cushman S a., Shirk AJ, Landguth EL (2013) Landscape genetics and limiting factors.
497 *Conservation Genetics*, **14**, 263–274.

498 Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G (2009) Multiple
499 ecological pathways to extinction in mammals. *Proceedings of the National*
500 *Academy of Sciences of the United States of America*, **106**, 10702–10705.

501 Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads
502 on cougar movement in southern California. *Journal of Wildlife Management*, **69**,
503 264–276.

504 Diva-GIS (2014) Download data by country.

505 Durand E, Jay F, Gaggiotti OE, François O (2009) Spatial inference of admixture
506 proportions and secondary contact zones. *Molecular Biology and Evolution*, **26**,
507 1963–1973.

508 Dutta T, Sharma S, Maldonado JE *et al.* (2013) Fine-scale population genetic structure
509 in a wide-ranging carnivore, the leopard (*Panthera pardus fusca*) in central India (J
510 Austin, Ed.). *Diversity and Distributions*, **19**, 760–771.

511 Dyer RJ, Nason JD (2004) Population Graphs: the graph theoretic shape of genetic
512 structure. *Molecular ecology*, **13**, 1713–27.

513 Eizirik E, Kim J-HH, Menotti-Raymond M *et al.* (2001) Phylogeography, population
514 history and conservation genetics of jaguars (*Panthera onca*, Mammalia, Felidae).
515 *Molecular Ecology*, **10**, 65–79.

516 Van Etten J (2012) gdistance: Distances and routes on geographical grids.

517 Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals
518 using the software STRUCTURE: a simulation study. *Molecular Ecology*, **14**,
519 2611–20.

520 Ewers RM, Didham RK (2006) Confounding factors in the detection of species
521 responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

522 Ewers RM, Didham RK, Pearse WD *et al.* (2013) Using landscape history to predict
523 biodiversity patterns in fragmented landscapes (M Bonsall, Ed.). *Ecology Letters*,
524 **16**, 1221–1233.

525 Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using
526 multilocus genotype data: linked loci and correlated allele frequencies. *Genetics*,
527 **164**, 1567–1587.

528 Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation:
529 A synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

530 Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: the
531 relative importance of habitat amount and arrangement. *The American Naturalist*,
532 **159**, 40–56.

533 François O, Ancelet S, Guillot G (2006) Bayesian clustering using hidden Markov
534 random fields in spatial population genetics. *Genetics*, **174**, 805–16.

535 François O, Durand E (2010) Spatially explicit Bayesian clustering models in
536 population genetics. *Molecular ecology resources*, **10**, 773–784.

537 Frantz a. C, Cellina S, Krier a., Schley L, Burke T (2009) Using spatial Bayesian
538 methods to determine the genetic structure of a continuously distributed
539 population: clusters or isolation by distance? *Journal of Applied Ecology*, **46**, 493–
540 505.

541 Frantz a. C, Pope LC, Carpenter PJ *et al.* (2003) Reliable microsatellite genotyping of
542 the Eurasian badger (*Meles meles*) using faecal DNA. *Molecular Ecology*, **12**,
543 1649–1661.

544 Galetti M, Eizirik E, Beisiegel B *et al.* (2013) Atlantic Rainforest’s jaguars in decline.
545 *Science*, **342**, 930.

546 Goudet J (2002) FSTAT: a computer program to calculate F-statistics.

547 Guillot G, Estoup A, Mortier F, Cosson JF (2005) A spatial statistical model for
548 landscape genetics. *Genetics*, **170**, 1261–80.

549 Haag T, Santos AS, Sana DA *et al.* (2010) The effect of habitat fragmentation on the
550 genetic structure of a top predator: loss of diversity and high differentiation among
551 remnant populations of Atlantic Forest jaguars (*Panthera onca*). *Molecular*
552 *Ecology*, **19**, 4906–4921.

553 Hardy O, Vekemans X (2013) SPAGeDi.

554 Hostetler J a, Onorato DP, Jansen D, Oli MK (2012) A cat’s tale: the impact of genetic
555 restoration on Florida panther population dynamics and persistence. *The Journal of*
556 *Animal Ecology*, **82**, 608–620.

557 Hylander K, Ehrlén J (2013) The mechanisms causing extinction debts. *Trends in*
558 *Ecology & Evolution*, **28**, 341–346.

559 IUCN (2013) The IUCN red list of threatened Species.

560 Jakobsson M, Rosenberg N a (2007) CLUMPP: a cluster matching and permutation
561 program for dealing with label switching and multimodality in analysis of
562 population structure. *Bioinformatics (Oxford, England)*, **23**, 1801–1806.

563 Jaquiéry J, Broquet T, Hirzel a H, Yearsley J, Perrin N (2011) Inferring landscape
564 effects on dispersal from genetic distances: how far can we go? *Molecular*
565 *Ecology*, **20**, 692–705.

566 Jombart T, Ahmed I (2011) adegenet 1.3-1: new tools for the analysis of genome-wide
567 SNP data. *Bioinformatics*, **27**, 3070–1.

568 Jombart T, Devillard S, Dufour a-B, Pontier D (2008) Revealing cryptic spatial patterns
569 in genetic variability by a new multivariate method. *Heredity*, **101**, 92–103.

570 Kalinowski ST (2005) Hp-Rare 1.0: a Computer program for performing rarefaction on
571 measures of allelic richness. *Molecular Ecology Notes*, **5**, 187–189.

572 Kurushima JD, Collins J a., Well J a., Ernest HB (2006) Development of 21
573 microsatellite loci for puma (*Puma concolor*) ecology and forensics. *Molecular*
574 *Ecology Notes*, **6**, 1260–1262.

575 Legendre P, Legendre L (1998) *Numerical ecology*. Elsevier Science, Amsterdam.

576 Lenormand T (2002) Gene flow and the limits to natural selection. *Trends in Ecology &*
577 *Evolution*, **17**, 183–189.

578 Loxterman JL (2011) Fine scale population genetic structure of pumas in the
579 Intermountain West. *Conservation Genetics*, **12**, 1049–1059.

580 McRae BH (2006) Isolation by resistance. *Evolution*, **60**, 1551–1561.

581 Menotti-Raymond M, David V a, Lyons L a *et al.* (1999) A genetic linkage map of
582 microsatellites in the domestic cat (*Felis catus*). *Genomics*, **57**, 9–23.

583 Miotto RA, Cervini M, Figueiredo MG, Begotti RA, Galetti PM (2011) Genetic
584 diversity and population structure of pumas (*Puma concolor*) in southeastern

585 Brazil: implications for conservation in a human-dominated landscape.
586 *Conservation Genetics*, **12**, 1447–1455.

587 Mondol S, Ullas Karanth K, Samba Kumar N *et al.* (2009) Evaluation of non-invasive
588 genetic sampling methods for estimating tiger population size. *Biological*
589 *Conservation*, **142**, 2350–2360.

590 Moran PAP (1948) The interpretation of statistical maps. *Journal of the Royal*
591 *Statistical Society Series B*, **10**, 243–251.

592 Moran PAP (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37**, 17–23.

593 Morrison JC, Sechrest W, Dinerstein E, Wilcove DS, Lamoreux JF (2007) Persistence
594 of large mammal faunas as indicators of global human impacts. *Journal of*
595 *Mammalogy*, **88**, 1363–1380.

