# Amenazas actuales de los grandes felinos neotropicales

## La ganadería en el punto de mira

Pablo Villalva Aguilar

Tesis Doctoral

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# AMENAZAS ACTUALES DE LOS GRANDES FELINOS NEOTROPICALES:

## *La ganadería en el punto de mira*

*Memoria presentada por el Ldo.* ***Pablo Villalva Aguilar*** *para optar al título de Doctor por la Universidad de Sevilla*

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## Resumen:

Jaguares (*Panthera onca*) y pumas (*Puma concolor*) son los mayores depredadores del Neotropico y comparten rasgos de su biología, historia evolutiva, modos de vida y conflictos con el ser humano. Sin embargo, el nivel de amenaza entre ambas especies difiere. La distribución actual del jaguar se encuentra profundamente reducida y se categoriza como especie cercana a la extinción (*Near Threaten*), mientras que el puma, ampliamente distribuido por el Neotropico, se categoriza como de preocupación menor (*Least Concern*). En esta tesis doctoral estudio los mecanismos que subyacen a estas diferencias, profundizando en la interacción entre la ecología de las especies y las relaciones con el ser humano con la motivación de comprender el efecto que la presión antrópica ejerce sobre estas especies.

En el **primer capítulo** analizamos cómo los patrones climáticos pasados y presentes han afectado a las poblaciones de grandes felinos de manera dispar. Los pumas responden a paisajes climáticos antiguos mientras que los jaguares responden tanto a paisajes climáticos antiguos como modernos, mostrando una mayor vulnerabilidad al cambio climático. Mediante el uso de predicciones climáticas evaluamos distintos escenarios sobre cada especie, obteniendo una aproximación del efecto potencial del cambio climático sobre cada especie en el futuro próximo.

En el **segundo capítulo** usamos el jaguar como modelo de estudio. A través de un modelado ecológico a escala continental comprobamos si las causas de extinción se relacionan con características intrínsecas (e.g. distancia al borde de la distribución) o extrínsecas (e.g. presiones humanas) a la especie. Observamos que el patrón de extinción de la especie es una combinación de ambas causas, destacando la ganadería como la principal de ellas.

Una vez establecida la ganadería como impulsor de extinción de los jaguares, en el **tercer capítulo** estudiamos cómo la presión humana muestra un profundo efecto, no sólo sobre las especies de felino de forma aislada, sino sobre sus relaciones de dominancia. Encontramos que las relaciones intragremiales naturales se ven moduladas por la presión humana y se discute cómo la comunidad de carnívoros neotropical está siendo desestabilizada por la mayor tolerancia de los pumas a las presiones humanas. Se muestra el efecto en cascada de las distintas presiones sobre la comunidad de carnívoros y en última instancia sobre el ecosistema completo.

En el **capítulo cuarto** nos aproximamos al conflicto ganadero a través de una perspectiva socio-ecológica. A través de entrevistas a ganaderos de la Chiquitanía y del

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Pantanal bolivianos estudiamos la magnitud del conflicto y la percepción local hacia los felinos en estas dos ecoregiones. Encontramos que el conflicto ganadero está ampliamente extendido, aunque las pérdidas ganaderas se encuentran dentro de los límites de depredación de ganado establecidos para otros grandes carnívoros. La percepción local de estas especies es generalmente negativa y su persecución está generalizada afectando directamente al declive de sus poblaciones.

En el **quinto capítulo** nos aproximamos a la emergente amenaza que supone el uso de felinos como sustitutos del tigre (*Panthera tigris*). A través de una revisión bibliográfica explicamos cómo la demanda de productos derivados del tigre, usados en medicina tradicional asiática, supone una amenaza a las poblaciones de grandes felinos de todo el mundo, incluyendo a los felinos neotropicales que habitan a miles de kilómetros.

Los resultados de esta tesis nos permiten comprender mejor las amenazas a las que se encuentran sometidas las especies de felinos neotropicales, en muchos casos aplicable a la generalidad de grandes carnívoros. Destacamos el profundo efecto que la ganadería extensiva ejerce sobre sus poblaciones y recalcamos la importancia de la coexistencia con el ser humano para la conservación de los grandes carnívoros, que son piezas clave en el mantenimiento del equilibrio del ecosistema.

# Chapter 1

# General introduction

## Introducción general

La actual crisis de biodiversidad se asocia con la actividad del ser humano a escala planetaria. El continuo crecimiento de la población humana tiene un penetrante efecto sobre los ecosistemas, encontrándose más del 80 % de la superficie terrestre bajo la influencia directa de sus actividades, gran parte relacionadas con la producción de alimentos (Sanderson *et al*. 2002 a). Actualmente existen 7.7 billones (americanos) de personas que, según las predicciones de la ONU, incrementará en 2 billones para 2050 (UN 2021). Esta escalada de la población humana ha originado grandes cambios a nivel planetario afectando a los ecosistemas desde distintos ángulos. La conversión de habitats nativos en sistemas de producción agropecuaria o el efecto del cambio climático tienen efectos sobre los ecosistemas completos que, en muchos casos, son modificados radicalmente. Actividades dirigidas como la sobreexplotación por cacería afectan a especies concretas suponiendo cambios importantes para las dinámicas poblacionales e incluso para su supervivencia. Se espera que el incremento de población humana provoque un aumento proporcional de la demanda de alimentos que, previsiblemente, tendrá importantes consecuencias para la mayoría de los ecosistemas (FAO 2017). En 2021, más de 1700 especies de mamíferos terrestres (el 29.8 % de ellas) se encontraban bajo algún grado de amenaza de extinción (UICN 2021). Por ello la supervivencia de los mamíferos terrestres depende enormemente de la capacidad de estas especies de coexistir con el hombre en ambientes cada vez más humanizados, así como de la tolerancia del hombre a coexistir con ellas.

### Importancia ecológica y problemática ambiental de los carnívoros

Los mamíferos carnívoros se distribuyen globalmente y muchas de sus poblaciones han sufrido importantes declives durante las últimas décadas. Los carnívoros que muestran contracciones de rango más acusadas son aquellos de mayor tamaño, reducido rango de distribución y que viven en bajas densidades (Gittleman *et al*. 2001). Estas especies son escasas por definición (Lindeman 1942, Colinvaux 1979), pero en la mayoría de los casos las amenazas a sus poblaciones no provienen de su inherente rareza, sino de las presiones antrópicas a las que se encuentran sometidos

(Cardillo *et al.* 2004). Algunos ejemplos de grandes carnívoros que han sufrido importantes contracciones de rango por acción directa del hombre son los tigres *Panthera tigris*, que han experimentado una reducción del 95 % de su rango de distribución, los leones africanos *Panthera leo* un 94 %, los jaguares *Panthera onca* un 49%, los osos grizzlys *Ursus arctos horribilis* un 42 % o los lobos *Canis lupus* un 26 % (Wolf and Ripple 2017, Quigley et al. 2017). En general, el 38.7 % de los carnívoros se encuentra actualmente bajo algún grado de amenaza de extinción (IUCN 2021), un 10 % más que hace tan solo 15 años (Foster 2007).

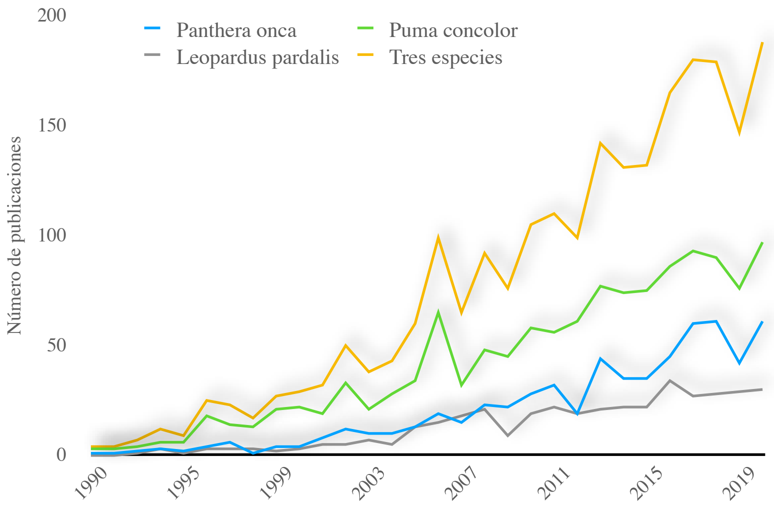
Muchos de estos carnívoros son especies clave (*Keystone species*) cuyo efecto en el ecosistema es mucho mayor del que cabría esperar por su abundancia (Paine 1980, Jordán, 2009), y su ausencia puede provocar efectos en cascada en las redes tróficas (Ripple *et al.* 2016). Cuando un depredador *top* es eliminado de un ecosistema puede ocurrir una liberación de predadores menores (*mesopredator release*) que desestabiliza los niveles tróficos inferiores (Soulé *et al.* 1988, Crooks & Soulé 1999, Palomares *et al.* 1995). Esta regulación *top-down* depende normalmente de una compleja red de relaciones intragremiales más que de la clásica visión de una sola especie reguladora, dando idea de cómo la coexistencia del gremio de carnívoros puede funcionar en el mantenimiento del ecosistema (Monterroso, 2020). Muchos carnívoros son también predadores apicales (*apex predators*), es decir no tienen depredadores naturales aparte del hombre. Por ello suelen verse envueltos en conflictos con los intereses humanos por causar daños, bien por ser percibidos o reales, a las empresas humanas. Estos conflictos suelen tener importantes implicaciones ecológicas para las especies que terminan siendo desplazadas por el hombre de su posición de depredador último a penúltimo (Oriol-Cotterill *et al.* 2015).

Cuando los depredadores apicales desaparecen, los herbívoros aumentan sus densidades incrementando el consumo de plantas y afectando así al ecosistema completo (Hairston *et al.* 1960; Leopold *et al.* 1947). Además, su ausencia puede provocar alteraciones en el comportamiento de los herbívoros que instan a que ocupen nuevos hábitats y/o a consumir nuevas especies. Por ejemplo, tras la supresión de los leopardos y perros salvajes, depredadores *top* del Parque Nacional Gongorosa en Mozambique, los antílopes extendieron sus poblaciones colonizando nuevos ecosistemas donde consumieron nuevas especies de plantas acuáticas llegando a suprimirlas localmente y modificando la dinámica ecológica del río (Atkins *et al*. 2020). En este caso de estudio el daño provocado pudo ser restablecido rápidamente tras la reintroducción de los carnívoros. Es así como los carnívoros ejercen un servicio en la regulación de los ecosistemas, siendo el principal motivo de que algunas políticas ambientales de la última década se hayan enfocado en promover programas de reintroducción de depredadores amenazados para reparar los daños generados por su ausencia. Algunos ejemplos: el lobo rojo (*Canis rufus*) ha sido reintroducido en Carolina del Norte; el licaón (*Lycaon pictus*) en Sudáfrica, Namibia, Zimbabwe y Kenia; el puma (*Puma concolor*) en el norte de Florida; el oso (*Ursus arctos*) en Polonia, Austria, Francia e Italia (Gittleman & Gomper 2001) y el lince ibérico en el sur de España (Iberlince 2016).

Los efectos de la supresión de la comunidad de depredadores también pueden tener efectos directos sobre el bienestar humano, no sólo a través del valioso servicio ecosistémico que aportan como piezas reguladoras, sino a través de efectos indirectos que su ausencia puede ocasionar por la generación de conflictos con repercusiones sociales. Por ejemplo, cuando se diezmaron las poblaciones de leones y leopardos del África subsahariana el número de babuinos incrementó y no sólo ejerció una presión excesiva sobre los ungulados -con sus consiguientes efectos ecológicos en cascada- sino que además se generaron grupos de babuinos saqueadores de cultivos que obligaron a las familias a sacar los niños de la escuela para ayudar a proteger los campos, con un impacto directo sobre la tasa de escolarización rural (Brashares *et al*. 2010).

## Felinos neotropicales como caso de estudio

Los felinos son un grupo especialmente importante dentro del gremio de los carnívoros neotropicales, no sólo por su elevado número de especies, sino por su importancia como especies claves para mantener la estructura del gremio. Los jaguares *Panthera onca*, los pumas *Puma concolor* y los ocelotes *Leopardus pardalis* las tres especies de felinos más robustas del neotropico han sido sugeridas como las especies que estructuran el gremio de los carnívoros al estar en la cima de la cadena trófica



Publicaciones sobre jaguares, pumas y ocelotes desde 1990.
Fuente: *Scopus 2021*

Neotropical (Oliveira *et al*. 2014). Estas tres especies coexisten en buena parte del neotropico y se encuentran bajo similares escenarios de presión antrópica aunque su grado de amenaza es distinto. La IUCN cataloga a los jaguares como *Near Threatened* mientras que pumas y ocelotes están catalogados como *Least Concern*.

Durante las últimas dos décadas ha existido un gran interés en conocer la ecología de los felinos neotropicales, así como sus interacciones con el hombre siendo objeto de exhaustivas investigaciones ecológicas. Las compilaciones como Medellin *et al*. (2016), Nagy-Reis *et al*. 2020 o Castaño-Uribe *et al*. 2017 sin duda destacan entre las últimas obras que engrosan la bibliografía sobre estas especies, caracterizadas por la colaboración de equipos de investigación de todo el mundo. Desde 2018 se han publicado más de 400 artículos científicos en relación con los jaguares, pumas y ocelotes (Scopus, febrero 2021) ofreciendo una imagen bastante completa sobre la ecología de estas especies. Por ello su uso como modelo de estudio permite no sólo conocer el efecto de las actividades humanas sobre cada especie a escala continental, validando los resultados mediante la extensa bibliografía existente, sino también sobre sus interacciones intragremiales, importantes elementos estructurantes de la comunidad. Estas especies se brindan a ser utilizadas en la conservación de ecosistemas a gran escala ya que se distribuyen (aún) por la mayor parte del Neotrópico habitando hábitats diversos.

Como ocurre con la mayor parte de los grandes carnívoros, existe una polarización en la percepción social hacia los grandes felinos. Es común encontrar percepciones negativas hacia estas especies en las áreas rurales donde la coexistencia diaria con el hombre genera tensiones continuas. Sin embargo, existe una clara tendencia de aceptación en las ciudades, donde sus habitantes son ajenos a las realidades rurales. Esta polarización en la opinión de distintos sectores poblacionales permite una interesante integración de las ciencias sociales y la ecología, necesaria para obtener una visión más completa a la hora de implementar medidas efectivas para la coexistencia entre la fauna y el hombre. Por este motivo, estas especies icónicas sirven de modelo para involucrar a diferentes gobiernos, organismos internacionales y ONGs en la elaboración de planes de conservación a gran escala, necesarios para el mantenimiento de las especies y los ecosistemas a largo plazo (Sanderson *et al.* 2002 b).

## Perspectiva prehistórica e histórica de las amenazas de los grandes felinos Neotropicales

Tanto jaguares como pumas tienen amplias distribuciones y han sufrido cambios en sus rangos de distribución mediados por la acción conjunta de los cambios paleoclimáticos y las presiones antrópicas (Barnoski *et al.* 2004). La distribución actual del jaguar se extiende desde el norte de México hasta la provincia de Corrientes al norte de Argentina. El puma tiene una distribución más amplia comprendiendo prácticamente todo el continente americano, desde Canadá hasta el sur de Chile (IUCN 2017). Ambas especies, con historias filogenéticas similares, han coexistido desde el Pleistoceno temprano a lo largo del continente americano durante (probablemente) más de un millón de años hasta la llegada al nuevo mundo del *Homo sapiens* en el Pleistoceno tardío.

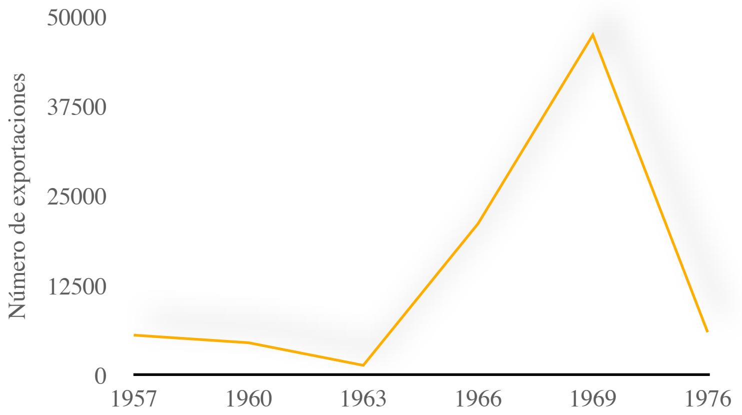
Existe cierta controversia sobre la llegada del *H. sapiens* a América (Cooper *et al.* 2019, Manning 2020, Cooper *et al.* 2020) pero parece claro que su llegada ocurrió no antes de 30.000 años a través de Beringia, durante la glaciación de Wisconsin (o para los europeos Würm) (Goebel *et al.* 2008). Hace tan solo 16.500 años se abrió el pasillo del Pacífico permitiendo la migración hacia el Sur y el acceso al resto del continente americano (Lesnek *et al.* 2018, Batchelor *et al.* 2019). A partir de este momento el *H. sapiens,* que había permanecido retenido en el refugio glacial norteamericano, pudo avanzar hacia el sur colonizando el continente, comenzando la (pre)histórica coexistencia con los felinos americanos.