596 Oksanen J (2012) Vegan: ecological diversity.

597 Ovaskainen O, Hanski I (2003) How much does an individual habitat fragment
598 contribute to metapopulation dynamics and persistence? *Theoretical Population*
599 *Biology*, **64**, 481–495.

600 Paetkau D, Amstrup SC, Born EW *et al.* (1999) Genetic structure of the world's polar
601 bear populations. *Molecular ecology*, **8**, 1571–1584.

602 Palomares F, Godoy J a, Piriz A, O'Brien SJ, Johnson WE (2002) Faecal genetic
603 analysis to determine the presence and distribution of elusive carnivores: design
604 and feasibility for the Iberian lynx. *Molecular Ecology*, **11**, 2171–2182.

605 Perez I, Geffen E, Mokady O (2006) Critically Endangered Arabian leopards *Panthera*
606 *pardus nimr* in Israel: estimating population parameters using molecular scatology.
607 *Oryx*, **40**, 295.

608 Pérez-Espona S, McLeod JE, Franks NR (2012) Landscape genetics of a top neotropical
609 predator. *Molecular Ecology*, **21**, 5969–5985.

610 Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using
611 multilocus genotype data. *Genetics*, **155**, 945–959.

612 R Core Team (2013) R: A language and environment for statistical computing.

613 Reed DH (2004) Extinction risk in fragmented habitats. *Animal Conservation*, **7**, 181–
614 191.

615 Rice WR (1989) Analysing tables of statistical tests. *Evolution*, **43**, 223–225.

616 Roques S, Adrados B, Chavez C *et al.* (2011) Identification of neotropical felid faeces
617 using RCP-PCR. *Molecular Ecology Resources*, **11**, 171–5.

618 Roques S, Furtado M, Jácomo ATA *et al.* (2014) Monitoring jaguar populations
619 (*Panthera onca*) with non-invasive genetics : a pilot study in Brazilian ecosystems.
620 *Oryx*, In press.

621 Ryall KL, Fahrig L (2006) Response of predators to loss and fragmentation of prey
622 habitat: a review of theory. *Ecology*, **87**, 1086–1093.

623 Schmidt K, Ratkiewicz M, Konopínski MK (2011) The importance of genetic
624 variability and population differentiation in the Eurasian lynx *Lynx lynx* for
625 conservation, in the context of habitat and climate change. *Mammal Review*, **41**,
626 112–124.

627 Slatkin M (1985) Gene flow in natural populations. *Annual Review of Ecology and*
628 *Systematics*, **16**, 393–430.

629 Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of
630 model complexity and fit. *Journal of the Royal Statistical Society: Series B*
631 (*Statistical Methodology*), **64**, 583–639.

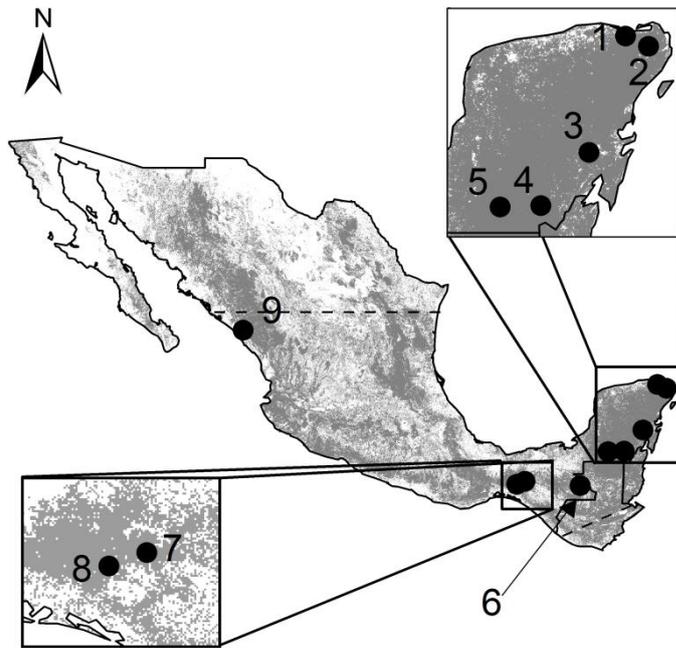
632 Thioulouse J, Chessel D, Champely. S (1995) Multivariate analysis of spatial patterns: a
633 unified approach to local and global structures. *Environmental and Ecological*
634 *Statistics*, **2**, 1–14.

- 635 Thornton DH, Branch LC, Sunquist ME (2011) The relative influence of habitat loss
636 and fragmentation: Do tropical mammals meet the temperate paradigm? *Ecological*
637 *Applications*, **21**, 2324–2333.
- 638 Vandergast AG, Bohonak AJ, Weissman DB, Fisher RN (2007) Understanding the
639 genetic effects of recent habitat fragmentation in the context of evolutionary
640 history: phylogeography and landscape genetics of a southern California endemic
641 Jerusalem cricket (Orthoptera: Stenopelmatidae: Stenopelmatus). *Molecular*
642 *Ecology*, **16**, 977–992.
- 643 Villard M-A, Metzger JP (2013) Beyond the fragmentation debate: a conceptual model
644 to predict when habitat configuration really matters. *Journal of Applied Ecology*,
645 online version.
- 646 Villela PMS, Verdade LM, Adrados BA *et al.* (2014) Evaluation of a suitable
647 microsatellite marker set for individual identification, parentage test and genetic
648 structure in noninvasive samples of *Puma concolor*.
- 649 Wagner HH, Fortin M-J (2013) A conceptual framework for the spatial analysis of
650 landscape genetic data. *Conservation Genetics*, **14**, 253–261.
- 651 Walker FM, Sunnucks P, Taylor AC (2008) Evidence for habitat fragmentation altering
652 within-population processes in wombats. *Molecular Ecology*, **17**, 1674–1684.
- 653 Whitmee S, Orme CDL (2013) Predicting dispersal distance in mammals: a trait-based
654 approach. *The Journal of Animal Ecology*, **82**, 211–21.
- 655 Wright S (1943) Isolation by distance. *Genetics*, **28**, 114–128.

656 Table 1. Genetic diversity estimates for puma and jaguar subpopulations. AR –rarefied
 657 allelic richness averaged over loci; Ho – observed heterozygosity; He – expected
 658 heterozygosity; SD – standard deviation.