Coincidiendo con el proceso de expansión postglacial, ocurrió el evento de *Extinción de Megafauna del Cuaternario*, una extinción masiva que acabó con el 80 % de las especies de megafauna mundial (Grayson & Meltzler, 2003, Wroe *et al.* 2004, Johnson, 2009). El origen de esta extinción masiva ha sido foco de un histórico debate para elucidar si la extinción fue mediada por los cambios climáticos o por la acción directa del hombre. Las evidencias apuntan a que, más que un factor único, fue el efecto aditivo de ambos factores la causa de este suceso (Barnoski *et al.* 2004); sin embargo, el papel de cada uno de ellos parece haber sido diferente en cada continente. Parece claro que en el norte de Eurasia los eventos de extinción de megafauna coincidieron con los pulsos climáticos, mientras que en Norteamérica fue el avance de la colonización del *Homo sapiens* (las culturas *Clovis* de cazadores-recolectores) la que se ha relacionado robustamente con la extinción de megafauna (Becerra-Valdivia & Highman 2019). En lo que respecta a los felinos, tanto las evidencias fósiles (Seymour 1989, Rodriguez *et al.* 2018) como las genéticas (Eizirik *et al.* 2001, Culver & Pecor-Slattery 2000) sugieren que los pumas y jaguares también fueron eliminados de Centro y Norteamérica coincidiendo con el paso de esta nueva especie de depredador top, y que posteriormente ocurrió la recolonización por individuos procedentes de poblaciones suramericanas. Estos datos sugieren que, en las etapas primigenias de la coexistencia los grandes felinos americanos ya entraban en conflicto con los humanos y que la combinación hombre-clima supone un tándem sumamente penetrante para la extinción de las especies, como muestran las diversas especies de felinos extintas durante dicho periodo expansivo (i.e *Smilodon* o *P. onca augusta*) y de las cuales sólo persistieron los actuales jaguares y pumas.

A pesar de este primer encuentro exterminador para las especies de felino, las culturas paleoindias - evolucionadas a partir de la cultura *Clovis* - se caracterizaron por tener una visión *homofelina,* entendida como la capacidad de proyección en la imagen y virtudes propias del felino (algo así como un *alter ego*). Esta visión idólatra se puede encontrar por todos los rincones y culturas indígenas, como muestran las artes rupestres de Chiribiquete (Colombia), el templo al dios jaguar en Tikal (Guatemala), en las cabezas deformadas con forma felina por los Olmecas (Perry 1970), en la creencia de los pueblos Guaraníes de que el jaguar era el causante de los eclipses (Cadogan 1973) o los innumerables casos de emulación y proyección cultural en el imaginario histórico y mítico que encontramos hasta nuestros días (Castaño-Uribe 2017). Probablemente esta visión integradora, culturalmente más evolucionada que la de los pueblos *Clovis,* pudo propiciar la coexistencia y recolonización de Centro y Norteamérica por los grandes felinos, durante el Pleistoceno tardío, a partir de las poblaciones suramericanas (Eizirik 2001, Culver & Pecor-Slattery 2000).

La llegada del hombre blanco al nuevo continente supuso una transición en cómo los humanos percibían a estas especies. Gradualmente se diluyó la proyección de los felinos como *alter ego* a través de la satanización de su figura, simbolizando una idolatría propia de de los herejes (Reichel-Dolmatoff 1978). Esta visión *felino-fóbica* se fue consolidando a medida que avanzaba por el continente la conversión de los pueblos indígenas al cristianismo que, sin duda, marcó un importante hito para la actual percepción hacia los grandes felinos americanos. Estas dos percepciones conceptuales (*homofelina* vs *felino-fóbica*) son el origen, o al menos un reflejo, de las diferentes percepciones sociales que encontramos en la actualidad.

A partir del siglo XVI nació una estrecha relación entre indígenas y colonos a través del comercio de pieles. En un principio los indios americanos comerciaban con pieles de pequeños animales para conseguir las herramientas de acero del hombre moderno. Este trueque primigenio fue sustituido paulatinamente por una verdadera industria internacional que abastecía el mercado *de moda* norteamericano y europeo en el que las pieles de felinos eran muy demandadas (Carlos & Lewis 2015). Esta industria tuvo su auge durante los años 60 del siglo XX, afectando gran cantidad de especies de mamíferos y reptiles incluyendo a los grandes felinos. Se estima que unos 15.000 jaguares y 80.000 ocelotes fueron cazados cada año para el comercio peletero durante la década de los años 60 (Smith, 1976) y se incrementó, durante tan solo una década, en un orden de magnitud la exportación de grandes felinos (jaguares y pumas) desde Brasil hacia Estados Unidos y Europa (Dowghty & Myers 1971). Durante este corto período de tiempo la industria peletera fue la mayor amenaza para las poblaciones de grandes felinos, especialmente los *gatos pintados,* como jaguares, ocelotes y margays, que vieron reducidas sus poblaciones drásticamente (Swank & Teer 1987). Con la aparición del convenio CITES se prohibió el comercio internacional de muchas especies silvestres, entre ellas el jaguar, incluido en el Apéndice I en el año 1973. A pesar de que el comercio se mantuvo durante los años 70, la industria peletera prácticamente desapareció a principio de los años 80 y, a través de la reducción de la demanda, los precios de las pieles disminuyeron drásticamente, haciendo insostenible el negocio de peletería de felinos salvajes (Swank & Teer 1987).



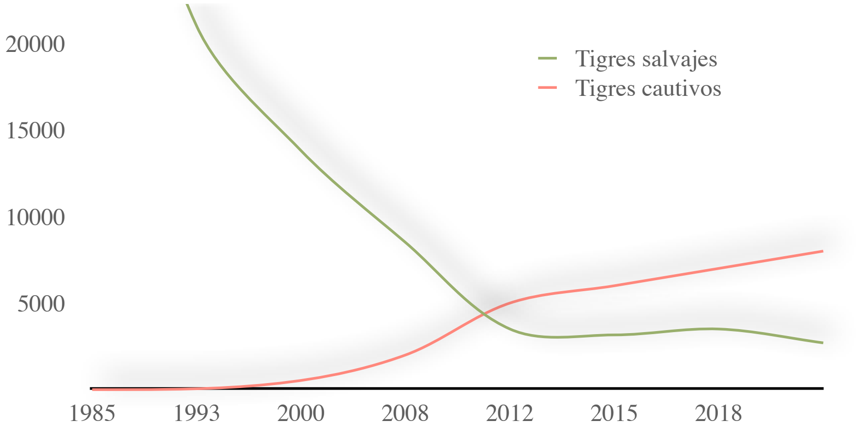
Exportaciones de *Panthera onca* y probablemente *Puma concolor* desde Brasil a US, UK, Alemania e Italia.
Adaptación de Dowgly & Myers (1971) & Smith (1976)

**Principales amenazas actuales para la conservación de los felinos**

Desde entonces y hasta hoy las principales amenazas de los grandes felinos neotropicales se han relacionado con la pérdida de hábitat y la persecución directa (Quigley *et al*. 2017, Nielsen *et al*. 2015). Es abrumadora la reciente documentación sobre el declive poblacional - especialmente sobre el jaguar- por la pérdida de hábitat (por ejemplo, Ceballos *et al*. 2011, Espinosa *et al*. 2016, Hoogesteijn *et al*. 2016, Di Bitetti *et al*. 2016, Paviolo *et al*. 2016, Jedrzejewski *et al*. 2016). La cacería actual de felinos ocurre por distintos motivos, y está generalizada a lo largo del Neotrópico (Medellín *et al*. 2017). Es común que el conflicto que supone la depredación de ganado promueva su cacería (Castaño-Uribe *et al*. 2017). Durante el pasado siglo la ganadería bovina ha crecido de manera muy acusada en Latinoamérica, dominando el paisaje neotropical (Gilbert *et al*. 2018, Robinson *et al*. 2014). Ésta ha modificado ya biomas completos y afecta a los ecosistemas en los que se establece (véase el caso del cerrado brasileño, modificado por la combinación de la ganadería y los sistemas agrícolas intensivos). Actualmente el 27% de la producción mundial de carne es producida en Latinoamérica (FAO, 2020), aunque su superficie abarque poco más del 12 % de la superficie terrestre, dando una idea de la intensidad de esta industria en el Neotrópico. La ganadería supone quizás la mayor amenaza actual a los grandes felinos neotropicales a través del enraizado conflicto que emerge por la depredación de ganado. Conocer en profundidad el conflicto ganadero es uno de los objetivos transversales de esta tesis.

Por otro lado, además del conflicto ganadero existen otros motivos para la persecución y cacería de los grandes felinos neotropicales. Existe una creciente demanda de productos derivados del tigre por parte de países asiáticos cuyo efecto ya ha salpicado al resto de grandes felinos del mundo. Las poblaciones de tigre asiático *Panthera tigris* no han podido soportar la presión de cacería de las últimas décadas hasta tal punto que existen tan solo unos 3000 individuos salvajes en libertad (Goodrich *et al*. 2015). Sin embargo la gran demanda de productos derivados del tigre ha promovido el millonario negocio de la cría de tigres en cautividad (EIA 2017) y ya ha afectado a las poblaciones de leopardos (*P. uncia, P. pardus, N.nebulosa)* y leones (*P. leo)* a través de su uso como sustitutos (Maheshwari & Niraj 2018, Nowell & Pervushina 2015, Williams et al. 2017). Parece que este emergente foco de persecución puede afectar a las poblaciones de otros felinos, entre ellos los neotropicales, como ya lo ha hecho a las de tigre.

El cambio climático es otra de las amenazas actuales. Afecta a buena parte de las especies animales del mundo (Thomas 2010) y sin duda puede tener un importante



**Número de tigres salvajes y tigres cautivos.**
Fuentes: CITES SC70 Doc. 51 Annex 2 (Rev. 1) & EIA 2017. Cultivating demand. The growing threat of tiger farms.

efecto sobre las especies de grandes felinos. Como ya se puso de manifiesto durante las oscilaciones climáticas del Pleistoceno, los cambios climáticos pueden suponer grandes eventos de extinción especialmente si se presentan en combinación con otras presiones. Dada la tendencia humana a repetir el pasado (Freud 1914) no es descabellado imaginar que en la actualidad nos encontremos en un escenario paralelo a la E*xtinción de Megafauna del Cuaternario,* donde - de nuevo - un cambio climático combinado con la presión de cacería amenazan a las especies de gran tamaño. De mantenerse en la línea actual, el efecto del rápido cambio climático (esta vez con una eminente componente antrópica) en combinación con la persecución y caza de los grandes felinos (motivados por la ganadería y el tráfico ilegal) con certeza desembocará en una nueva extinción. Esta vez, el nuevo evento de extinción que se ha denominado la *Sexta Extinción Masiva* (Wake & Vredenburg 2008) tiene un indiscutible origen antropogénico (Estes *et al*. 2011).

El objetivo de esta tesis es profundizar en el conocimiento de los factores que amenazan la conservación de los felinos neotropicales para poder ofrecer información fidedigna que pueda ser utilizada como base de políticas ambientales asistiendo su conservación a largo plazo. He hecho un especial esfuerzo para comprender las relaciones de los grandes felinos con la ganadería tanto desde un punto de vista ecológico como social, ambos necesarios para ofrecer soluciones realistas y factibles ante el preocupante problema. Cada capítulo tiene una aproximación metodológica diferente -análisis genéticos, entrevistas estructuradas, modelado ecológico o revisión bibliográfica- permitiendo aproximamos a las amenazas de los felinos a nivel local y continental, esperando contribuir con una visión lo más completa posible sobre cómo las actividades humanas afectan a estas especies. Las distintas aproximaciones metodológicas, escalas y contextos permiten profundizar en los efectos que las perturbaciones humanas ejercen en los felinos. Por un lado, investigando las principales amenazas a escala global para entender el efecto e implicaciones macroecológicas del ser humano sobre los grandes depredadores ofreciendo, al mismo tiempo, una imagen de su estado de conservación actual. Por otro lado, profundizando en el escenario de coexistencia entre hombre y felinos a través de una visión socio-ecológica del conflicto ganadero que, como veremos, resulta ser la mayor amenaza actual de estas especies. Por último, ofrezco una revisión sobre la amenaza emergente que supone el tráfico de felinos hacia Asia y sus potenciales efectos en las poblaciones de felinos.

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# Chapter 2

## The differential genetic signatures related to climatic landscapes for jaguars and pumas on a continental scale

*Integrative Zoology* 2021

## Abstract

Modern and paleoclimate changes may have altered species dynamics by shifting species' niche suitability over space and time. We analyze whether the current genetic structure and isolation of the two large American felids, jaguar (*Panthera onca*) and puma (*Puma concolor*), are mediated by changes in climatic suitability and connection routes over modern and paleoclimatic landscapes. We estimate species distribution under 5 climatic landscapes (modern, Holocene, last maximum glaciations [LMG], average suitability, and climatic instability) and correlate them with individuals' genetic isolation through causal modeling on a resemblance matrix. Both species exhibit genetic isolation patterns correlated with LMG climatic suitability, suggesting that these areas may have worked as "allele refuges." However, the jaguar showed higher vulnerability to climate changes, responding to modern climatic suitability and connection routes, whereas the puma showed a continuous and gradual transition of genetic variation. Despite differential responsiveness to climate change, both species are subjected to the climatic effects on genetic configuration, which may make them susceptible to future climatic changes, since these are progressing faster and with higher intensity than changes in the paleoclimate. Thus, the effects of climatic changes should be considered in the design of conservation strategies to ensure evolutionary and demographic processes mediated by gene flow for both species.

**Key words:** causal modeling, climatic landscape, ecological niche modeling, gene flow, linear mixed model

## INTRODUCTION

The distribution and spatial arrangement of suitable niches determine the locations, sizes, and connectivity of populations (Guisan & Thuiller 2005; Soberón & Nakamura 2009), which in turn regulate gene flow and drive genetic patterns from the local to the continental scales (Barrientos *et al.* 2014; Loveless *et al.* 2016; Carvalho *et al.* 2017; Inoue & Berg 2017; Mairal *et al.* 2017; Noguerales *et al.* 2017; Koch *et al.* 2018). Changes in the climate have led to range shifts and the alteration of niche suitability across species distributions, making population connectivity transient over space and time (Aguilée *et al.* 2009; Licona-Vera *et al.* 2018; Koch *et al.* 2018). Consequently, gene flow has occurred in different directions and intensity throughout population history, leading to climatic landscape signatures in the current genetic structure of species (Pauls *et al.* 2013; Habel *et al.* 2015).

Jaguar [*Panthera onca* (Linnaeus, 1758)] and puma [*Puma concolor* (Linnaeus, 1771)] are large-bodied and widely distributed felids that likely underwent range shifts mediated by paleoclimatic changes. The current jaguar distribution extends from the southwestern United States to Rio Negro province in northern Argentinean Patagonia (IUCN 2017). However, its late Pleistocene distribution extended somewhat further, from the southern half of the United States to Chilean Patagonia (Rodriguez *et al.* 2018). The puma has a wider current distribution, ranging from Canada to southern Chile (IUCN 2017), though its late Pleistocene distribution encompassed all of North America (Kurtén & Anderson 1980) and reached southwards to the Mar del Plata region in central-eastern Argentina (Chimento & Dondas 2018).

Despite advances in molecular techniques, including non-invasive methods that have been used effectively for jaguar and puma (Roques *et al.* 2014; Palomares *et al.* 2016, 2017; Zanin *et al.* 2016), investigations of the genetic diversity and structure of both species have largely been limited to the local or regional scales (Ernest *et al.* 2003; Haag *et al.* 2010; Miotto *et al.* 2011; Pflüger & Balkenhol 2014; Balkenhol *et al.* 2014; Salzano *et al.* 2015; Srbek-Araujo *et al.* 2018). Some of these studies have shown that both species are susceptible to genetic isolation at the landscape scale due to habitat loss and fragmentation (Haag *et al*. 2010; Miotto *et al*. 2011; Balkenhol *et al*. 2014; Srbek-Araujo *et al*. 2018). However, the patterns of genetic isolation of both species at the continental scale and the possible effects of climate changes on their genetic structure are not well understood. Continental studies on jaguar and puma have focused on niche prediction and its relationship to ecological patterns, which shows the effectiveness of climatic variables as predictors of felid niches (Tôrres *et al*. 2012; MartínezMeyer *et al*. 2013; Caruso *et al*. 2015; Silva *et al*. 2017; Zanin & Neves 2019).

This study aims to estimate the effect of climate changes on the jaguar and puma, assessing whether the modern and paleoclimatic landscape influenced the modern isolation patterns of individuals and the genetic population structure across the Neotropics. Our main hypothesis was that current genetic patterns are an amalgamation of spatial and temporal changes in the distribution of suitable areas and connection routes for the species, which in turn have been driven by climatic landscapes. We expected a stronger genetic signature from climatic landscapes for jaguars than for pumas, at both individual and population levels, since pumas have a higher tolerance to climatic variation (Zanin & Neves 2019) that enables a more stable distribution over space and time.

## MATERIAL AND METHODS

### Genetic data sampling, DNA extraction, and individual identification

Surveys for fecal samples were conducted in 21 localities within the historical sympatric distribution of the species. Jaguar samples were found in 15 of these localities and puma samples in 20 (Fig. 1 and Table 1). Fecal samples were collected between 2000 and 2017 by active search, by experienced researchers and field technicians, along dirt roads and trails. Samples were stored in 100 mL plastic containers with silica gel, and the sites were georeferenced by GPS.

DNA was extracted from the fecal samples using protocols based on the GuSCN/silica method (Boom *et al*. 1990; Frantz *et al*. 2003), and then purified and concentrated by ultra-filtration using Microcon-30 (Millipore). Each batch of extractions (*n* = 12–15) included 1 negative PCR control to monitor contamination by exogenous DNA. DNA extractions of fecal samples were performed in a UV-sterilized laminar flow hood in an isolated laboratory that was specially designated for the manipulation of non-invasively sourced biological material. Fecal samples were screened for species identity using species-specific primers (Roques *et al*. 2011).

Individual genotyping was conducted using an optimized set of 11 microsatellite markers for jaguar and 12 microsatellite markers for puma, following the protocols described in Roques *et al*. (2014) and Zanin *et al*. (2016), respectively. A consensus genotype was constructed for each sample after 4 repetitions. Homozygous loci were assigned when the same allele was observed in at least 3 replicates as long as a different allele was not observed in the fourth. Heterozygous loci were those with 2 different alleles in at least 2 replicates.

## Climatic landscapes

Climatic landscapes were generated by ecological niche modeling, for which we adopted 4 algorithms that use a correlative approach between

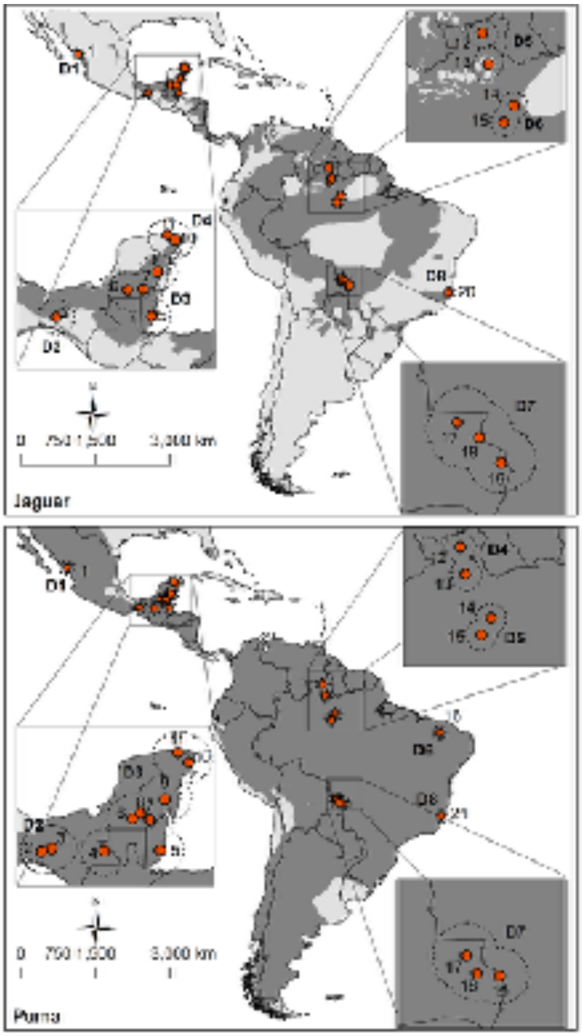

**Figure 1** Sampling localities of feces distributed across the Neotropics for jaguar ($N = 15$) and puma ($N = 20$). In dark gray, species distribution extends according to the IUCN red list (IUCN 2017). Sampling localities were aggregated in demes to population-level analysis. Table 1 provides the names of sam- pling sites and demes.

species occurrence data and climatic variables. The selected algorithms were as follows: generalized linear models—GLM (McCullagh & Nelder 1989), multivariate adaptive regression splines—MARS (Friedman 1991), maximum entropy modeling—MaxEnt (Phillips *et al*. 2006), and random forest (Breiman 2001).

The data on species occurrence is from a recently published database of Felidae occurrences (Zanin & Neves 2019), comprised of records sampled between 1990 and 2016. The database is highly effective for macroecological studies due to the random point-pattern of occurrences and climatic niche predictability at a spatial resolution of 0.5 decimal degrees. Therefore, our modeling approach used the 214 spatially unique occurrences for jaguar and the 538 for puma available in the database (Zanin & Neves 2019). This study thus used a spatial resolution of 0.5 decimal degrees for consistency with the occurrence data.

The current literature warns about the reconstruction of species paleoclimatic distribution by using only the current occurrences of species, which could underestimate the niche breadth and compromise the niche transferability to other temporal scenarios (MartínezFreiría *et al*. 2016; Faurby & Araújo 2018). Here, we opted against including species occurrences from historical distributions for several reasons. Firstly, the adopted dataset covers a wide variety of ecosystems, so our modeling should capture a broad range of climatic niches. Moreover, most recent contractions in the range of jaguar and puma in the Neotropics have occurred locally across different ecosystems. Thus, our estimation should generate an effective approximation of the species' climatic niches since sampled occurrences cover areas environmentally similar to those in which the species has become extinct (similar to the study on elephants by Martínez-Freiría *et al*. 2016). Lastly, the addition of other occurrences can compromise the verified reliability and effectiveness of the dataset by inserting spatial bias, since historical occurrence registers can be less precise than recent ones (Matthews & Heath 2008; Tingley & Beissinger 2009).

All of the selected algorithms employ pseudo-absences in the modeling procedure (Fielding & Bell 1997). We used a random subset of occurrences of other felids of the

| ID | Sampling localities | Jaguar | | | | | | Puma | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NS | NI | QI | NL | Deme | Pop | NS | NI | QI | NL | Deme | Pop |
| 1 | El Carmen | 10 | 4 | 0.90 ± NA | 10.00 ± NA | 1 | JP1 | 25 | 14 | 0.85 ± 0.11 | 9.56 ± 1.12 | 1 | PP1 |
| 2 | Los Ocotones | 1 | 1 | 0.80 ± NA | 11.00 ± NA | 2 | JP2 | 20 | 3 | 0.90 ± 0.15 | 9.65 ± 1.60 | 2 | PP2 |
| 3 | SelvaOcote | | | | | | | 1 | 1 | 0.88 ± NA | 9.00 ± NA | 3 | PP2 |
| 4 | La Cojillita | | | | | | | 2 | 2 | 0.96 ± 0.01 | 11.00 ± 0.00 | 3 | PP2 |
| 5 | Cockscomb | 31 | 5 | 0.88 ± 0.13 | 9.97 ± 1.38 | 3 | JP2 | 3 | 2 | 0.76 ± 0.06 | 8.00 ± 1.00 | 3 | PP2 |
| 6 | Calakmul | 20 | 7 | 0.80 ± 0.15 | 9.14 ± 1.77 | 3 | JP2 | 20 | 9 | 0.85 ± 0.15 | 9.25 ± 1.77 | 3 | PP2 |
| 7 | Ejido Caoba | 14 | 4 | 0.81 ± 0.11 | 10.00 ± NA | 3 | JP2 | 11 | 4 | 0.86 ± 0.14 | 9.64 ± 1.43 | 3 | PP2 |
| 8 | Ejido 20 November | | | | | | | 1 | 1 | 0.83 ± NA | 11.00 ± NA | 3 | PP2 |
| 9 | Petcacab | 18 | 5 | 0.88 ± NA | 8.00 ± 1.41 | 3 | JP2 | 11 | 7 | 0.78 ± 0.14 | 9.09 ± 1.22 | 3 | PP2 |
| 10 | El Eden | 64 | 9 | 0.78 ± 0.18 | 8.81 ± 2.12 | 4 | JP2 | 36 | 14 | 0.84 ± 0.12 | 9.42 ± 1.50 | 3 | PP2 |
| 11 | El Zapotal | 51 | 7 | 0.87 ± 0.12 | 9.40 ± 2.19 | 4 | JP2 | 43 | 12 | 0.89 ± 0.10 | 9.77 ± 1.81 | 3 | PP2 |
| 12 | Viruá | 14 | 7 | 0.88 ± 0.06 | 10.67 ± 0.58 | 5 | JP3 | 28 | 9 | 0.84 ± 0.17 | 9.43 ± 1.67 | 4 | PP3 |
| 13 | Maracá | 2 | 1 | 0.95±0.07 | 9.00±0.00 | 5 | JP4 | 5 | 2 | 0.78 ± 0.17 | 8.80 ± 1.64 | 4 | PP3 |
| 14 | Uatumã | 10 | 6 | 0.79 ± 0.18 | 9.00 ± 2.12 | 6 | JP4 | 10 | 3 | 0.88 ± 0.14 | 9.60 ± 1.58 | 5 | PP3 |
| 15 | Ducke | 17 | 6 | 0.74 ±0.18 | 10.33 ± 0.58 | 6 | JP4 | 62 | 6 | 0.82 ± 0.13 | 9.44 ± 1.46 | 5 | PP4 |
| 16 | Serra Almas | | | | | | | 63 | 3 | 0.88 ± 0.12 | 9.27 ± 1.17 | 6 | PP4 |
| 17 | Candelaria | 9 | 5 | 0.74 ±0.14 | 8.86 ± 1.07 | 7 | JP5 | 17 | 11 | 0.95 ± 0.06 | 9.88 ± 0.49 | 7 | PP4 |
| 18 | La Gaiba | 4 | 3 | 0.86±0.09 | 9.50 ± 1.00 | 7 | JP5 | 1 | 1 | 1.00 ± NA | 10.00 ± NA | 7 | PP4 |
| 19 | CS Corazon | | | | | | | 1 | 1 | 1.00 ± NA | 11.00 ± NA | 7 | PP4 |
| 20 | Linhares | 5 | 1 | 0.77±0.17 | 8.75±2.63 | 8 | JP6 | | | | | | |
| 21 | Santa Teresa | | | | | | | 2 | 1 | 0.70 ± 0.07 | 8.00 ± 0.00 | 8 | PP4 |

**Table 1** DNA amplification success for samples of jaguars and pumas. NS, number of samples; NI, number of individuals identified; QI, quality index, calculated by amplification in 4 PCRs (mean ± SD); NL, number of loci (mean ± SD)

database on Felidae occurrences as pseudo-absences, which were spatially restricted to the Neotropics. We assumed that the observer (or equipment) responsible for a record would be able to determine the presence of other felid species at the same location and time of observation based on the taxonomical similarity and sampling methods used. We, therefore, considered that these pseudo-absences are a closer representation of real absence.

The climatic data comprised 19 temperature and precipitation variables that formed the following scenarios: last maximum glaciation (LMG), Holocene, and modern (1950–1999). The climatic data were generated by the Community Climate System Model (CCSM) and obtained from the Ecoclimate Project (Lima-Ribeiro 2015; Lima-Ribeiro *et al*. 2018).

In order to reduce the number of climatic variables, we began by performing niche modeling though 25 repetitions, in which the occurrences were randomly split at 75% and 25% of the amount of data to be used for model calibration and validation, respectively. We selected 7 variables that best described the climatic niche of the species and repeated the ecological niche modeling using 50 repetitions and the same split rules. The predictions were multiplied by true skill statistic (TSS) and averaged through an ensemble forecasting approach (Allouche *et al.* 2006) to generate the final climatic characterization of the species' ecological niche in which individual predictions contributed accordingly with their robustness (Araújo & New 2007). After characterizing each species' climatic niche, we projected it to modern and past scenarios to construct climatic suitability landscapes for the jaguar and puma. Final predictions were evaluated by TSS, area under ROC curve (AUC) analysis, and kappa (Allouche *et al.* 2006; Peterson *et al.* 2008). All analyses were conducted in R software (R Core Team 2019) with the *biomod2* package (Thuiller *et al.* 2009).

### Individual-based causal modeling of climatic and genetic landscapes

We used an individual pairwise comparison to test the influence of spatial and climatic distances (or dissimilarities) on genetic dissimilarities for the jaguar and puma. Genetic dissimilarities were calculated using the Kosman Index (Kosman & Leonard 2005). Geographical (Euclidean) distance among individuals was used to test the pure effect of spatial distance or the isolation by distance hypothesis. The pure effect of climate was estimated by differences in climatic suitability through pairwise sites. The functional distances (i.e. the connectivity among individuals) were estimated by the least-cost route (*sensu* Adriaensen *et al.* 2003) and resistance surface (*sensu* McRae 2006), both assuming the climatic niche suitability map as a surface of permeability.

The least-cost analysis draws the most efficient path between 2 sites according to the landscape permeability (Adriaensen *et al.* 2003). The resistance surface, on the other hand, has a more complex approach since it estimates the expected commute time between 2 sites by random walk movement (McRae 2006). The transition rule among grid cells was the same for both methods, calculated by mean permeability and considering a potential move to any of the 8 grid cells surrounding the focal one.

The pure climatic effect and functional distances were calculated for each climatic landscape (modern, Holocene, and LMG), for the average climatic landscape (mean suitability among climatic landscapes), and for climatic instability (coefficient of variation of suitability among climatic landscapes). We thus tested 16 hypotheses of how the environment and species genetics could be correlated, with each hypothesis represented by a different geographical and/or climatic distance matrix. The dissimilarity matrices were calculated using the *mmod* (Winter 2013), *vegan* (Oksanen *et al.* 2019), and *gdistance* (van Etten 2012) packages in the R software.

Hypothesis tests were conducted by causal modeling on resemblance matrix, which uses Mantel and partial Mantel tests to measure the degree of correlation among dissimilarity matrices using a simple relationship or by comparing them with a third matrix, respectively (Legendre & Legendre 1998). The causal modeling framework is effective in identifying paths of gene flow in complex landscapes, allowing the simultaneous test of spatial and non-spatial hypotheses (Cushman & Landguth 2010; Cushman *et al.* 2013). We tested a single response variable (genetic distance) against individual predictor variables (either climatic or geographical distance) either by a simple relationship or by controlling for the effect of the other predictor variable. All pairwise comparisons among predictor variables were tested, totaling 256 correlations for each species (16 Mantel and 240 partial Mantel tests). The Pearson correlation and Monte Carlo *P*-values were calculated over 10 000 permutations of the Mantel and partial Mantel tests using the *vegan* package in R software.

Causal modeling can result in reduced Type II errors (Cushman *et al.* 2013), suggesting a low probability of rejection of spatial or climatic effects when they do affect genetic structure. However, it can also show elevated rates of Type I errors, which lead to acceptance of spurious correlations as true patterns (Cushman & Landguth 2010;

Cushman *et al.* 2013). Spurious correlations can be identified by evaluating the tendencies of how each variable works across the entire causal modeling framework. We assumed that an influential predictive variable (true hypothesis) would have a good ability to explain genetic dissimilarities in all models where it appears as a causal variable. However, it should decrease the explanation power of models when inserted as a control variable.

To reduce the misinterpretation pattern generated by Type I and II errors in the causal modeling framework, we used linear mixed models to evaluate the conditional means of the Pearson correlation and the Monte Carlo *P*-value (response variables) as a linear function of the scenarios used as the causal variable (fixed effect) and controlled variable (random effect) (Gotelli & Ellison 2004). The random effect works as a grouping factor, which, in our study, allowed us to calculate shrinkage estimates of regression coefficients (Efron & Morris 1977). The ability of the full model (comprising fixed and random variables) to describe the tendencies of Pearson correlations and Monte Carlo *P*-values was evaluated by comparing it with the null model (composed only by random variables) through an analysis of variance (ANOVA), in which we adopted a 95% confidence interval. Linear mixed models were calculated with the *lme4* package (Bates *et al.* 2015) in R software.