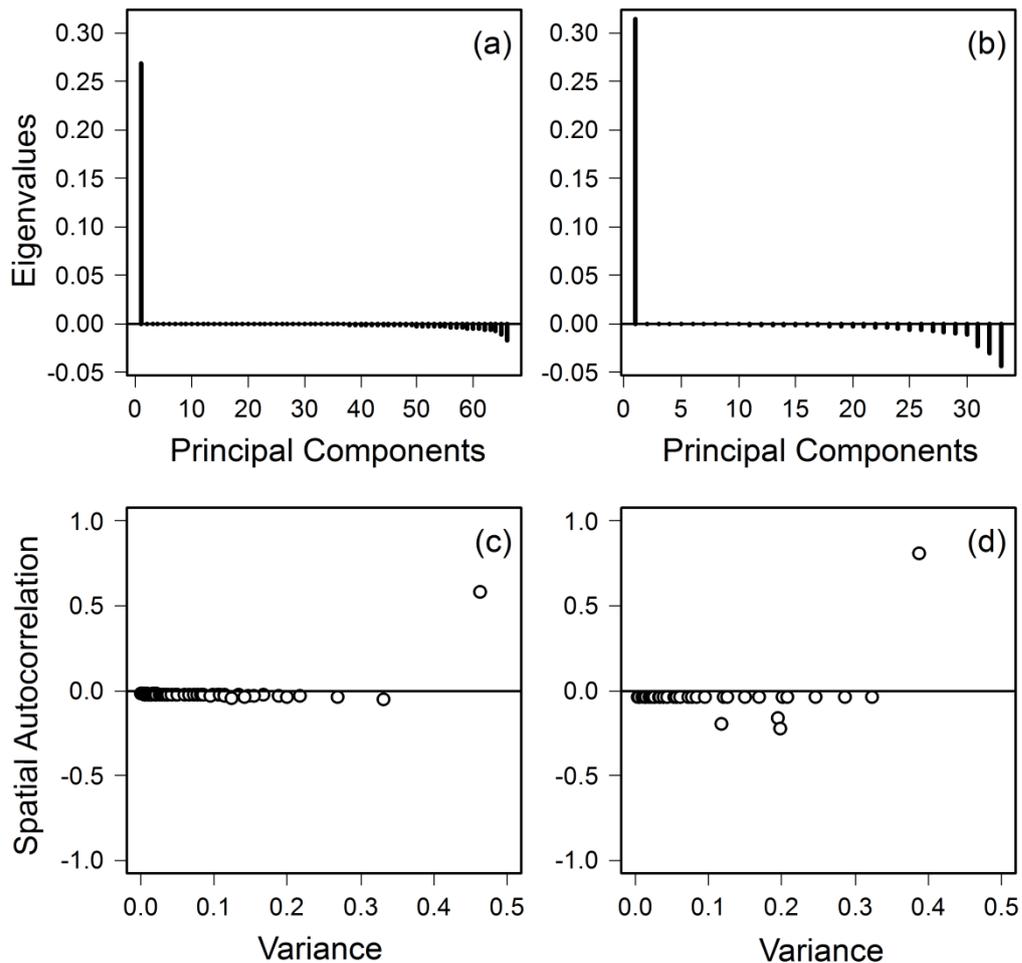
	AR	Ho (SD)	He (SD)	Fis
<i>Puma concolor</i>				
El Edén and Zapotal	3.22	0.61 (0.08)	0.65 (0.11)	0.12
Petcacab, Cojolita, Calakmul and Caobá	3.29	0.65 (0.11)	0.66 (0.11)	0.06
Selva el Ocone	2.50	-	-	-
Ocotones	1.67	0.69 (0.33)	0.55 (0.24)	-0.22
El Carmen	4.00	0.71 (0.11)	0.76 (0.11)	0.12
<i>Panthera onca</i>				
El Edén and Zapotal	2.79	0.62 (0.26)	0.58 (0.23)	-0.06
Petcacab, Caobá, Calakmul and Ocotones	3.24	0.70 (0.19)	0.66 (0.17)	-0.03
El Carmen	2.57	0.64 (0.20)	0.59 (0.16)	-0.03

659



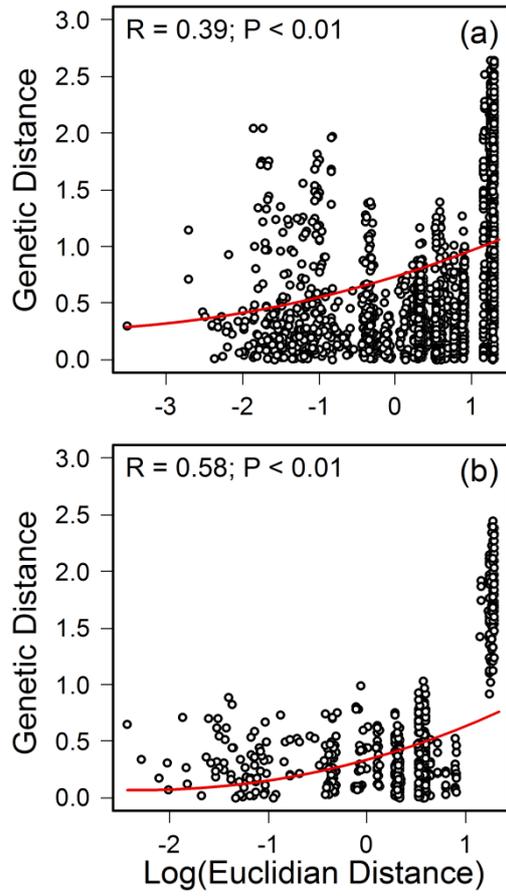
660

661 Figure 1. Sampling areas located in Mexico: (1) El Edén; (2) El Zapotal; (3) Petcacab;
 662 (4) Ejido Caoba; (5) Calakmul; (6) La Cojolita; (7) Selva El Ocone; (8) Los Ocotones;
 663 and (9) El Carmen. Dashed line is the limit of our study area used for cost and
 664 resistance models and gray color represents native vegetation cover.