### Population structure and diversity

The sampling sites were unevenly distributed within the species' range distribution (Fig. 1 and Table 1). Thus, we aggregated them based on the largest home-range of each species described in the literature to conduct the population-level analyses. These groups or demes were used as a maximum *k* value for the cluster analysis, minimizing the spatial dependence of sampling sites. The home-range area adopted was 690 km$^2$ for jaguar and 755 km$^2$ for puma (Gonzalez-Borrajo *et al.* 2017), resulting in 8 demes for each species (Table 1 and Fig. 1).

Population clusters were analyzed with TESS software (Chen *et al*. 2007; Durand *et al*. 2009), which employs a spatial Bayesian cluster analysis using Markov Chain Monte Carlo algorithms to identify *k* populations without a priori group definition. TESS assumes geographical continuity of allele frequencies, which would make neighboring sites more similar than distant sites (François *et al*. 2006). This approach enables cline and/ or cluster detection, making TESS effective for scenarios with isolation by distance (François & Durand 2010). We ran admixture models using 50 000 iterations after a burn-in period of 500 000 iterations, for *k* = 2–8 (maximum number of demes), with 20 independent runs for each *k*. The number of clusters was determined using the deviance information criterion (DIC) (Spiegelhalter *et al*. 2002).

Cluster analysis can be influenced by differences in the distribution of sampling units and gaps in the study area, so we performed a second-level analysis when a cluster was composed of more than one deme. In these cases, we performed TESS with 50 independent runs, for *k* varying from 2 up to the number of demes. When the first-order cluster was formed by 2 demes, the number of clusters was determined through the graphical distribution of ancestry coefficients.

CLUMPP software was used to average the admixture proportions of individuals over the replicates of the 20 most likely *k* (Jakobsson & Rosenberg 2007). Geographic maps of ancestry coefficients were drawn in the R software by the *tess3r* package (Caye *et al*. 2016) to enable a spatial visualization of cluster distribution, following Caye *et al*. (2016). The strength of genetic differentiation was estimated with Jost's D, which is more appropriate than FST to compare populations with contrasting levels of genetic diversity (Jost 2008; Whitlock 2011; Assis *et al*. 2018).

We evaluated genetic diversity for populations through allele richness, rarefied allele richness, and observed (*Ho*) and expected (*He*) heterozygosity under Hardy–Weinberg assumptions. The significance of the Hardy–Weinberg equilibrium was evaluated through a Bonferroni correction of *P*-values (Rice 1989). We also estimated inbreeding to measure the degree of substructure among them. We calculated $F_{\mathrm{IS}}$ over the populations and loci using 10 000 permutations. These genetic diversity estimators were performed in the R software using the *adegenet* (Jombart 2008), *hierfstat* (Goudet & Jombart 2011), and *genetics* (Warnes *et al*. 2019) packages.

## RESULTS

### Genetic extraction and genotyping success

We genotyped 270 samples from jaguars and 363 from pumas. Both amplification and extraction were efficient, as indicated by the quality index and the number of complete loci (Table 1). We identified 71 unique genotypes (individuals) for jaguar and 106 for puma (Table 1). The number of individuals per sampling locality ranged between 0 and 9 for jaguar and between 0 and 14 for puma (Table 1), while the number of individuals per deme ranged between 1 and 21 for jaguar and 1 and 51 for puma.

### Climatic landscape effects on genetic similarity between individuals

The evaluating statistics of niche predictions were, on average, higher for jaguars (TSS = 0.85 ± 0.05; AUC = 0.96 ± 0.02; Kappa = 0.80 ± 0.08) than for pumas (TSS = 0.73 ± 0.11; AUC = 0.91 ± 0.025 Kappa = 0.73 ± 0.11). Despite these differences, climatic

| Model | logLik | deviance | Chisq | df | *P* |
|---|---|---|---|---|---|
| *Jaguar* | | | | | |
| FM–Pearson correlation | 34.992 | –69.983 | | | |
| NM–Pearson correlation | 79.940 | –159.881 | 89.898 | 15 | <0.001 |
| FM–*P*-value | –64.208 | 128.417 | | | |
| NM–*P*-value | –36.813 | 73.625 | 54.792 | 15 | <0.001 |
| *Puma* | | | | | |
| FM–Pearson correlation | 159.25 | –318.50 | | | |
| NM–Pearson correlation | –279.12 | –558.25 | 239.740 | 15 | <0.001 |
| FM–*P*-value | –94.232 | 188.464 | | | |
| NM–*P*-value | –19.503 | 39.005 | 149.460 | 15 | <0.001 |

**Table 2** Chi-square (Chisq) test to evaluate the ability of the mixed model (full model, FM) to describe the causal modeling results (Pearson correlation and Monte Carlo *P*-value) when compared with the null model (NM).

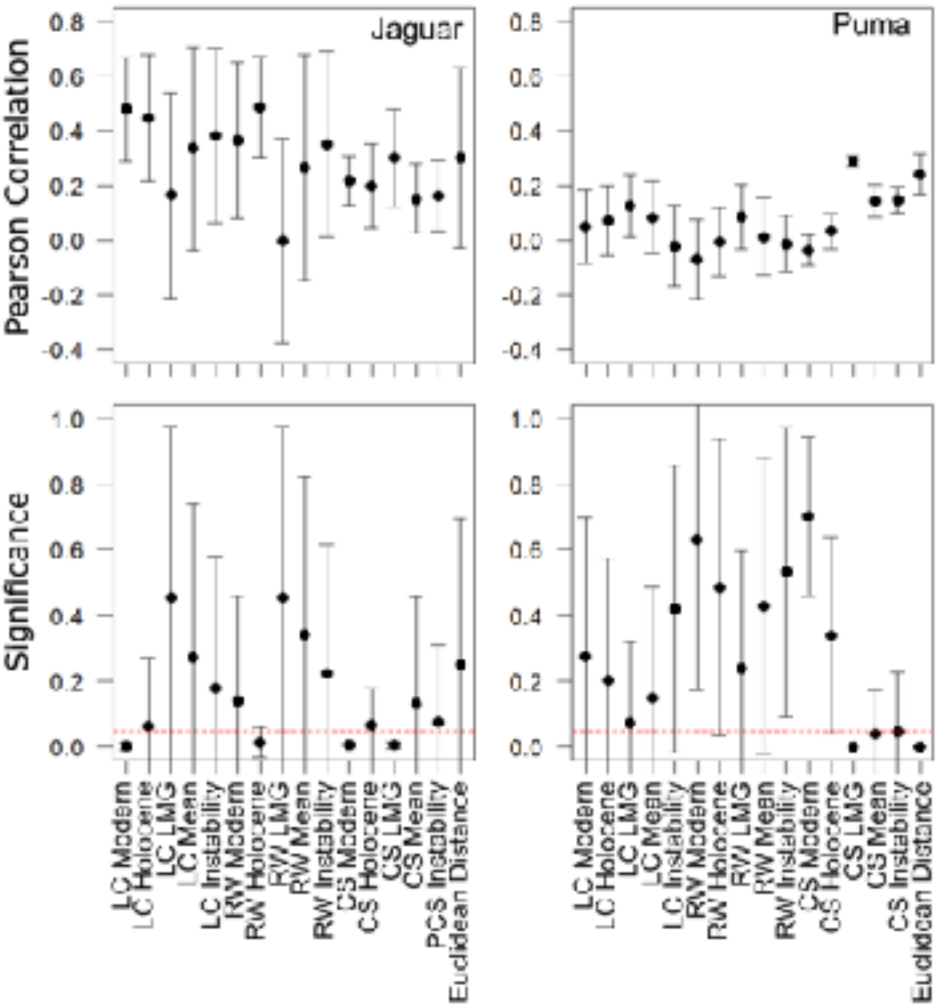

**Figure 2** Average and standard deviation of Pearson correlation and significance of causal modeling framework used to explain genetic distance of jaguars (left panel) and pumas (right panel), according to climatic or geographic scenarios and different hypothesis of isolation. LC, least-cost distance; RW, random walk probability; CS, climatic suitability. Dashed red lines show the limit of significance probability at 0.05.

suitability predictions performed well for both species, which supports their use in our study (see Table S1, Supporting Information, for complete values of model evaluation statistics).

Climatic landscapes and geographical distance affected genetic dissimilarities. The full linear mixed model (composed of fixed and random variables) was better than the null model to describe Pearson's correlation and Monte Carlo *P*-value derived from causal

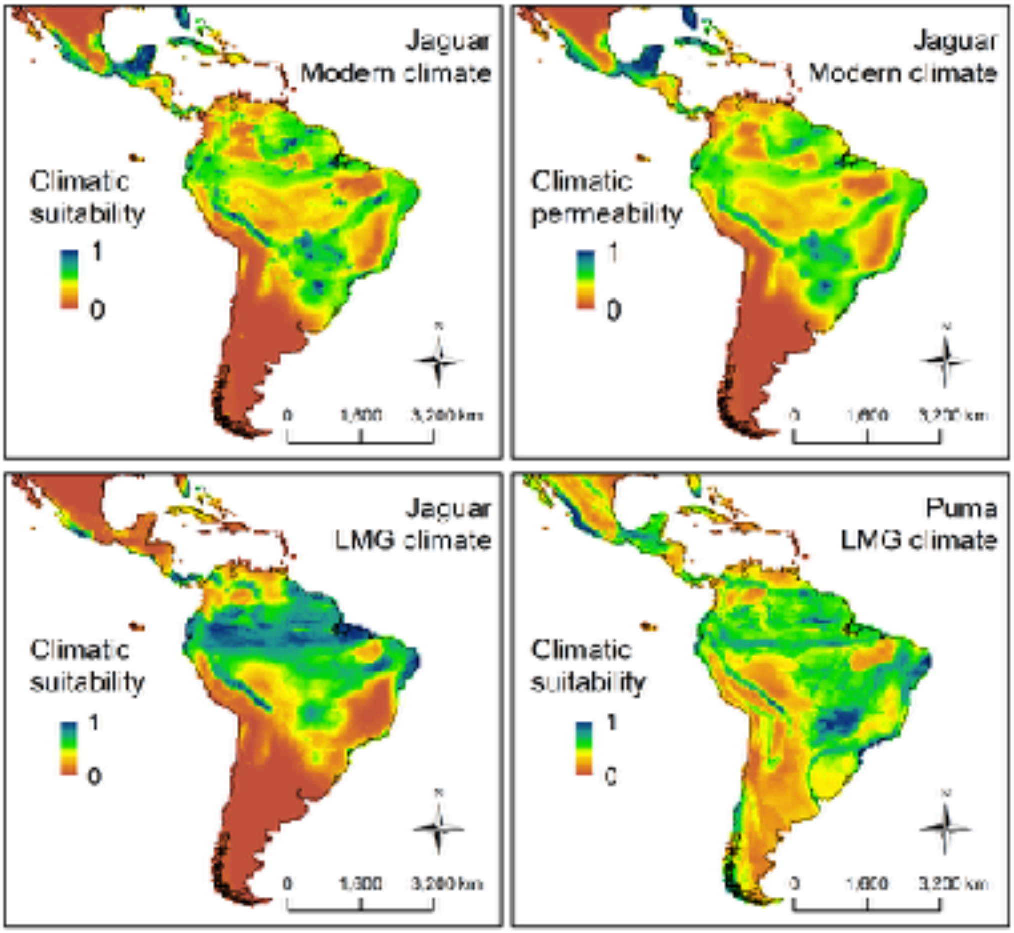

**Figure 3** Climatic suitability and permeability maps correlated with genetic distance of the jaguar and puma.

modeling (Table 2). The genetic distances of the jaguar correlated with the least-cost distances of the modern climatic landscape, the pure effect of current, and LGM climatic niche suitability (Fig. 2, left panel). The genetic distances of puma were, on the other hand, better explained by the pure effect of LGM niche suitability and geographic distance (Fig. 2, right panel).

The climatic landscapes correlated with the genetic similarity of jaguars and pumas are depicted in Fig. 3 (Figs S1 and S2, Supporting Information, for all climatic suitability and permeability maps). Across LMG scenarios, the areas with the highest climatic suitability (closest to 1, mapped in blue) were quite different for both species. These areas were concentrated at the equatorial latitudes for jaguars, while they were spread throughout the Pacific coast of Mexico and the middle mainland and the Atlantic coast of South America for pumas. For the jaguar, the modern climatic scenario shows high niche suitability in the Yucatan peninsula, as well as widely distributed routes of climatic permeability.

### Genetic clusters and diversity

The first-level analyses of genetic clusters inferred 3 ancestral populations for the jaguar, all of which consist of more than 1 deme (Figs 4 and 5a). Second-level analyses split all of them into 2 ancestral populations each (Figs 4 and 5a). Two were located in the Brazilian Amazon, where demes showed a gradual transition of individuals leading to a split into 2 populations. We opted to interpret both ancestral populations as different clusters, even though they exhibited a low Jost's D index (Table 3) because populations structured across cline patterns should exhibit a bias to estimations such as Jost's D index, which is more effective at measuring differentiation force between populations with discrete structures.

Therefore, our cluster analysis suggested that jaguars are organized into 6 genetic populations, as follows: jaguar population 1 (JP1)—El Carmen, Mexico; JP2— South Mexico and Belize; JP3—Viruá and Maracá, Brazilian Amazon; JP4—Ducke and Uatumã, Brazilian

|  | JP1 | JP2 | JP3 | JP4 | JP5 |
|---|---|---|---|---|---|
| JP2 | 0.26 |  |  |  |  |
| JP3 | 0.44 | 0.46 |  |  |  |
| JP4 | 0.47 | 0.39 | 0.07 |  |  |
| JP5 | 0.59 | 0.55 | 0.43 | 0.34 |  |
| JP6 | 0.59 | 0.70 | 0.45 | 0.52 | 0.56 |

**Table 3** Jost's D index showing pairwise genetic differentiation between jaguar populations (JP). JP1, El Carmen; JP2, South Mexico and Belize; JP3, Viruá and Maracá; JP4, Ducke and Uatuma, JP5, Chaco; JP6, Linhares.

|  | PP1 | PP2 | PP3 |
|---|---|---|---|
| PP2 | 0.33 |  |  |
| PP3 | 0.31 | 0.03 |  |
| PP4 | 0.37 | 0.14 | 0.07 |

**Table 4** Jost's D Index showing pairwise genetic differentiation between puma populations (PP). PP1, El Carmen (Mexico); PP2, South Mexico Belize; PP3, Brazilian Amazon; PP4, Chaco (Bolivia), Santa Teresa, and Serra das Almas (Brazil).

Amazon; JP5—Bolivian Chaco; and JP6—Linhares, Brazilian Atlantic Forest (see Table 1 and Fig. 5 for sampling localities and demes belonging to each population). Jost's D showed intermediate to high differentiation between all pairs of clusters, except between both populations from the Brazilian Amazon, as mentioned before (Table 3).