665

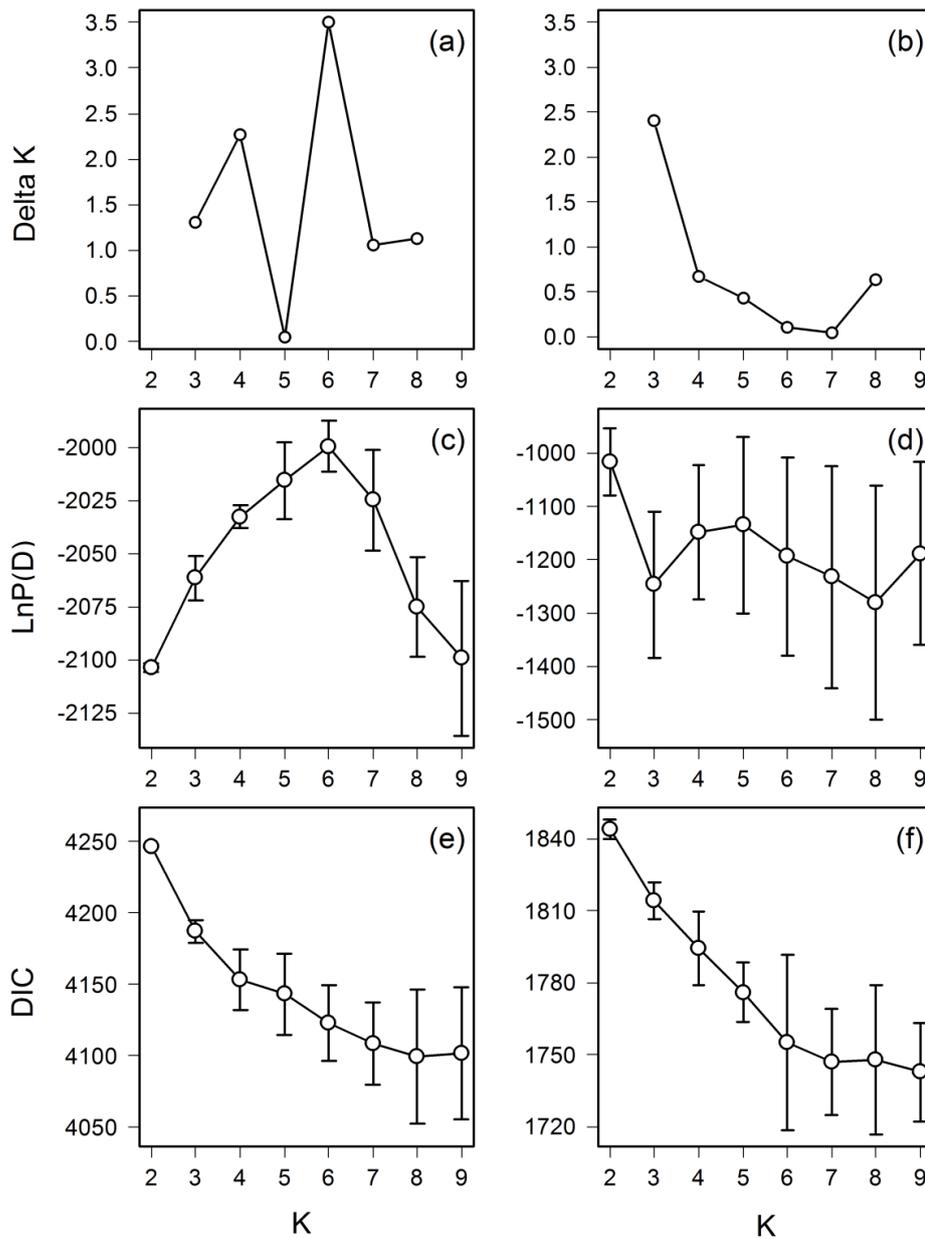
666 Figure 2. Selection of principal components of the Spatial Principal Components
 667 Analysis (sPCA) for puma (left) and jaguar (right). Upper graphs (a and b) are
 668 eigenvalues expressing the explanatory power of the principal components. Lower
 669 graphs (c and d) display the genetic variance and spatial autocorrelation (measured by
 670 Moran's Index) contained in each principal component. For both species, the first
 671 principal component is the only one that captures spatial structure and substantial
 672 genetic variation, which corresponds to the outlier point in both graphs c and d.



673

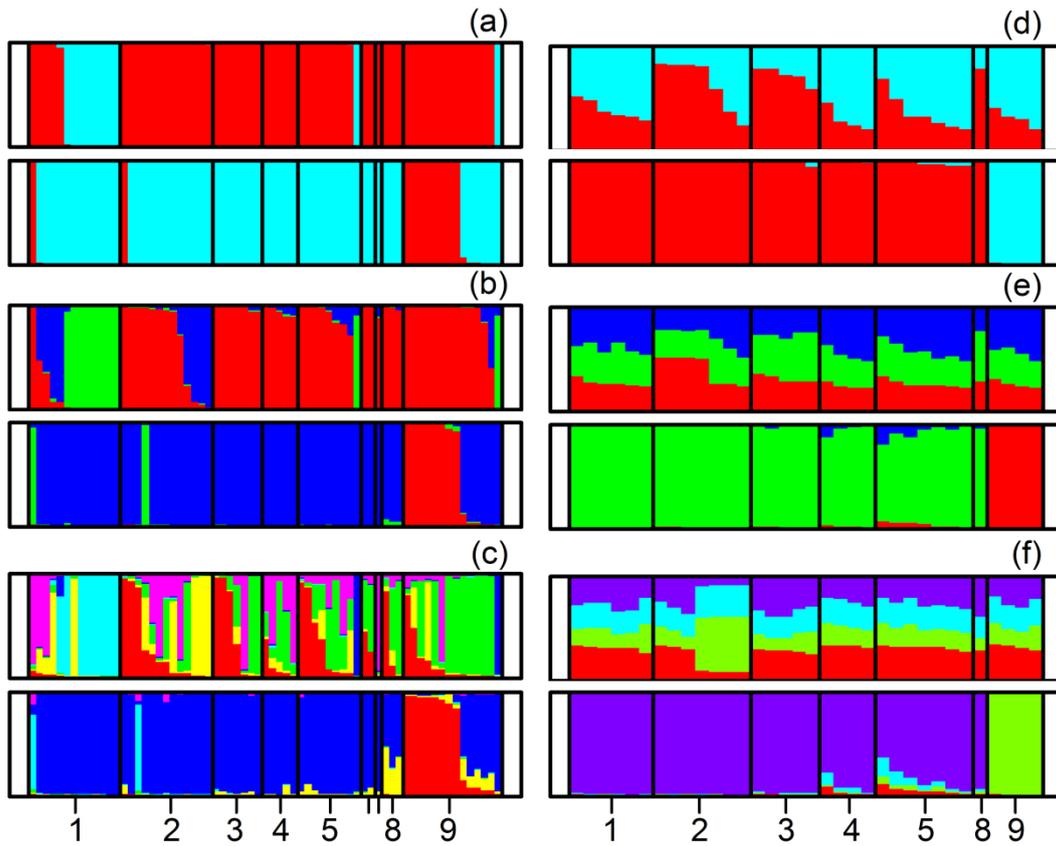
674 Figure 3. Correlations between genetic and logarithm of Euclidian distance for puma (a)

675 and jaguar (b).



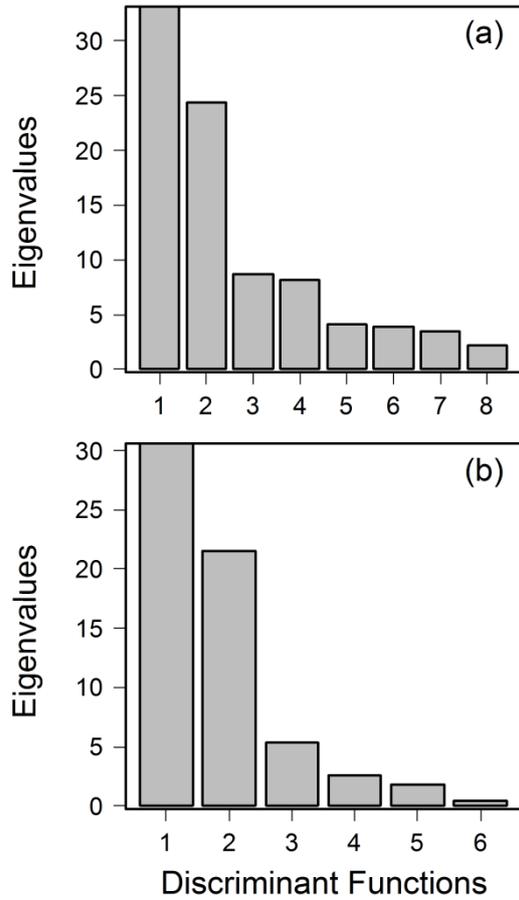
676

677 Figure 4. Number of genetic clusters (k) estimated by STRUCTURE (a-d) and TESS (e
678 and f) for pumas (left panels) and jaguars (right panels). Δk and average log likelihood
679 $\text{LnP}(D)$ results show $k = 6$ for pumas (a and c, respectively) as the best fit of the data for
680 the highest level of hierarchical genetic structure; for jaguars, the best fit was $k = 3$ (b)
681 and $k = 2$ (d) for Δk and $\text{LnP}(D)$ respectively. The deviance information criterion (DIC)
682 scores computed by the TESS admixture model indicated $k = 3$ for pumas (e) and $k = 4$
683 for jaguars (f). The intervals represented in figures c-f are the standard deviations.



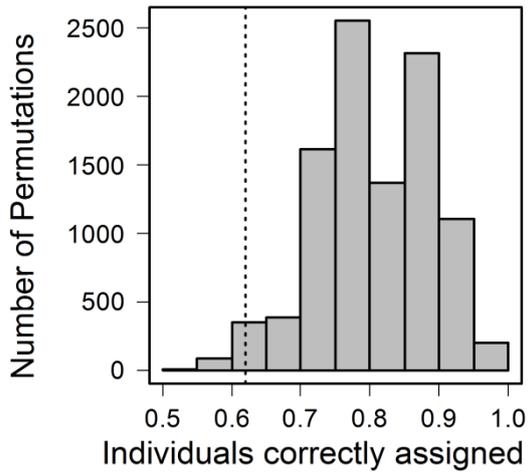
684

685 Figure 5. Bar plots showing the assignment proportions of individuals for
 686 STRUCTURE (top) and TESS (bottom). Left-hand-side panels are puma-assigned
 687 groups for $k = 2$ (a), $k = 3$ (b), and $k = 6$ (c). Right-hand-side panels are jaguar-assigned
 688 groups for $k = 2$ (d), $k = 3$ (e), and $k = 4$ (f). Numbers along the bottom of (c) and (f)
 689 indicate the sampling location of individuals (see Figure 1).



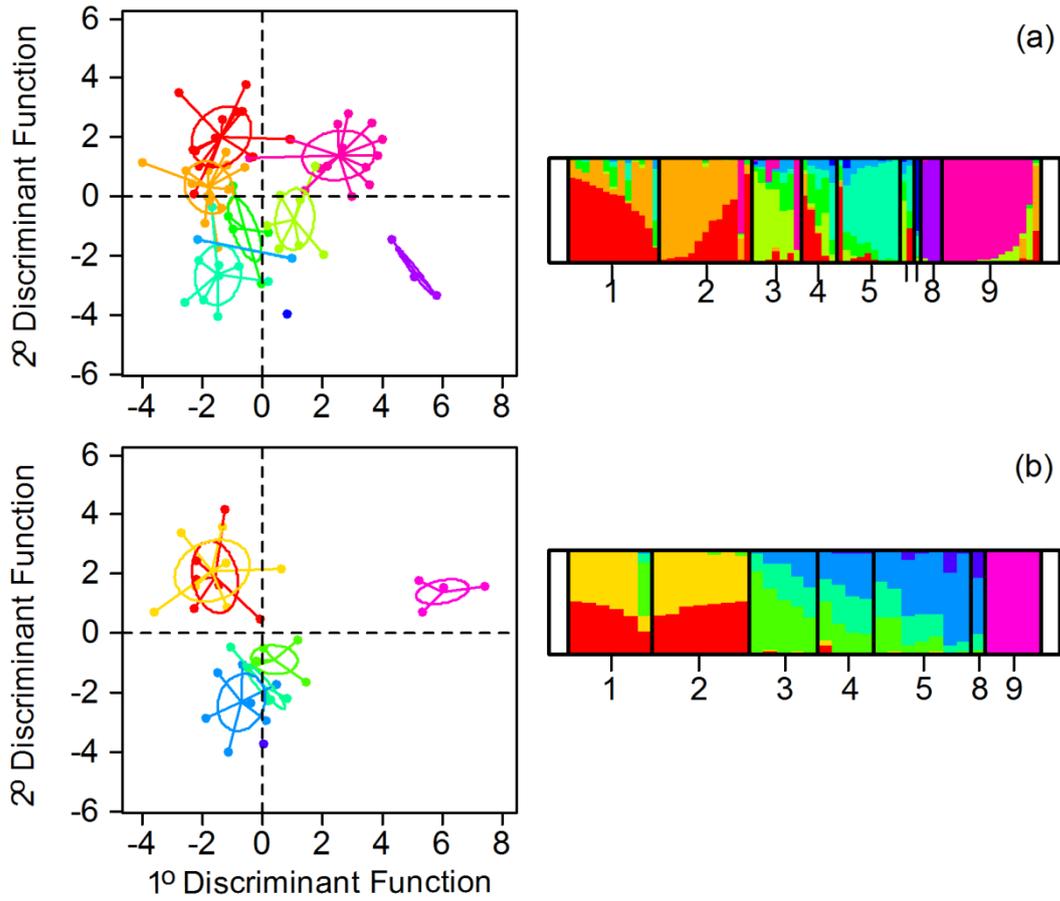
690

691 Figure 6. Eigenvalues expressing the explanatory power of the linear discriminant
 692 function of the Discriminant Analysis of Principal Component analysis for puma (a) and
 693 jaguar (b).



694

695 Figure 7. Proportion of pumas correctly assigned into 10,000 random subsamples to
 696 evaluate the assignment efficiency of the Discriminant Analysis of Principal
 697 Component analysis due to differences in sample size for puma and jaguar. Dashed line
 698 marks the average assignment proportion for jaguar, which was often lower than the
 699 average assignment proportion of puma subsamples (Mean = 0.80).



700

701 Figure 8. Summary of Discriminant Analysis of Principal Component results. Genotype
 702 ordination for pumas (a) and jaguars (b) are given in the left-hand-side panels, showing
 703 differentiation into groups (points and circle of the same color) and between group
 704 variation (distance of one group centroid to another). The right-hand-side panels show
 705 the assignment proportions of individuals for each sampling location (numbers along
 706 bottom; see Figure 1 legend for spatial location).

Appendix A. Raster creation representing landscape permeability for jaguars and pumas

Jaguar

We used three variables to calculate the permeability of the landscape for jaguars: distance to roads, human population density and landcover. These variables were selected based on the studies of (Conde *et al.* 2010; Colchero *et al.* 2011). These studies uncovered sex-biased differences in habitat use and movement, so we constructed different permeability rasters for each sex.

Distance to roads

Firstly, we created a raster of distance to road (in kilometers) through the function map calculator of ArcGIS using road shapefiles from Mexico, Guatemala and Belize (Diva-GIS 2014). Then, we applied the logistic function representing the model of habitat selection reported by (Colchero *et al.* 2011) using the map calculator in ArcGIS:

$$\text{Female} = \text{Exp}([\text{Road Distance}] * 0.776) / (1 + \text{Exp}([\text{Road Distance}] * 0.776))$$

$$\text{Male} = \text{Exp}([\text{Road Distance}] * 0.305) / (1 + \text{Exp}([\text{Road Distance}] * 0.305))$$

Human population density

We converted the raster of human population (Diva-GIS 2014) into a human population density (HPD) function and calculated the model function of (Colchero *et al.* 2011):

$$\text{Female} = \text{Exp}([\text{HPD}] * (-2.386)) / (1 + \text{Exp}([\text{HPD}] * (-2.386)))$$

$$\text{Male} = \text{Exp}([\text{HPD}] * 0.219) / (1 + \text{Exp}([\text{HPD}] * 0.219))$$

Landcover

We used coefficients of the models of Conde *et al.* (2010) to express transformed landcover type suitability; to mirror other variables used in the distance models, they were linearly transformed to vary from zero to one. The transformation was done taking account of the range of variation of both sexes and capturing the differences between females and males (Table S1). We attributed the linear scores to the landcover map (Bontemps *et al.* 2011) based on the similarity of cover types described in the landcover map of Conde *et al.* (2010) (Table S2).