For pumas, the first-level analyses suggested 5 ancestral populations (Fig. 4), but we observed only 3 clusters when individuals were assigned using the ancestry coefficient (Fig. 5c). All South American individuals were assigned to the same cluster (Fig. 5c),

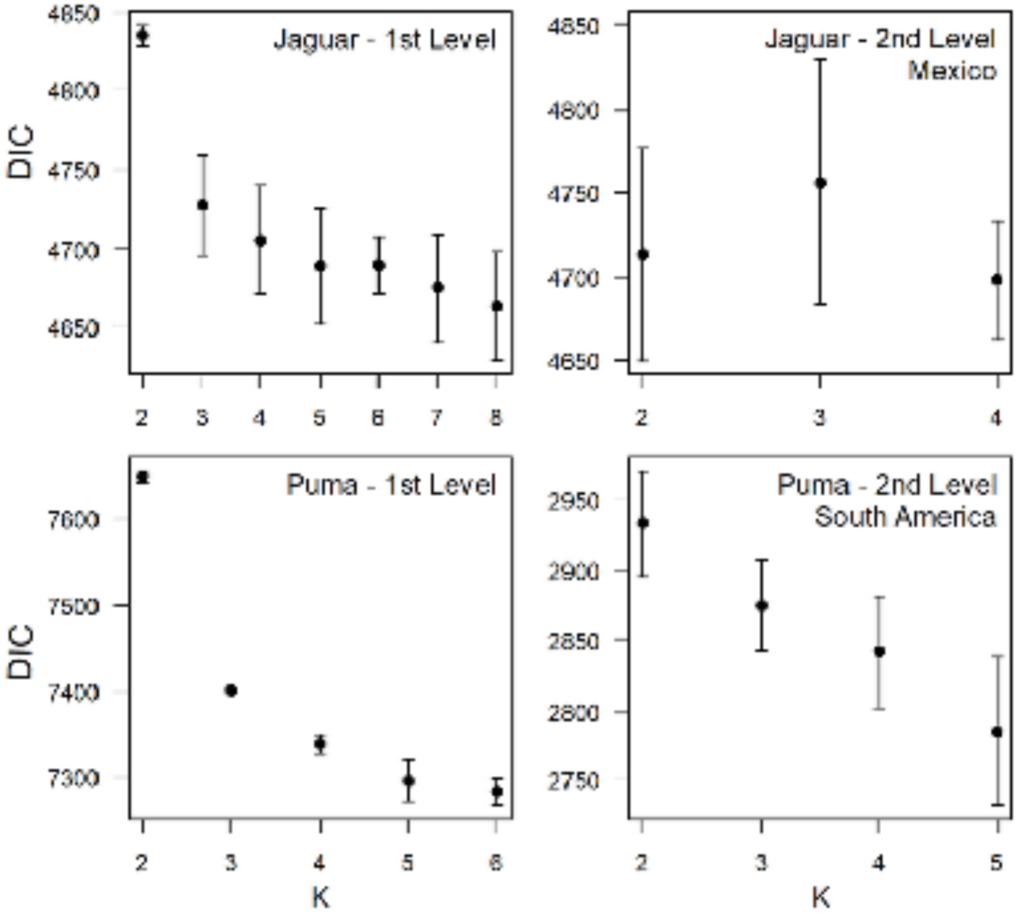

**Figure 4** Number of genetic clusters (*k*) estimated by deviance information criterion (DIC) scores computed by the TESS admixture model for jaguar (top) and puma (bottom). First-level analyses were performed with whole datasets, and second-level analyses were performed for clusters identified in the first-level analyses; so they differed between species.

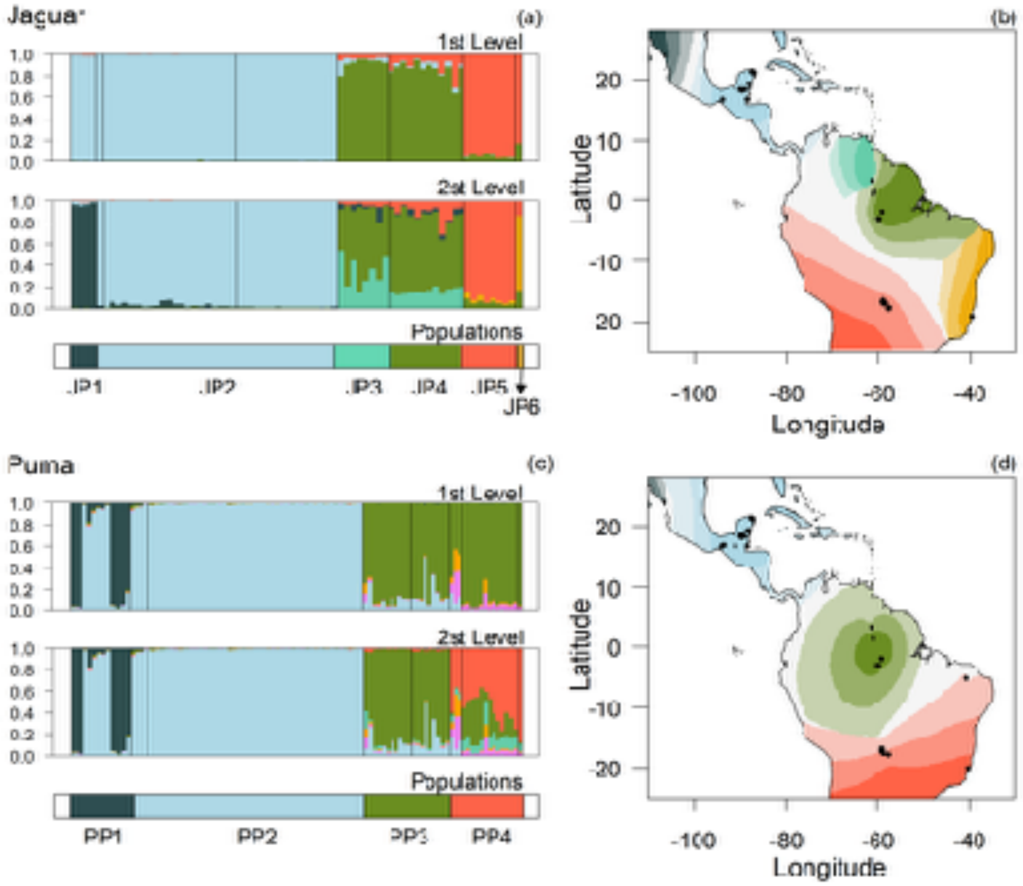

**Figure 5** Cluster analysis computed by the TESS admixture model for jaguar (top) and puma (bottom). Bar plots (a,c) show the assignment proportions (ancestry coefficient) of individuals in the first-level analyses (using the whole dataset) and the second-level analysis (performed for first-order clusters). The black lines inside bar plots delimit demes of individuals, defined by grouped sampling localities limited by the species' home-range size (the complete list of sampling localities and their respective demes are available in Table 1). The horizontal bar below each set of bar plots shows the proportion of individuals that belong to each jaguar population (JP) and puma population (PP). The reference colors were maintained in the maps (b,d), which were spatial representations of populations based on individual assignment proportions. Black points represent individual sites.

so we performed a second-level analysis for them. South American pumas came from 3 ancestral populations (Fig. 4), but the ancestry coefficient analysis suggested only 2 clusters (Fig. 5c,d). Our findings thus indicate a total of 4 populations for pumas (Fig. 5c,d), as follows: puma population 1 (PP1)—El Carmen, Mexico; PP2—South Mexico and Belize; PP3—Brazilian Amazon; PP4—Bolivian Chaco, Santa Teresa in the Brazilian Atlantic Forest, and Serra das Almas in the Brazilian Caatinga biome (see Table 1 for sampling localities and Fig. 5 for the demes that comprise each population).

Jost’s D index showed intermediate to low pairwise differentiation for puma’s genetic clusters (Table 4).

Jaguars had a higher number of clusters than pumas. The spatial congruence of clusters between species occurred only in northern populations (El Carmen and South Mexico/ Belize) (Fig. 5). Moreover, the average pairwise genetic differentiation (Jost’s D) was higher for jaguars than for pumas (average Jost’s D for jaguar = 0.45 ± 0.15 and puma = 0.30 ± 0.24) (Tables 3 and 4), suggesting a more effective mechanism of population isolation for jaguars.

The number of alleles per locus ranged between 4–12 for pumas and 2–16 for jaguars (Table 1). All loci were polymorphic for both species, with an average rarified allele richness ranging between 4.64 and 11.05 for jaguars and only between 5.71 and 6.36 for pumas (Table 5). Both species exhibited similar variation in genetic diversity and expected and observed heterozygosity (Table 5). Jaguars and pumas showed linkage equilibrium for most loci (Tables S2 and S3, Supporting Information) with no evidence of population inbreeding (Table 5).

| Population | *N* | AR | *Ho* | *He* | $F_{IS}$ |
|---|---|---|---|---|---|
| *Jaguar* | | | | | |
| JP1 | 4 | 11.05 ± 3.77 | 1.00 ± 0.00 | 0.63 ± 0.07 | –0.62 ± 0.20 |
| JP2 | 38 | 4.64 ± 1.36 | 1.00 ± 0.00 | 0.67 ± 0.07 | –0.51 ± 0.16 |
| JP3 | 8 | 11.04 ± 3.77 | 1.00 ± 0.00 | 0.73 ± 0.07 | –0.39 ± 0.14 |
| JP4 | 12 | 6.29 ± 2.31 | 1.00 ± 0.00 | 0.72 ± 0.09 | –0.40 ± 0.19 |
| JP5 | 8 | 11.04 ± 3.77 | 1.00 ± 0.00 | 0.71 ± 0.07 | –0.41 ± 0.15 |
| JP6 | 1 | 11.04 ± 3.77 | 1.00 ± 0.00 | | |
| *Puma* | | | | | |
| PP1 | 14 | 6.09 ± 1.29 | 1.00 ± 0.00 | 0.73 ± 0.05 | –0.37 ± 0.10 |
| PP2 | 55 | 5.71 ± 1.39 | 1.00 ± 0.00 | 0.72 ± 0.07 | –0.40 ± 0.14 |
| PP3 | 20 | 5.90 ± 1.54 | 1.00 ± 0.00 | 0.72 ± 0.07 | –0.41 ± 0.16 |
| PP4 | 17 | 6.36 ± 1.54 | 1.00 ± 0.00 | 0.72 ± 0.05 | –0.40 ± 0.12 |

**Table 5** Intrapopulation genetic diversity estimates for jaguar (11 microsatellite markers) and puma (12 microsatellite markers) across populations *N*, number of individuals genotyped; AR, rarefied allelic richness averaged over loci; *Ho*, observed heterozygosity; *He*, expected heterozygosity; $F_{IS}$, inbreeding rate within population.

## DISCUSSION

Jaguars and pumas are the largest American felids and generally have similar ecological and biogeographical patterns of distribution (Wilson & Reeder 2005). Our analysis showed similar patterns of variation in genetic similarity based on climate suitability in the LMG scenario. However, the jaguar seems more vulnerable to climate changes than the puma because the modern climatic landscape has also led to differences between individuals. The higher susceptibility of jaguars to climate change is a likely reason why the species has more genetically structured populations than pumas, especially in South America. Meanwhile, changes in genetic variation in pumas have been continuous and gradual, suggesting a low influence of recent landscape changes, which is in line with the isolation by distance pattern observed between individuals.

For both species, individuals located in LGM climatically suitable areas exhibited higher similarity if compared with individuals from climatically unsuitable areas, despite the distance among them, suggesting an effect of climatic exposure on the genetic configuration. LMG is largely recognized as a period of range contraction and the emergence of environmental refuges for many species (Stewart & Lister 2001; Provan & Bennett 2008; Sandel *et al*. 2011). However, jaguars and pumas have a large climatic niche (Zanin & Neves 2019) with a high dispersion capacity (Morato *et al*. 2016; Gonzalez-Borrajo *et al*. 2017), which enables them to move through less-suitable areas. As a result, this hinders the applicability of climatic refuge hypotheses in the classical interpretation as sites of high genetic diversification and speciation (Provan & Bennett 2008). On the other hand, some species with wide ranges seem to maintain large population sizes in climatically suitable areas (Tôrres *et al*. 2012; MartínezMeyer *et al*. 2013; Martínez-Gutiérrez *et al*. 2018). Therefore, these areas may function as a source of individuals by maintaining a larger population and thereby keeping a larger pool of alleles.

The broad climatic tolerances and dispersion abilities of jaguars and pumas also suggest that the effect of climatic exposure was not a sudden event that isolated or connected individuals and populations. The most probable hypothesis is that paleoclimate changes may have generated gradual and dynamic cycles of expansion and retraction of populations. These smoothing changes reduce the probability of allele fixation, reducing the risk of alleles disappearing in the population, and thereby enhancing genetic similarities (Aguilée *et al.* 2009). As a result, climatically suitable areas may have housed a diminished genetic differentiation and functioned as an "allele refuge" for both the jaguar and puma.

The suitability of the modern climate also interacts positively with genetic similarity for jaguars. These areas could, therefore, also be keeping an allelic pool in their populations. Moreover, the connection routes between climatically suitable areas in the modern day seem to result in genetic exchange between individuals. Therefore, the effects of the modern climatic landscape on the jaguar probably go beyond those from the LMG landscape, suggesting vulnerability to recent anthropogenic impacts coming from climate changes. This result represents an alarming prospect for jaguar conservation, since it suggests the existence of fragile populations and a relatively short-term response of jaguars to climate changes.

The genetic diversity of jaguars found in our study corroborates this warning since our estimates were similar to previous studies in which authors drew attention to the low genetic diversity and population bottlenecks (Roques *et al.* 2016; Srbek-Araujo *et al.* 2018). These results show the emerging need for securing populations located in climatically suitable areas, as well as providing connections over climatically suitable routes to facilitate range shifts into optimum areas. The threats can be more intense for marginal populations, which were poorly sampled in our study because they usually have a small population size and lower genetic diversity than core populations, which can drive genetic losses in marginal populations (Lesica & Allendorf 1995; Blevins *et al.* 2011; Davis *et al.* 2015).

This study provides a map of climatic connection routes for jaguars (Fig. 3); however, our map does not incorporate land cover changes, one of the major threats (IUCN

2020) affecting the jaguar's genetic structure and demography (Haag *et al.* 2010; Zanin *et al.* 2015). Although some studies and field experiences have designed and implemented dispersion corridors for the jaguar from distributional up to local scales (Rabinowitz & Zeller 2010; Petracca *et al.* 2013, 2014; Rodríguez-Soto *et al.* 2013; Silveira *et al.* 2014; de la Torre *et al.* 2017), climatic suitability is not a common parameter to delineate the connection routes. Therefore, the design of corridors must integrate both threats, and existing corridors should be re-evaluated to guarantee their maximum effectiveness and long-term performance.

Unlike jaguars, pumas have not been affected by the modern climatic landscape, showing that the latter species has not experienced a substantial change in genetic configuration between the study sites in recent times. This pattern is probably due to the broad climatic niche of the puma, the largest among felids (Zanin & Neves 2019). This enables pumas to occupy areas ranging from cold climates such as the Rocky Mountains to semi-arid environments like the Brazilian Caatinga. Despite the climatic plasticity, the positive effect of LMG on the puma's genetic isolation shows its responsiveness to climatic depletion. Therefore, the current scenario of the puma's genetic configuration must be viewed with caution because future climate changes are predicted to reach higher rates and velocity than paleoclimatic changes (Loarie *et al.* 2009; Schloss *et al.* 2012; Zanin & Albernaz 2016). The current genetic scenario of the puma, therefore, represents an opportunity to design appropriate conservation plans to avoid further genetic erosion.

Some limitations of our approach may be considered concerning the interpretation and application of results. The grid cell resolution (0.5 decimal degrees) can considerably overestimate ecological niche breadth when compared with a higher resolution (Trived *et al.* 2008). Another relevant consideration has to do with the distance measured by the least-cost routes, which is constrained to only one connection path. Thus, the method ignores alternative routes and solutions (Rayfield *et al.* 2010; Parks *et al.* 2020). Moreover, the least-cost routes can be influenced by the resolution scale and by the method chosen to weight geographic and environmental distances (Adriaensen *et al.*

2003; Beier *et al*. 2009). The resolution we use is appropriate for the macroecological investigation since it provides a good balance between suitable environmental representation and logistical feasibility (Zanin & Neves 2019), and may also present a large amount of biological information (Soberón 2010). However, a higher resolution and more realistic representation of species' movement are essential to investigations in which precise inferences are needed, such as conservation actions or studies at local or regional scales.

Despite these limitations, our results provide valuable information on the effects of climatic conditions

on jaguars and pumas. Our findings lead us to suppose that future climate changes will create genetic isolation and diversity losses for pumas and aggravate the already alarming situation of jaguars. The impacts of climate changes on genetic diversity of species have been increasingly documented in the literature (Aitken *et al*. 2008; Rubidge *et al*. 2012; Row *et al*. 2014; Loveless *et al*. 2016; Lima *et al*. 2017). This amount of evidence makes clear that climatic projection scenarios have to be included in species conservation agendas to ensure evolutionary and demographic processes mediated by gene flow. In this way, providing refuges in suitable areas of climatic stability and dispersion routes among climatically vulnerable populations is essential to the conservation of the species. It is important to highlight that our sampling localities were in areas with relatively homogeneous land cover, meaning that our inferences are only an approximation of the species' natural response to past climate change. However, jaguars and pumas are subjected to strong range contraction due to habitat loss and fragmentation, which can exacerbate the effects of climate changes on genetic population patterns.