Pumas

We also used three variables in the distance models for pumas: road density, topography and landcover. Unfortunately, we did not find studies of habitat selection and movement for pumas in our study area, so the variables were selected according to studies conducted in different environments. We assumed that the hierarchical relationship of habitat preferences is the same, independently of region. These other puma studies did not evaluate sex-biased habitat selection, so we created only one permeability raster for each variable.

Road density

We adapted the results of Dickson *et al.* (2005), who state that “*total paved road density was about 21% lower on cougar travel paths (4.20m/km², $x=0.10$ +/- 0.20m/km² [SD]) compared to available paths (5.30m/km², $x=0.12$ +/- 0.22m/km²; $t=-2.16$, $P=0.04$, $n=44$)*”. Thus, we assumed a road resistance of 21% (79% permeability). However, tracks facilitate puma movement: “*density of dirt roads was slightly higher on paths used by cougars (62.50m/km² $x=1.42$ +/- 1.04m/km²)*”

compared to available paths (59.17m/km², $x=1.34 \pm 0.78\text{m/km}^2$; $t=1.48$, $P=0.15$, $n=44$). Buffered movement segments intersected dirt roads in all but 2 sessions, during which no dirt roads were available. All tracked individuals encountered or used dirt roads (368 occasions during 41 sessions)” (Dickson *et al.* 2005). Therefore, tracks do not impede puma movement, but instead facilitate movement 5.63% more than for native landcover. These values of permeability (79% and 105.63%) were linearly transformed to vary from zero to one, resulting in scores of 0.75 and 1 for tracks and roads, respectively.

Landcover

The model coefficients of (Burdett *et al.* 2010) were used as a measure of landcover suitability. As for the other variables, the coefficients were linearly transformed to vary from zero to one (Table S3) and the resulting scores were attributed to the landcover map (Bontemps *et al.* 2011) based on the similarity of cover types (Table S2).

Topography

We converted the altitude raster (Diva-GIS 2014) through the function described in (Burdett *et al.* 2010) using the map calculator tool of the ArcGIS software:

$$\text{Puma Topography} = \text{Exp}([\text{Altitude}] * 12.11) / (1 + \text{Exp}([\text{Altitude}] * 12.11))$$

Table S1. Linearly transformed scores from (Conde *et al.* 2010) describing permeability of landcover type for jaguars.

Vegetation Type	Coefficient	Linear transformation
Female		
Agriculture-cattle	-2.784	0.075
Secondary vegetation	-3.034	0.000
Short forest	0.021	0.917
Tall forest	-0.364	0.802
Male		
Agriculture-cattle	-0.270	0.830
Secondary vegetation	-0.834	0.660
Short forest	-0.563	0.742
Tall forest	0.297	1.000
Swamps	-0.492	0.763

Table S2. Attribution of linear scores to landcover types in the (Bontemps *et al.* 2011) landuse map.

Vegetation Type	Jaguar (female)	Jaguar (male)	Puma
Rainfed croplands	0.075	0.830	0.199
Mosaic Croplands/Vegetation	0.075	0.830	0.199
Mosaic Vegetation/Croplands	0.075	0.830	0.199
Closed to open broadleaved evergreen or semi-deciduous forest	0.802	1.00	0.199
Closed broadleaved deciduous forest	0.802	1.000	1.000
Open broadleaved deciduous forest	0.802	1.000	1.000
Closed needleleaved evergreen forest	0.802	1.000	1.000
Closed to open mixed broadleaved and needleleaved forest	0.802	1.000	1.000
Mosaic Forest-Shrubland/Grassland	0.917	0.742	1.000
Mosaic Grassland/Forest-Shrubland	0.917	0.742	0.251
Closed to open shrubland	0.917	0.742	0.251
Closed to open grassland	0.917	0.742	0.251
Sparse vegetation	0.000	0.660	0.000
Closed to open broadleaved forest, regularly flooded (fresh-brackish water)	0.000	0.763	0.000
Closed broadleaved forest, permanently flooded (saline-brackish water)	0.000	0.763	0.199
Closed to open vegetation, regularly flooded	0.000	0.763	0.251

Table S3. Linearly transformed scores from (Burdett *et al.* 2010) describing permeability of landcover type for puma.

Vegetation Type	Coefficient	Linear
Barren	-0.870	0.035
Coastal scrub	-0.250	0.251
Grassland	-0.970	0.000
Riparian	1.900	1.000
Oak woodland	0.650	0.564
Exurban	-0.400	0.199
Suburban/Urban	-0.800	0.059

Table S4. Number of identified scats collected in each sampling location for pumas and jaguars (males:females indicated in brackets).

Location	Puma	Jaguar
El Edén	36 (6:7)	37 (6:0)
El Zapotal	57 (5:8)	51 (7:0)
Petcacab	14 (2:5)	18 (4:1)
Ejido Caoba	12 (1:3)	14 (3:1)
Calakmul	27 (3:6)	20 (6:1)
La Cojolita	3 (1:1)	0 (0:0)
Selva El Ocone	1 (0:1)	0 (0:0)
Los Ocotones	23 (2:1)	1 (1:0)
El Carmen	31 (7:7)	10 (2:2)

Table S5. Measures of diversity at 12 microsatellite loci in the five puma subpopulations identified in the study.

Loci	El Edén and Zapotal							Petcacab, Cojolita, Calakmul and Caobá							Selva el Ocone							Ocotones							El Carmen							Global Data			
	N	A	AR	PA	Ho	He	Fis	N	A	AR	PA	Ho	He	Fis	N	A	AR	PA	Ho	He	Fis	N	A	AR	PA	Ho	He	Fis	N	A	AR	PA	Ho	He	Fis	N	A	Ho	He
Fca077	26	6	2.49	0.42	0.54	0.56	0.07	23	3	2.60	0.65	0.52	0.59	0.11	1	2	1.00	0.00	-	-	-	3	1	2.00	0.00	0.00	0.00	-	14	8	4.65	3.11	0.71	0.84	0.15	67	11	0.55	0.57
Fca126	26	6	3.20	0.65	0.69	0.62	<-0.01	23	6	2.86	0.54	0.52	0.50	0.04	1	1	2.00	0.00	-	-	-	2	2	1.00	0.04	1.00	0.50-1.00	14	5	3.46	0.73	0.64	0.72	0.11	66	7	0.56	0.55	
Fca547b	23	5	3.16	0.83	0.70	0.71	0.06	21	6	3.28	0.70	0.62	0.67	0.21	1	1	2.00	0.00	-	-	-	3	2	1.00	0.00	1.00	0.50-1.00	4	2	3.00	0.00	0.8	0.50	-0.33	52	6	0.57	0.6	
Fca82b	23	7	4.47	1.13	0.74	0.86	0.17	21	7	4.12	0.63	0.71	0.80	0.11	1	1	2.00	0.00	-	-	-	3	2	1.00	0.08	0.33	0.33	0.00	13	8	4.60	1.85	0.77	0.81	0.05	61	11	0.51	0.65
PcoA208	26	5	2.58	0.53	0.54	0.56	0.03	23	4	2.67	0.14	0.56	0.60	0.09	1	2	4.00	0.00	-	-	-	3	4	2.00	1.09	0.67	0.83	0.20	14	7	4.36	1.61	0.93	0.80	-0.16	67	9	0.77	0.7
PcoA216	26	6	3.08	0.64	0.54	0.56	0.10	20	5	2.85	0.53	0.70	0.58	-0.11	1	2	2.00	0.37	-	-	-	3	2	2.00	0.34	0.67	0.50	0.00	14	8	3.83	2.00	0.57	0.76	0.25	64	10	0.64	0.65
PcoA339	24	8	4.26	1.51	0.62	0.79	0.28*	23	9	4.21	1.42	0.83	0.77	-0.02	1	1	4.00	0.00	-	-	-	3	3	1.00	1.35	1.00	0.8-0.33	14	8	4.23	2.37	0.78	0.85	0.17	65	14	0.62	0.74	
PcoB003	21	6	2.94	0.09	0.57	0.62	0.11	22	5	3.37	0.31	0.55	0.64	0.18	1	2	2.00	0.07	-	-	-	2	2	2.00	0.05	1.00	0.50-1.00	10	7	4.55	1.80	0.70	0.87	0.34	56	8	0.73	0.73	
PcoB010	24	7	3.57	0.85	0.50	0.71	0.48**	20	7	4.26	0.88	0.7	0.82	0.29	1	2	3.00	0.00	-	-	-	3	3	2.00	1.10	1.00	0.67-0.50	14	7	4.50	2.17	0.78	0.79	0.06	62	12	0.74	0.80	
PcoB210	26	7	3.59	0.39	0.65	0.75	0.15	23	7	3.96	0.16	0.87	0.78	-0.1	1	2	2.00	0.52	-	-	-	3	2	2.00	0.14	0.33	0.67	0.50	13	9	4.70	2.41	0.77	0.87	0.1	66	11	0.72	0.79
PcoC108	24	3	2.10	0.15	0.54	0.47	-0.16	23	2	1.99	0.00	0.61	0.50	-0.18	1	2	2.00	0.00	-	-	-	3	2	2.00	0.00	0.67	0.50-0.33	13	3	2.25	0.32	0.61	0.57	0.23	64	4	0.65	0.56	
PcoC108	24	6	3.22	0.00	0.71	0.67	-0.02	23	6	3.37	0.00	0.70	0.71	0.03	1	2	4.00	0.72	-	-	-	3	4	2.00	0.04	0.67	0.92	0.27	10	4	3.87	0.71	0.50	0.8	0.41	61	6	0.69	0.79

Sample size (N), allelic richness (A), rarefaction of allelic richness (AR), private alleles (PA), observed (Ho) and expected (He) heterozygosities, and inbreeding coefficient (Fis).

Allele richness and private alleles calculated with the HP-Rare software based on seven genes.

* p<0.01

** p< 0.001

Table S6. Measures of diversity at 11 microsatellite loci in the three jaguar subpopulations of the study.

Loci	El Edén and Zapotal							Petcacab, Caobá, Calakmul and Ocotones							El Carmen							Global Data			
	N	A	AR	PA	Ho	He	Fis	N	A	AR	PA	Ho	He	Fis	N	A	AR	PA	Ho	He	Fis	N	A	Ho	He
FC24	11	3	2.64	0.02	0.85	0.60	-0.36	14	3	2.39	0.00	0.56	0.58	0.13	4	2	2.00	0.20	0.8	0.50	-0.50	29	3	0.69	0.56
FC26	12	3	2.60	0.85	0.92	0.59	-0.55	13	5	2.97	0.54	0.94	0.64	-0.43	3	2	2.00	0.32	0.8	0.50	-0.33	28	5	0.83	0.58
FC43	13	2	1.99	0.00	0.54	0.52	-0.04	17	4	2.56	0.21	0.65	0.59	-0.09	3	2	2.00	0.63	0.3	0.67	1.00	33	4	0.39	0.56
FC77	13	5	3.58	0.30	0.77	0.8	-0.03	15	6	3.78	0.44	0.70	0.78	0.15	4	3	3.00	0.14	0.8	0.71	-0.06	32	6	0.73	0.75
FC82	13	1	1.00	0.00	0.00	0.00	-	17	2	1.62	0.00	0.23	0.21	-0.10	4	2	2.00	0.38	0.8	0.50	-0.50	34	2	0.33	0.23
FC90	11	3	2.21	0.02	0.50	0.39	-0.16	14	5	3.60	1.29	0.81	0.73	-0.07	4	3	2.88	0.24	0.8	0.67	-0.12	29	5	0.66	0.59
FC115	12	7	4.35	2.25	0.54	0.83	0.40	17	12	4.77	2.67	0.76	0.85	0.10	4	3	3.00	2.00	0.8	0.71	-0.06	33	16	0.67	0.81
FC126	12	4	2.86	0.56	0.85	0.62	-0.34	16	4	2.85	0.55	0.65	0.62	-0.01	4	2	1.88	0.88	0.3	0.3	0.00	32	6	0.57	0.50
FC176	12	3	2.47	0.06	0.61	0.56	-0.03	14	5	3.45	0.75	0.73	0.74	0.03	4	3	2.75	1.07	0.50	0.46	-0.09	30	6	0.60	0.59
FC547	13	4	3.05	0.09	0.54	0.70	0.27	16	5	3.73	0.90	0.87	0.78	-0.17	4	4	3.75	1.91	0.8	0.8	0.00	33	7	0.72	0.74
FC566	13	5	3.96	0.83	0.77	0.80	0.04	14	6	3.93	0.81	0.82	0.79	0.01	4	3	3.00	1.01	0.8	0.8	0.00	31	7	0.77	0.78

Sample size (N), allelic richness (A), rarefaction of allelic richness (AR), private alleles (PA), observed (Ho) and expected (He) heterozygosities, and inbreeding coefficient (Fis).

Allele richness and private alleles calculated with the HP-Rare software based on seven genes.

No loci exhibited significant Fis values.

DISCUSSÃO GERAL

Em nossa pesquisa, estudamos aspectos referentes ao efeito da perda e fragmentação de habitat sobre felinos, testando hipóteses ecológicas relacionadas ao tema e investigando aspectos socio-ambientais relevantes para a conservação das espécies. Compreender os efeitos da perda e fragmentação do habitat sobre os felinos consiste em um aspecto relevante não apenas para o grupo em questão, mas também para todo o ecossistema onde ocorrem, devido a função ecológica exercida por eles (Ritchie & Johnson, 2009). A extinção de predadores de topo de cadeia alimentar, função ecológica amplamente desenvolvida pelos felinos, gera uma série de eventos em cascata com graves consequências para ambiente. O primeiro desses eventos é o crescimento populacional de mesopredadores que, por sua vez, leva as populações de pequenos predadores e presas ao declínio ou até mesmo a extinção (Prugh et al., 2009).