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## SUPLEMENTARY MATERIAL

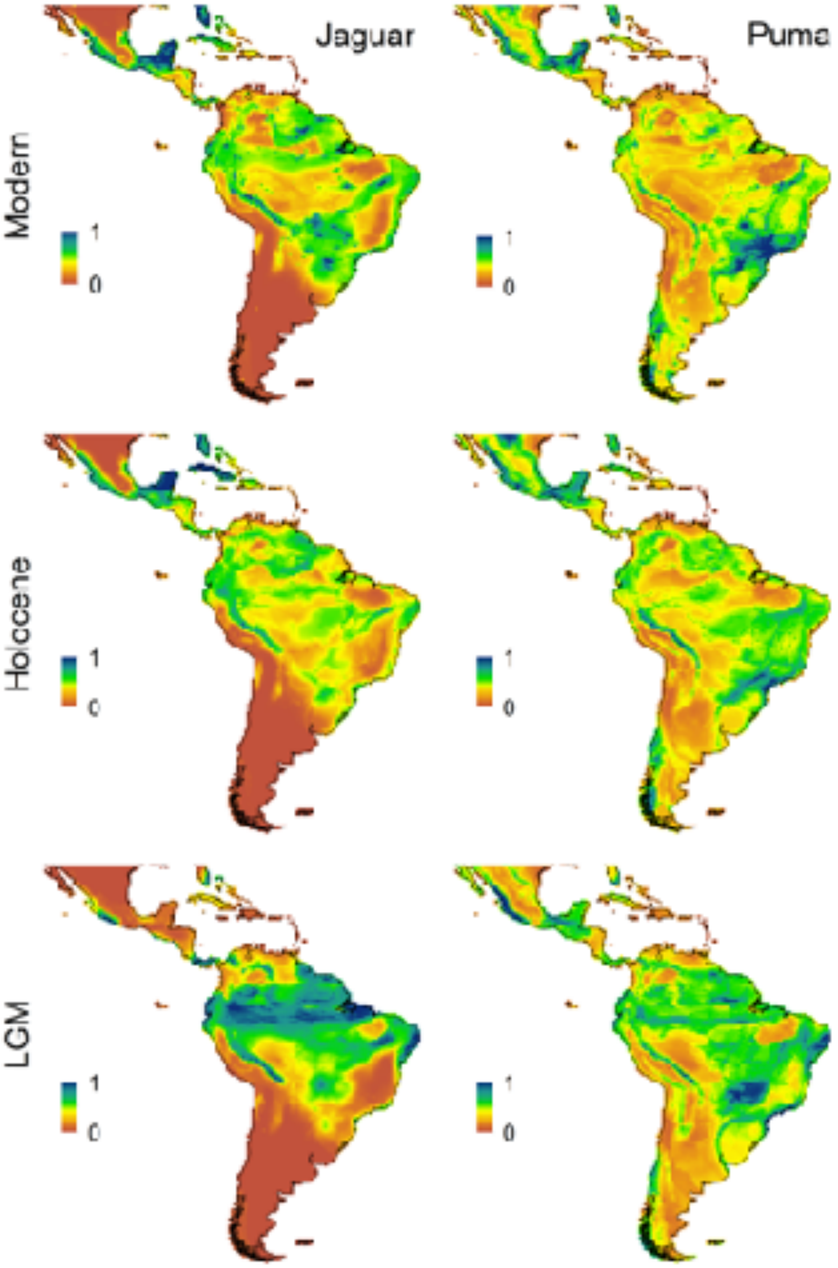

**Figure S1** Jaguar and puma climatic suitability maps generated by climatic niche modeling by ensemble forecast. The predictions were generated for three climatic scenarios: modern (1950-1999), Holocene, and Last Glaciation Maximum (LGM).

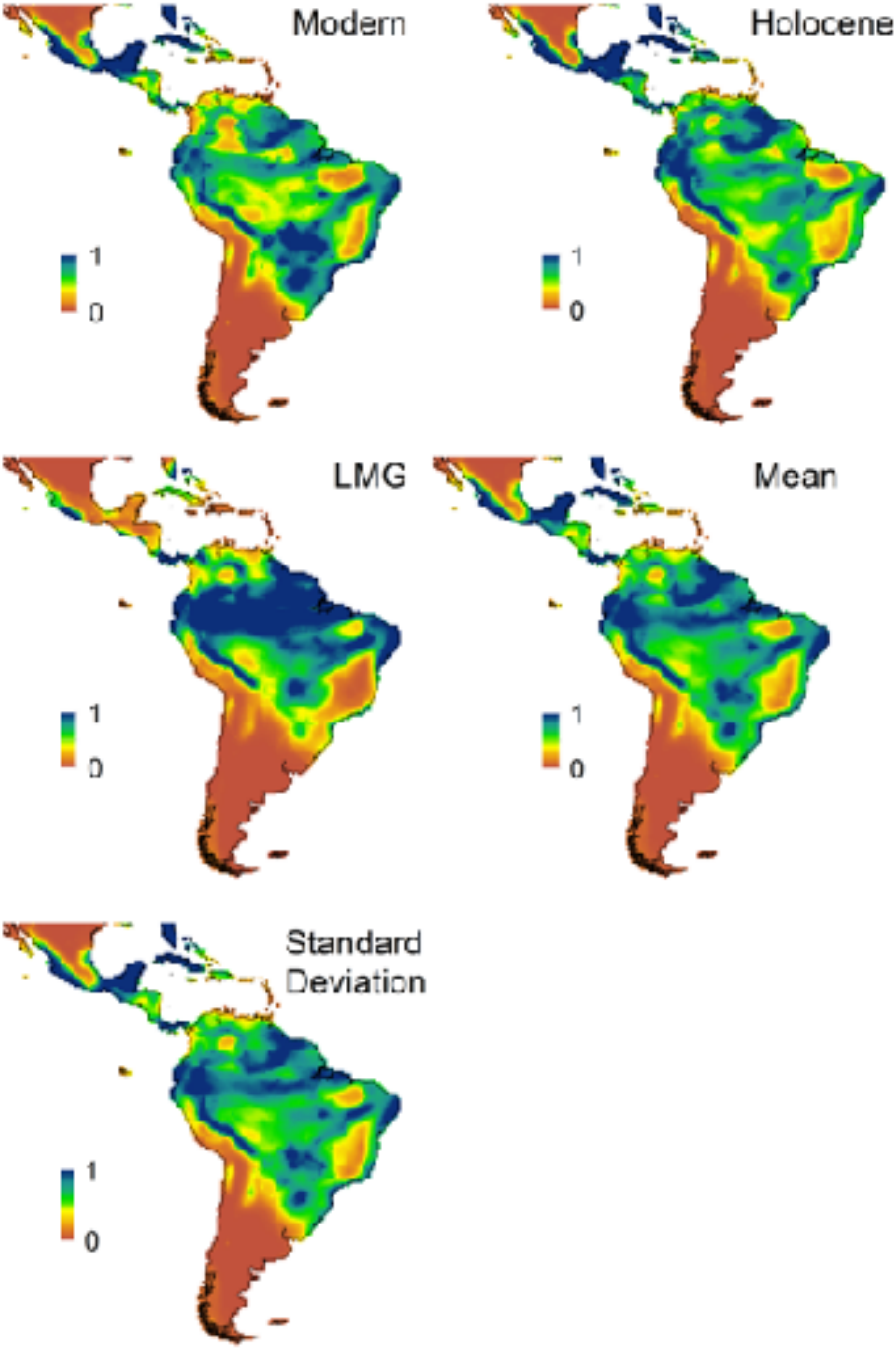

**Figure S2** Jaguar climatic permeability maps.

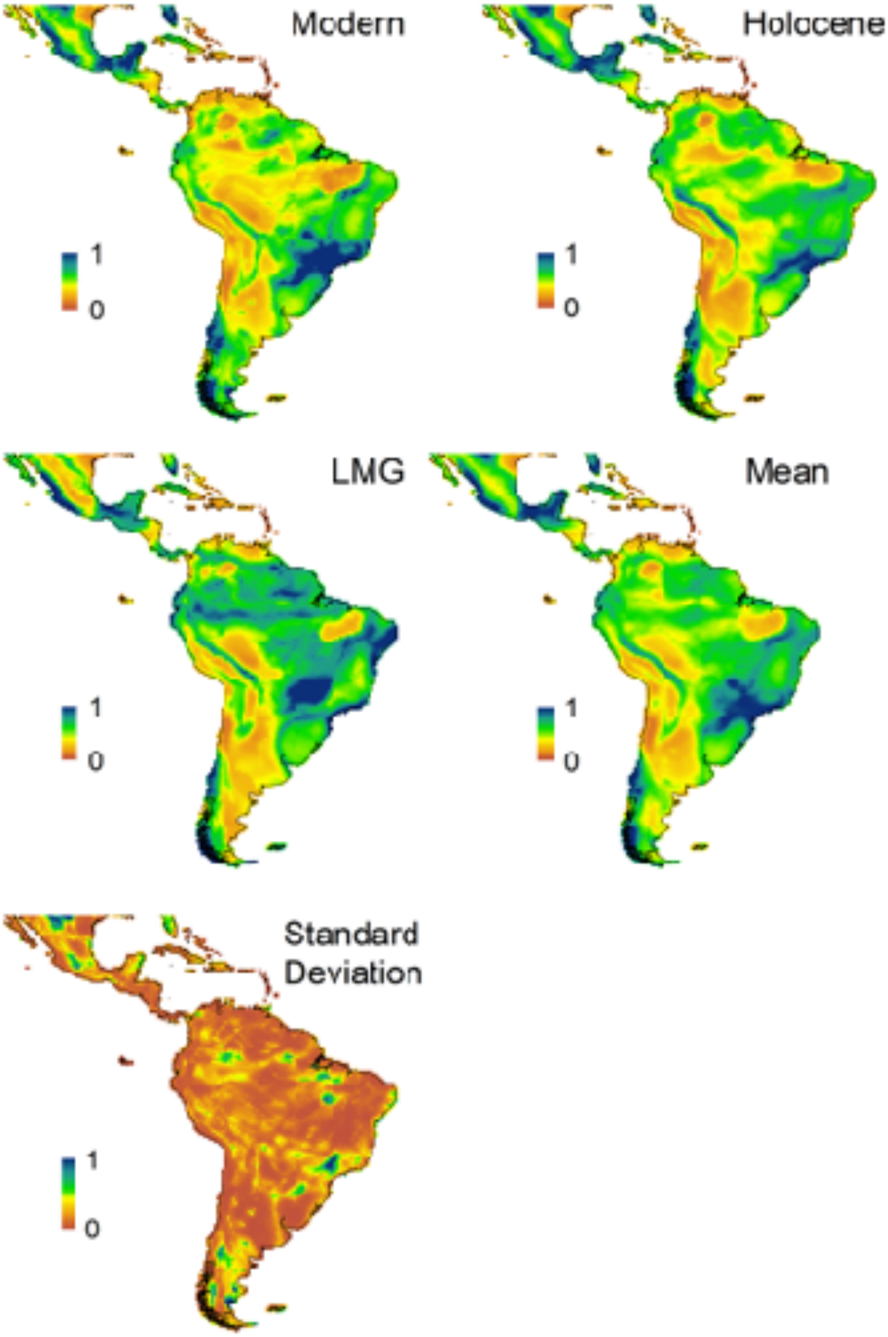

**Figure S3** Puma climatic permeability maps.

| | TSS | ROC | KAPPA |
|---|---|---|---|
| *Jaguar* | | | |
| GLM | 0.8092 | 0.9528 | 0.7368 |
| MARS | 0.8332 | 0.9586 | 0.7746 |
| RF | 0.9390 | 0.9934 | 0.9378 |
| ANN | 0.8164 | 0.9430 | 0.7576 |
| MAXENT.Phillips | 0.8240 | 0.9640 | 0.7762 |
| *Puma* | | | |
| GLM | 0.6262 | 0.8748 | 0.6266 |
| MARS | 0.7336 | 0.9266 | 0.7338 |
| RF | 0.9044 | 0.9864 | 0.9040 |
| ANN | 0.7108 | 0.8742 | 0.7110 |
| MAXENT.Phillips | 0.6652 | 0.8942 | 0.6654 |

**Table S1** Evaluation statistics of algorithms performed to predict jaguar and puma climatic niche. TSS - True Skill Statistic, AUC - Area Under ROC Curve, and Kappa were calculated according to Allouche et al. (2006) and Peterson et al. (2008).

| | chi$^2$ | df | Pr(chi$^2$ >) | Pr.exact |
|---|---|---|---|---|
| FC24 | 32.53577 | 21 | 5.16E-02 | 0.0296 |
| FC26 | 211.0862 | 105 | 4.03E-09 | 0 |
| FC43 | 38.63029 | 10 | 2.95E-05 | 0.0151 |
| FC77 | 124.5507 | 120 | 3.70E-01 | 0.0038 |
| FC82 | 44.90812 | 28 | 2.25E-02 | 0.0033 |
| FC90 | 59.19476 | 28 | 5.16E-04 | 0.0008 |
| FC115 | 462.3036 | 253 | 1.95E-14 | 0 |
| FC126 | 116.8237 | 36 | 1.81E-10 | 0.1026 |
| FC17 | 84.81723 | 55 | 6.05E-03 | 0 |
| FC547 | 123.9771 | 66 | 2.06E-05 | 0.1298 |
| FC566 | 245499 | 105 | 2.88E-13 | 1 |

**Table S2** Hardy-Weinberg linkage equilibrium over loci for jaguars

| | chi^2 | df | Pr(chi^2>) | Pr.exact |
|---|---|---|---|---|
| locus3 | 375.0657 | 105 | 0.00E+00 | 0 |
| locus10 | 217.4087 | 153 | 4.82E-04 | 0 |
| locus77 | 200.6454 | 55 | 0.00E+00 | 0.0002 |
| locus82 | 221.7449 | 66 | 0.00E+00 | 0 |
| locus108 | 25.49544 | 15 | 4.37E-02 | 0.0463 |
| locus112 | 79.46914 | 36 | 4.06E-05 | 2 |
| locus126 | 61.60862 | 45 | 5.04E-02 | 0.0064 |
| locus208 | 98.68517 | 55 | 2.74E-04 | 0.1246 |
| locus210 | 297.7771 | 120 | 0.00E+00 | 0 |
| locus216 | 126.5838 | 91 | 8.11E-03 | 0 |
| locus339 | 428.3287 | 171 | 0.00E+00 | 0 |
| locus547 | 71.03211 | 28 | 1.33E-05 | 0 |

**Table S3** Hardy-Weinberg linkage equilibrium over loci for pumas

# Chapter 3

## A continental approach to jaguar extirpation: a tradeoff between anthropic and intrinsic causes

*Journal for Nature Conservation 2022*

## Abstract

Human impacts are blamed for range contraction in several animal species worldwide. Remarkably, carnivores and particularly top predators are threatened by humans despite their key role in maintaining ecosystem balance and functions. Conservation strategies to allow human-carnivore coexistence are urgently needed and must be built on evidence and driven by knowledge of population risk at a broad scale. However, knowledge on wide distributed species is often based on regional expert opinions in which uncertainty is not quantifiable, making data incomparable across regions. Here we develop a method to assess endangerment status using information on range contraction and main threats using the jaguar *Panthera onca* as model species. The use of GLM with the main intrinsic and extrinsic drivers of jaguar extinction allowed us to assess endangerment status at continental and population scale. We found this method to be a valuable tool to obtain a broad picture of human-induced endangerment in a species. Intrinsic traits (summarized in the demographic contraction theory) and anthropic traits (based on agriculture, cattle and human densities) explained jaguar extinction highlighting the particular importance of livestock activity. Our results suggest that livestock ranching has a pervasive effect on the species likely due to habitat loss combined with retaliatory hunting. We highlight the need to rethink policies, practice and law enforcement in relation to livestock and suggest the development of action plans based in local evidence in those countries where endangered populations have been detected. We also recommend involving and encouraging land owners and private companies in the conservation of private lands that comprise much of the endangered jaguar range.

***Key words:***
Human-carnivore coexistence, extinction risk modelling, jaguar, retaliatory hunting.

## INTRODUCTION:

Species extinctions generally start with the vanishing of particular populations that continues until no populations remain (Yackulic et al. 2011). Understanding the general dynamics of species range contraction is key for effective conservation, and predicting population extinction risk is an important step toward achieve this goal (Safi & Pettorelli, 2010). There are two main factors determining carnivores' extinction risk (Purvis, 2000): 1) intrinsic traits, such as body mass (Inskip & Zimmermann, 2009), life history (Pearson et al., 2014) or population genetics (Frankham, 2005), and 2) extrinsic causes based on modern exposure to external anthropogenic threats (Bruskotter et al., 2017), including human-driven disease expansion (Pedersen et al., 2007). Extrinsic causes have been repeatedly suggested as important traits that affect direct or indirectly carnivore populations. In fact, human density (Woodrooffe, 2000), prey depletion (Craige et al., 2010), habitat loss (Cardinale et al., 2012) or retaliation (Jedrezewski et al., 2017) have been highlighted as the most important drivers of many carnivore species. Intrinsic traits may be summarized by the demographic contraction theory (Lawton 1993, Brown, 1995), which is derived from basic population dynamics. It assumes that environmental conditions and resources for species at the center of their distribution are more suitable than at the border, resulting in higher population growth rates and thus, higher abundance in central areas. This theory predicts that populations would be first extirpated along the range border (where density is lower) and would continue toward the center. On the other hand, more humanized landscapes are associated with higher risk of extirpation (Laliberte and Ripple 2004, Schipper et al. 2008, Hoffmann et al. 2010, Fisher 2011, Pomara et al. 2014), predicting that populations would be first extirpated in areas where human activities such as agriculture, cattle raising and urbanization dominate.