Apesar da importância, observamos que existe uma grande lacuna de conhecimento sobre o tema, mesmo sendo os felinos um dos grupos taxonomicos mais estudados (Brodie, 2009). Algumas espécies agregam um número considerável de artigos científicos (*Puma concolor*, *Panthera tigris*, *Lynx pardinus*, *Lynx lynx* e *Lynx rufus*) e mesmo para essas há lacuna de conhecimento, pois os trabalhos são frequentemente redundantes quanto às perguntas ecológicas que visam responder. No entanto, verificamos que as pressões sofridas pelas espécies de felinos são distintas, mesmo consistindo em um grupo relativamente homogêneo quanto aos traços ecológicos. Os efeitos da perda e fragmentação encontrados nos mais de 100 artigos revisados variam de acordo com o tipo de resposta avaliada. Variações de resultado como essa não são uma particularidade do grupo ou das áreas de estudos, pois são observadas frequentemente em outros trabalhos (Baguette & Van Dyck, 2007; Lord & Norton, 1990). Tais padrões consistem em um importante constatação ecológica e com consequências para a conservação (Baguette & Van Dyck, 2007; Lord & Norton, 1990).

O contraste entre os resultados encontrados no capítulo 2 e 3 elucidam a variação dos efeitos ou intensidade dos processos de acordo com a abordagem usada, pois observamos que a principal ameaça às populações de onça-pintadas estão no nível demográfico. Dentre as populações estudadas no capítulo 2 (N = 28), apenas duas tiveram uma combinação adequada de número de indivíduos e estrutura da paisagem que assegurassem a persistência no longo prazo. Em contrapartida, observamos que a diversidade genética da onça-pintada parece não ter sido afetada pela perda e fragmentação em várias localidades do México. É esperado um efeito mais intenso da perda e fragmentação sobre respostas demográfica que genéticas para qualquer espécie, pois existe um ‘tempo de resposta’ diferente para tais mudanças (Wagner & Fortin, 2013). Esse tempo de resposta está positivamente relacionado à capacidade de dispersão e ao tempo de vida das espécies, que são particularmente altos para os felinos. Dessa forma, podemos esperar grandes tempos de resposta dos felinos à perda e fragmentação de habitat e, conseqüentemente, que os impactos das alterações antrópicas sobre a estrutura e diversidade genética dessas espécies são frequentemente subestimados.

Subestimados ou não, os efeitos da perda e fragmentação sobre os felinos são inquestionáveis. As altas taxas de conversão de hábitat nos países de maior riqueza de felinos demonstra a ameaça crescente sobre essas espécies (ver mapa da introdução geral). Nesse contexto, faz-se necessário também um rápido avanço científico, pois muitas são as perguntas ecológicas sem respostas acerca do tema, que permitiriam suporte científico às estratégias de conservação a serem adotadas.

Referências

- Baguette, M., & Van Dyck, H. (2007). Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology*, 22(8), 1117–1129.
- Brodie, J. F. (2009). Is research effort allocated efficiently for conservation? Felidae as a global case study. *Biodiversity and Conservation*, 18(11), 2927–2939.
doi:10.1007/s10531-009-9617-3
- Lord, J. M., & Norton, D. A. (1990). Scale and the spatial concept of fragmentation. *Conservation Biology*, 4(2), 197–202. doi:10.1111/j.1523-1739.1990.tb00109.x
- Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *BioScience*, 59(9), 779–791.
doi:10.1525/bio.2009.59.9.9
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12(9), 982–998. doi:10.1111/j.1461-0248.2009.01347.x
- Wagner, H. H., & Fortin, M.-J. (2013). A conceptual framework for the spatial analysis of landscape genetic data. *Conservation Genetics*, 14(2), 253–261.
doi:10.1007/s10592-012-0391-5

ANEXOS

Anexo 1

30/1/2014

ScholarOne Manuscripts

Decision Letter (Oryx-13-R-0132.R1)

From: oryx@fauna-flora.org

To: marinazaning@gmail.com, marina_zanin@hotmail.com

CC: oryx@fauna-flora.org, martin.fisher@fauna-flora.org

Subject: Oryx Oryx-13-R-0132.R1, What we (don't) know about the effects of habitat loss and fragmentation on felines

Body: 26-Nov-2013

Dear Marina

Oryx-13-R-0132.R1 What we (don't) know about the effects of habitat loss and fragmentation on felines

Thank you for submitting your revised article to Oryx. I am glad to accept it for publication.

The next step is for the article to be copy-edited into the journal's house style. In due course you will receive another e-mail from us asking you to check an edited copy of the article and respond to any final queries. Please note, however, that we are dealing with an unprecedented number of manuscripts at the moment and it will probably be at least a couple of months before you hear from us again.

PLEASE NOTE: Oryx offers authors the option to publish their article through an Open Access model (Cambridge Open Option, see <http://journals.cambridge.org/action/displaySpecialPage?pageId=4576> for details), on payment of a one-off fee. If you wish to do this, please send an e-mail stating this choice to oryx@fauna-flora.org and complete and return the alternative copyright transfer and order form which can be accessed by clicking the link below:

http://journals.cambridge.org/images/fileUpload/images/ORX_ctf_oa.pdf

I look forward to publishing your article and thank you for contributing it to Oryx.

Yours sincerely, Martin

Dr Martin Fisher
Editor, Oryx - The International Journal of Conservation
Fauna & Flora International, 4th Floor, Jupiter House
Station Road, Cambridge, CB1 2JD, UK

e-mail martin.fisher@fauna-flora.org
tel +44 (0)1223 571000

Everything you need to know about Oryx - The International Journal of Conservation is at <http://www.oryxthejournal.org>

http://mc.manuscriptcentral.com/oryx?NEXT_PAGE=VIEW_DECISION_LETTER_POPUP&DOCUMENT_ID=15917542&CURRENT_ROLE_ID=37570&CURRENT_USER_ID=32825830&DOCUMENT_HASHCODE=&SANIT... 1/2

Anexo 2

Submissions Needing Revision for Author Marina Zanin

A submission has been returned to you for revision. To revise the submission, click 'File Inventory' in the Actions menu to download any files requiring revision. When you are ready to submit the revised files, click 'Revise Submission' and then 'OK' to begin the submission process.

For more information, click [here](#), or view this short [tutorial](#) on submitting a revision.

If you do not want to submit a revised version, click 'Decline to Revise' and then 'OK'. Your submission will be moved to the Declined Revisions folder.

Page: 1 of 1 (1 total submissions)

Display results per page.

 Action 	Manuscript Number 	Title 	Initial Date Submitted 	Date Revision Due 	Status Date 	Current Status 	View Decision 
View Submission File Inventory Revise Submission Decline to Revise Send E-mail	JNC-D-13-00135	The jaguar's patches: the decline of jaguar populations	Jun 18, 2013	Mar 20, 2014	Dec 20, 2013	Revise	Major revision

Page: 1 of 1 (1 total submissions)

Display results per page.

[<< Author Main Menu](#)

You should use the free Adobe Acrobat Reader 6 or later for best PDF Viewing results.