Risk models have been widely used to provide valuable information for conservation purposes. Most risk model assessments, particularly for larger mammalian carnivores, are based on habitat suitability often omitting anthropic traits that are usually indicated as responsible for the non-explicated variation (Cardillo, 2004; Brashares et al. 2001; Harcourt et al. 2001; McKinney 2001; Ceballos & Ehrlich 2002; Parks & Harcourt 2002). Studies taking into account anthropic variables

(Rodriguez-Soto et al. 2011, 2013, 2017, Zarco-Gonzalez et al. 2013) become more realistic models but use to be local scaled (but see Jedrezejewski et al. 2018). However, knowledge of both drivers of population declines and ultimately species extinction should be one of the main focusses to facilitate the allocation of the limited resources to specific conservation interventions (Mace et al., 1993; Davies et al., 2008; Travers et al., 2016).

During the past decade, knowledge about the ecology and conservation of top predators has increased widely. In particular, jaguars (*Panthera onca*) have received great attention since they have suffered a reduction to at least 46% (Sanderson et al., 2002) of their historic range. Since Sanderson et al. (2002) defined the Jaguar Conservation Units (henceforth JCU), many updates and revisions of jaguar status have been made and this percentage has been currently set to 51% in the last IUCN expert assessment (Quigley et al., 2017). Global experts made contributions and reviewed the state of the art completing the actual conservation snapshot for many regions (i.e., Quigley et al. 2017 and Medellín et al. 2016). This effort generated a large amount of information that not only promotes jaguar conservation but also enables the use of the species as a model to test for specific hypotheses about species range contraction. Again, most of the continental scale research has been focused on niche prediction and its relation to ecological patterns, demonstrating the efficiency of climatic variables as predictors of the felid niche suitability (Torres et al., 2012; Martínez-Meyer et al., 2013; Caruso et al., 2015; Zanin et al., 2019). However most continental scale approaches ignore anthropic disturbances, vital to understand species decline, and have been only assessed at a regional scale (Cavalcanti et al., 2010; Zimmermann et al., 2005; Rodriguez-Soto et al. 2011, 2013; Marchini et al., 2012; Villalva and Palomares, 2019). Moreover, ecological research on jaguars has largely focused on populations inhabiting protected areas (Foster et al., 2020). Consequently, few data are available on jaguars occupying the mosaic of human settlements and agriculture. These areas comprise typical unprotected landscapes, including jaguar movement corridors and private properties (Hoogestijn et al, 2015) that have been identified as vital to maintaining the genetic connectivity of jaguars (Zeller et al., 2013). Furthermore, global estimates are based on “expert opinion” which is burdened with a high and unquantifiable level of uncertainty

(Akçakaya et al., 2000; Rodrigues et al., 2006) that may result in a possible over or underreporting of threats to jaguars in certain areas (Zeller, 2006). The role of spatially explicit models appears to be a valuable tool as they can be a compliment to expert-based information (Bernal, 2015).

The aim of this study is to identify the endangerment of jaguars across their current range. As mentioned, jaguars are mainly threatened by intrinsic and external factors. The intrinsic threats are related to their large size, high trophic level, slow population dynamics and fragmentation of its populations that increases their extinction risk (Purvis et al., 2000). Thus, we expect them to exhibit a periphery-to-center extinction pattern. The extrinsic threats are related to human activities such as habitat loss on behalf of agriculture, cattle ranching (including persecution by predation on livestock) and urbanization (Boron et al., 2016, Quigley et al., 2017). We expect the probability of jaguar extirpation to increase in areas with higher human pressures compared to more natural areas. More concisely, we expect to find jaguars especially affected by livestock due to the combined effect of habitat loss and the deeply rooted retaliatory killing used to minimize economic losses, while agriculture and urbanization may moderately affect the species due to the lower conflict level with the main economic interests. Accordingly, we build an extinction threat model based on aforementioned intrinsic and extrinsic traits that will contribute to generating a comprehensive snapshot of current jaguar endangerment that may help in the elaboration of conservation strategies.

## METHODS:

We examine the extinction probability of jaguars for their entire distribution range using General Linear Models (GLM). We used current and historic distribution to construct a binomial response variable, assigning value zero to areas where jaguars still persist and value one to areas where jaguars have been extirpated (Fig. 1. Supp. 1). Current range (Quigley et al., 2017) was subtracted from historic range (Seymour, 1989) to obtain the area where jaguars have been locally extinct. To generate the dataset, we randomly displayed a set of 1000 points on current and extirpated areas extracting the same amount of data in each to avoid overdispersion.

We used a set of predictor variables based on intrinsic and extrinsic traits. The intrinsic variable was defined as the distance to the border from the historic distribution grounded on the demographic range contraction hypothesis. The extrinsic predictors contained a selection of the main reported human drivers of jaguar extinction such as fragmentation, habitat loss and felid persecution by humans (Quigley et al., 2017). Thus, we selected urban, agriculture and cattle ranching as the main human disturbances related to the aforementioned drivers. Human density was used as a proxy for urban disturbance based on the SEDAC-NASA model GRUMP 2000 (CIESIN, 2017). This is a population estimate at the municipal level, corrected for night-light. Agriculture disturbance was based on Global Land Cover (Bartholome et al., 2002; Eva et al., 2004) from The European Council. We clustered all types of agriculture (Cultivated and managed areas, Mosaic cropland with tree and Mosaic cropland with shrub) and resampled from 1 to 10 $Km^2$ pixel size obtaining the percentage of agriculture cover. Livestock pressure was acquired from Global Livestock of the World (Robinson et al., 2014) based on livestock data at a municipal level representing cattle density (number of heads/$km^2$). All layers were unified at a pixel value of 100 $Km^2$ based on a conservative home range size for a jaguar male (Gonzalez-Borrajo et al., 2017). When redefining pixel size, human and livestock pressure data took the mean value of the underlying pixels, while agriculture pressure, as explained above, was obtained as a percentage of cover regarding the 100 underlying pixels of 1 $Km^2$ contained in each sample grid of 100 $km^2$.

We tested the effect of intrinsic and external traits on jaguar extinction using a logit link with species extinction as the response variable. We first constructed univariate models to graphically evince the relationship of extinction to each independent variable. Then, using an information-theoretic approach, we analyzed the effect of intrinsic and extrinsic variables on the probability of jaguar extinction by comparing the generated presence-absence data, guided by three general hypotheses: (i) extrinsic traits (human disturbance) caused jaguar extinction; (ii) intrinsic traits (inherent species contraction) caused extinction; and (iii) the combination of the two influenced extinction. We also constructed a null model that included no explanatory variables. Prior to modelling we searched for confounding effects among predictor variables using Pearson´s rank correlation to avoid multicollinearity (Zar, 1999).

We made the best model spatially explicit within the jaguar current range using the logit function. Note that the intrinsic variable used here was the distance to the border from the current distribution range rather than the distance to the historic distribution. All other variables remained unchanged.

Finally, we focused on Jaguar Conservation Units (Sanderson et al., 2002) to compare the endangerment status among the most important and stable jaguar

| | Variables | AIC | Ɓ | S.E. | *p value* |
|---|---|---|---|---|---|
| Natural contraction | | | | | |
| | *Intercept* | | 0.820 | 0.108 | <0.001 |
| | Distance to border | 1255 | -0.211 | 0.022 | <0.001 |
| Anthropic variables | | | | | |
| | *Intercept* | | -0.621 | 0.085 | <0.001 |
| | Cattle density | 1212 | 0.033 | 0.003 | <0.001 |
| | *Intercept* | | -0.532 | 0.082 | <0.001 |
| | Agriculture | 1258 | 0.023 | 0.002 | <0.001 |
| | *Intercept* | | -0.166 | 0.071 | 0.01 |
| | Human density | 1339 | 0.020 | 0.004 | <0.001 |

**Table 1.** Univariate models for jaguar extinction. Comparison of models based on AIC and Beta, Standard error (S.E.) and significance level (*p-value*) are also shown.

populations. Values for each Jaguar Conservation Unit were calculated as the mean value of pixels contained in the polygon.

We transformed and processed the data with Q-Gis (2.8.9-Wien), and raster (Hijmans, 2020), spatial (Venables & Ripple, 2002), terra (Hijman, 2021) and sf (Pebesma, 2018) packages in R, and carried out the statistical analyses using the MuMIn (Barton, 2020) package in R version 4.0.3 (R Development Core Team, 2021).

## RESULTS:

Univariant models showed the relationship of all predictors with jaguar extirpation (Table 1). Distance to the border relate negatively with extinction whereas anthropic variables showed a positive relationship. Cattle density showed the lowest AIC among univariant predictors. Each variable affected extinction differently (Fig. 1).

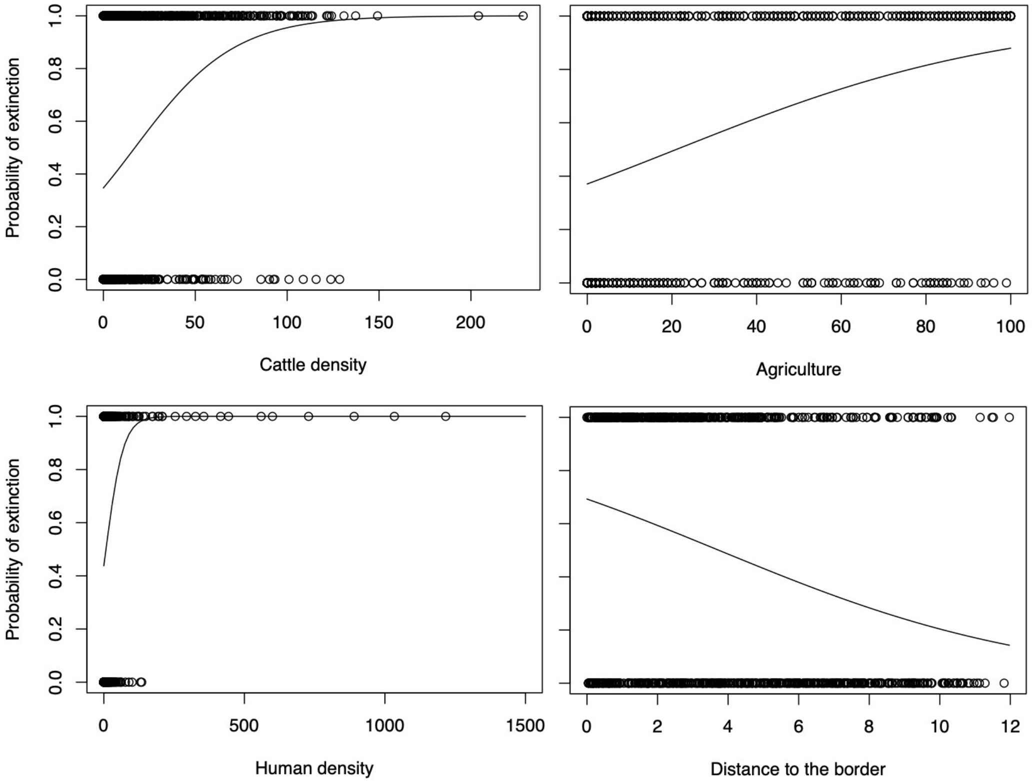

**Figure 1.** Univariate models for cattle density (heads/Km$^2$), agriculture coverage (%), human density (people/Km$^2$) and distance to the border (DD) related to probability of extinction.

Probability of extinction reached saturation with cattle and human densities, but not with agriculture or distance to the border. Saturation was reached over values of 150 and 350 (individuals/Km$^2$), respectively. Extinction likelihood reached a maximum value of 0.86 when agriculture cover was maximized.

Correlation tests showed cattle and agriculture as the most correlated variables with a marginal correlation of r pearson = 0.57 (Table 1. Supp. 1). Therefore, we retained all variables for multivariate models. Model selection showed that, in terms of AIC, extinction was better explained by anthropic variables rather than intrinsic traits, however both natural and human induced variables composed the best model characterized by the lowest AIC value among the tested hypotheses (Table 2) and with a goodness of fit $D^2 = 0.20$.

When the saturated model was made spatially explicit, we found 4.15 million Km$^2$ (corresponding to 46.9 % of current distribution) to have a probability of extinction over 0.5 while 4.7 million Km$^2$ (53.1 %) took values under this figure (Fig. 2). Four Jaguar Conservation Units are out of the current distribution range therefore appear to be entirely extinct and 68 % of JCUs (n = 51) showed a mean probability of extinction over 0.5. Regarding to the aggregated JCUs area more than 55 % of it took values over 0.5, corresponding to 886.834 Km$^2$ (Fig. 1, Table 1. Supp.2).

| Hypothesis | Intercept | Agriculture | Cattle density | Human density | Distance to border | AIC | delta |
|---|---|---|---|---|---|---|---|
| H1 | -0.008 | | | | -0.651 | 1287 | 174 |
| H2 | 0.150 | 0.409 | 0.659 | 1.043 | | 1199 | 86 |
| H3 | 0.094 | 0.291 | 0.876 | 0.396 | -0.728 | 1113 | 0 |

**Table 2.** Model selection (information theory approach) based on three hypotheses: H1. Natural contraction explains extinction; H2. Anthropic disturbance explains extinction; H3. The combination of intrinsic (H1) and extrinsic (H2) variables explain extinction.

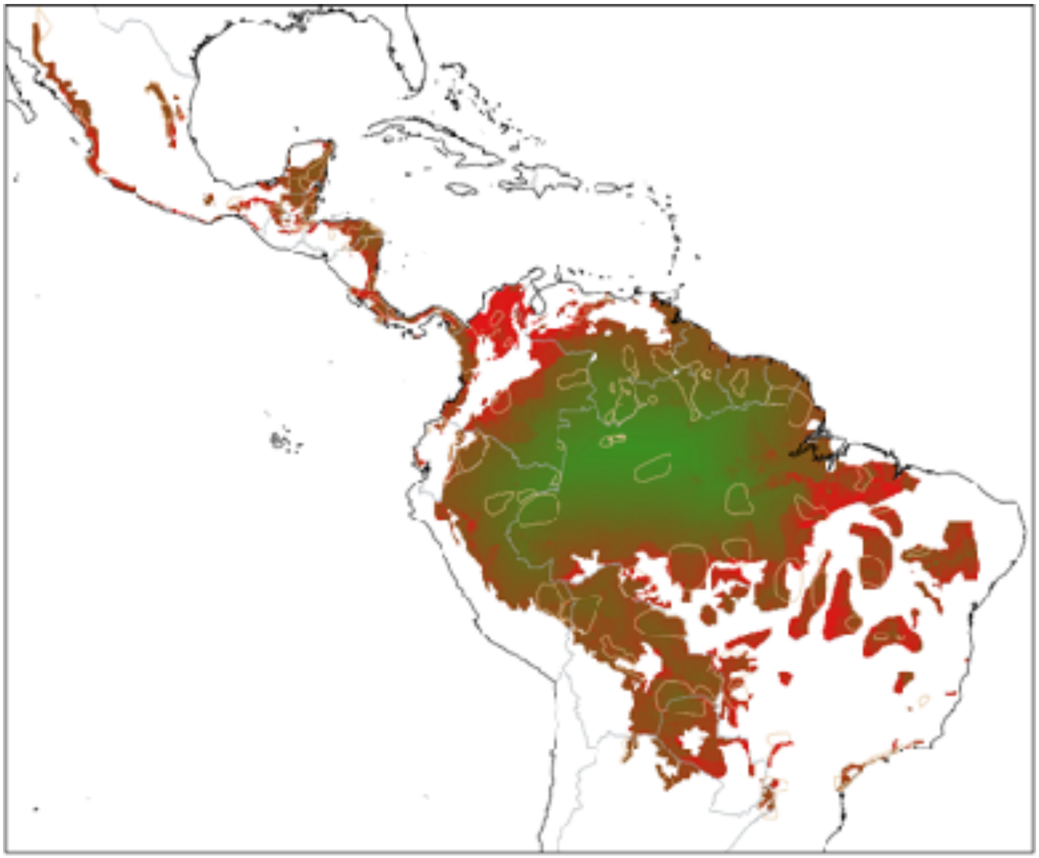

**Figure 2.** Probability of jaguar extinction in their current range based on the saturated model. Red pixels correspond to high endangerment levels while green pixels are related to low endangerment. Polygons demarcated in orange correspond to Jaguar Conservation Units (Sanderson et al., 2002). Probability frequency distribution is also shown (bottom-left).

## DISCUSSION:

In our study, anthropic drivers contributed the most to jaguar extirpations, suggesting that jaguar extinction is mostly human-driven. However, we also found that the edge effect is important for jaguar extinction as it takes part of the best model. This result likely indicates a combined effect among the limited jaguar recolonization from sources and the greater human pressure intensity at the distribution edge. Anthropic variables showed scarce correlation with distance to the border (Table 1. Supp. 1) however, human pressure may locally be more intense at the border than at the core of the distribution where ecosystems are more pristine and human industries have less impact. The lethal combination among edge effect and human induced mortality has been previously detected in protected areas for many large carnivore species, including jaguars (Woodroffe and Ginsberg, 1998) but, to our knowledge, it has not been detected in the entire range of any carnivore species. In summary, we found that both intrinsic and anthropic variables affect jaguar extirpations. We highlight the need to consider both human activities and natural intrinsic traits to understand the range contraction of a species, a conclusion recently shown for different mammalian species (Pacifici, 2020), in line with prior findings where combining distance to range border and human impacts are needed to define terrestrial vertebrate range contraction (Lucas et al., 2016).

From the set of extinction drivers we test here, cattle density showed the best performance in both univariant and multivariant models, suggesting the major role that cattle industry may have for jaguar extirpations. On the other hand, the rest of anthropic drivers didn't perform well to explain jaguar extinction compared to cattle ranching, even though agriculture (Petraca, 2014) and human density (De Angelo et al., 2013) are main factors limiting jaguar use of space at regional scales. We highlight the limited effect of agriculture, which only reached a moderate extinction risk in the univariant model even when agriculture cover was maximized. Still, agriculture and urbanization are important drivers of habitat loss but these human activities lack the deeply rooted motivation of retaliatory hunting that characterizes livestock ranching, which appears to be the main reason for human-induced jaguar extinction. The implications of these results are relevant at the continental scale, since livestock and agriculture are the essential drivers of habitat loss and fragmentation in Latin America (FAO & UNEP, 2020). Predictions of world population growth (UN, 2019) and the resulting increase on food demand (FAO, 2017) portends an increase in the area occupied by these industries in the neotropical region. Therefore, identifying livestock growth policies in particular may help to get ahead of jaguar extirpations in the near future.

The spatially explicit model revealed that more than 46 % of the current jaguar distribution may be endangered ($p > 0.5$). However, observing the frequency histogram of extinction probabilities in Fig. 2, there is a sharp decrease in extinction probability of 0.7. Thus, to avoid overestimation of endangered areas we may consider areas with a high endangerment level to be those with extinction probability values over 0.7, and those with values over 0.9 to be at a very high endangerment level. Thus, 14.5 % of the predicted jaguar distribution area would be highly endangered, and 3.5 % extremely endangered, suggesting that in these areas local extinction may have already occurred or will soon be complete. This area covers 1.5 million km$^2$, which implies that jaguar distribution may be currently occupying 40.1 % of its historic range, or will soon reach that level. Our results show higher range contraction than estimations from last decades (Zeller, 2006; Sanderson et a., 2002), but are aligned with the later estimations (Quigley et al., 2017), suggesting that jaguar extinction is still occuring at a broad scale. On the other hand, we find that 53.1 % of the current distribution (4.7 million Km$^2$) is under low endangerment levels ($p < 0.5$). Most of these areas correspond to the main jaguar sources located in the Amazon basin and surroundings where human business is still not magnified, seeming to be vital to maintain jaguar core populations and therefore to maintain their integral role in trophic cascades and prey regulation of neotropical ecosystems (Cavalcanti and Gese, 2009; Terbourg et al., 2001).

We noted that four Jaguar Conservation Units have currently been extirpated according to the last distribution range update. These populations corresponded to the northern Sierra Madre Occidental in Mexico, Honduras South, Mache-Chindul and Manglares Cayapas in Ecuador. Moreover, our model identified 15 highly endangered ($p > 0.7$) populations distributed throughout the current range, results supported by local assessments. Populations in Central America stand out due to their lack of connectivity and high extinction risk (Zeller and Rabinowitz, 2010), showing high endangerment in our model with the exception of Yucatan ($p = 0.55$), where anthropic pressure is more controlled (Cuauhtemoc et al., 2016), and Belize ($p = 0.57$), where conservation has been historically promoted through ecotourism (Kroshus, 2010). Additional Central American populations such as Guatemala and Honduras show high-risk values, which reveal their critical situation (Sanderson et al., 2002) due to conflicts with ranchers and inefficiency of protected areas (Mora et al., 2016). Most endangered populations in northern South America are located in Colombia and Venezuela, and have been identified as highly threatened key populations for maintaining connectivity between Central and South American populations (Zeller et al., 2013). Finally, our model shows endangered populations in Southern Brazil and Argentina corresponding to populations that have shown alarming conservation problems due to their reduced size (Srbek de Araújo et al., 2016; Paviolo et al., 2008). Overall, extremely endangered populations ($p > 0.9$) occupy 2.1 % (34,280 Km$^2$) of the aggregated Jaguar Conservation Units area, while 44.7 % (718,101 Km$^2$) of the area is under moderate or low ($p < 0.5$) extinction risk. These results show that high endangerment is less frequent in JCUs compared to the surrounding matrix, hinting at a hopeful scenario for the species in these areas.

Our model has some limitations, mainly related to the spatial data used, which were obtained in 2010 and 2000 for cattle and human densities, and agriculture, respectively. Some of these variables have increased over the last one or two decades (e.g., Hansen et al., 2013); therefore, we will expect that our model may overestimate potentially occupied areas, unveiling our results as conservative. Despite these limitations, we believe that this approach is useful for assessing the conservation status of jaguars as well as understanding carnivores range contraction at a broad scale.

Our conclusions demonstrate that livestock ranching, most likely via persecution and retaliatory hunting, has a pervasive effect on jaguars, becoming the main cause of the species extinction. Persecution and retaliatory hunting have been detected in most regions where jaguars coexist with livestock (review in Medellin et al., 2016). However, there are numerous examples to evince successful coexistence between livestock and big cats (Hoogesteijn et al., 2015; Tortato et al., 2017, Toratato and Izzo, 2017; Nassar et al., 2013), generally linked to ecotourism. Coexistence strategies such as the mentioned above need to be promoted for Neotropical big cat conservation. Moreover, our results show that most current jaguar range is unprotected and is highly affected by human industries, thus their conservation requires measures that ensure wide connected areas (Rabinowitz and Zeller, 2010; Sanderson et al., 2002) besides the protected-area strategy that fail to effectively protect top carnivores, including jaguars (Woodroffe and Ginsberg, 1998). Management of humanized landscapes should be a more realistic scenario for carnivores' long-term survival (Athreya et al., 2013; Chapron et al., 2014; but see Gilroy et al., 2015). In this context, we believe that it is essential to use livestock ranching as a tool for jaguar conservation and highlight the need to rethink law enforcement and livestock policies and practice. We suggest the development of action plans based on local evidence in those countries where endangered populations have been detected as well as to involve and encourage land owners and private companies to integrate conservation practices.

**Authors´ contributions:**

PV conceived the idea; PV and FP designed the methodology; PV analyzed the data and led the writing of the manuscript. FP revised the analysis and interpretation and revised the intellectual content. All authors contributed critically to the drafts and gave final approval for publication.

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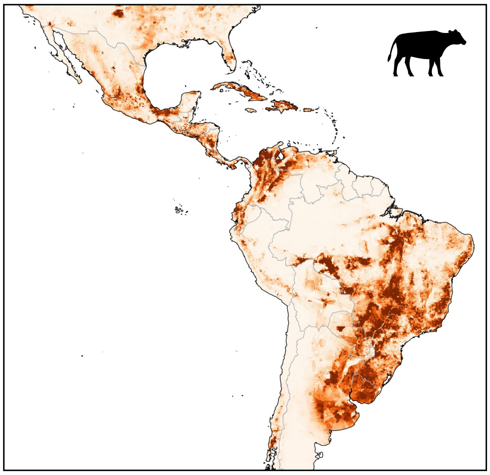
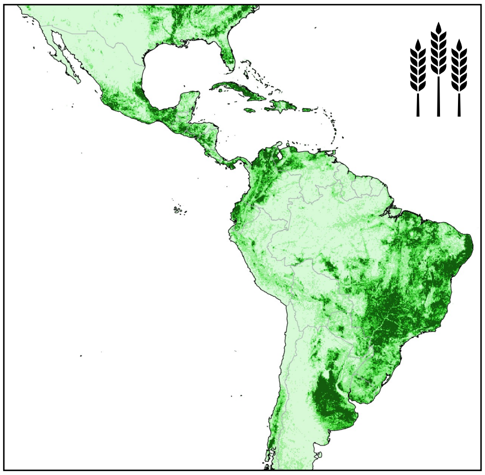
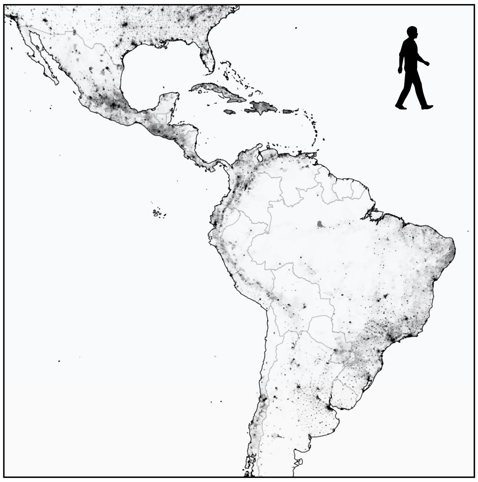
**Suplementary material 1**

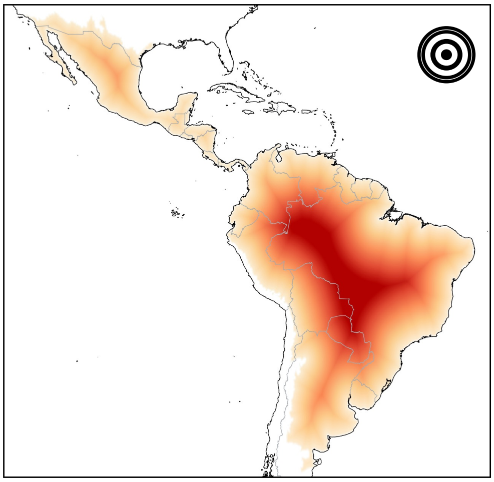
**Figure1.** Jaguar current and historic distribution range (1) used to generate the binomial response variable.

Cattle density (2), agriculture cover (3), human density (4) and distance to the border (5) are the independent variables used for modelling.









## Suplementary material 1

| | Distance to the border | Agriculture | Human density | Cattle density |
|---|---|---|---|---|
| **Distance to the border** | 1.000 | | | |
| **Agriculture** | -0.14 | 1.000 | | |
| **Human density** | -0.11 | 0.09 | 1.000 | |
| **Cattle density** | 0.03 | 0.57 | 0.09 | 1.000 |

**Table1.** Correlation matrix of the variables in jaguar historic range.

## Supplementary material 2

**Table 1.** Probability of extinction for Jaguar Conservation Units (JCUs) based on the mean values of the model contained in each JCU. Extinct area corresponds to the percentage of the area that is out of the current range. Name, country, size and estimated population size based on expert opinions (Zeller, 2007) are also shown.

| Id | **JCU Name** | **Country** | **Size (km²)** | **Population size** | **Probability of extinction** | **Extinct area (%)** |
|---|---|---|---|---|---|---|
| 1 | Sierra Madre Occidental | Mexico | 11724 | <50 | - | 100 |
| 2 | Sierra Madre Occidental | Mexico | 13606 | 50-100 | 0.61 | 0 |
| 3 | Sierra Madre Oriental | Mexico | 21570 | 50-100 | 0.59 | 0 |
| 4 | Sierra Madre Oriental | Mexico | 1384 | 50-100 | 0.63 | 0 |
| 5 | Nayarit | Mexico | 29329 | >500 | 0.77 | 0 |
| 6 | Veracruz | Mexico | 9547 | 100-200 | 0.67 | 46 |
| 7 | Yucatán | Mexico | 63349 | >500 | 0.55 | 1 |
| 8 | Belize | Belize | 8561 | >500 | 0.57 | 0 |
| 9 | Guatemala | Guatemala | 5334 | 50-100 | 0.75 | 4 |
| 10 | Honduras North | Honduras | 2824 | - | 0.80 | 0 |
| 11 | Honduras South | Honduras | 2206 | 50-100 | - | 100 |
| 12 | Reservas Tawatika, Rio Plátano | Honduras - Nicaragua | 36435 | 200-500 | 0.55 | 6 |
| 13 | Costa Rica NW | Costa Rica | 5302 | 50-100 | 0.78 | 5 |
| 14 | Reserva Indo Maiz | Nicaragua | 7018 | 100-200 | 0.60 | 0 |
| 15 | P.N La Amistad | Costa Rica - Panama | 14041 | 100-200 | 0.64 | 6 |
| 16 | P.N Corcovado | Costa Rica | 1801 | 100-200 | 0.60 | 0 |
| 17 | Panamá S. | Panama - Colombia | 69729 | 100-200 | 0.64 | 1 |
| 18 | Paramillo | Colombia | 8203 | 200-500 | 0.85 | 3 |
| 19 | Cienaga Mogua | Colombia | 6887 | 50-100 | 0.81 | 0 |
| 20 | Rio Magdalena | Colombia | 2619 | <50 | 0.90 | 0 |

| Id | JCU Name | Country | Size ($km^2$) | Population size | Probability of extinction | Extinct area (%) |
|---|---|---|---|---|---|---|
| 21 | Rio Apure | Venezuela | 1422 | <50 | 0.87 | 0 |
| 22 | Arismendi | Venezuela | 973 | 50-100 | 0.90 | 12 |
| 23 | El Baul | Venezuela | 7095 | 50-100 | 0.82 | 2 |
| 24 | Laguna de Tacarigua | Venezuela | 1616 | <50 | 0.64 | 0 |
| 25 | Tinigua | Colombia | 20948 | 50-100 | 0.73 | 0 |
| 26 | Tuparro | Colombia | 22614 | 50-100 | 0.37 | 0 |
| 27 | Jaua-Sarisariñama | Venezuela | 18654 | 200-500 | 0.40 | 0 |
| 28 | Canaima | Venezuela - Brazil - Guyana | 81458 | - | 0.38 | 0 |
| 29 | Guyana | Guyana | 3716 | - | 0.39 | 0 |
| 30 | Surinam | Surinam | 16183 | - | 0.39 | 0 |
| 31 | Guayana Francesa | French Guyana - Brazil | 71437 | >500 | 0.45 | 0 |
| 32 | Parima Tapirapeco | Venezuela | 56414 | 200-500 | 0.22 | 0 |
| 33 | Ilha de Maraca | Brazil | 2807 | <50 | 0.27 | 0 |
| 34 | Mache-Chindul | Ecuador | 1350 | 50-100 | - | 100 |
| 35 | Cotachi Cayapas | Ecuador | 2450 | 50-100 | 0.59 | 5 |
| 36 | Manglares Cayapas | Ecuador | 210 | <50 | - | 100 |
| 37 | Awa Territory | Ecuador | 896 | <50 | 0.64 | 0 |
| 38 | Sumaco Galeras | Ecuador | 5748 | 200-500 | 0.59 | 17 |
| 39 | Yasuni | Ecuador | 47372 | >500 | 0.49 | 0 |
| 40 | Yaigoje Apaporis | Colombia | 4126 | <50 | 0.20 | 0 |
| 41 | Pico da Nebuna | Brazil | 11705 | 50-100 | 0.13 | 0 |
| 42 | Condor Kutuku | Ecuador | 7505 | 200-500 | 0.60 | 0 |
| 43 | Jaú | Brazil | 37991 | 50-100 | 0.15 | 0 |
| 44 | Rio Marañón | Peru | 22830 | 200-500 | 0.35 | 0 |

| Id | **JCU Name** | **Country** | **Size (km²)** | **Population size** | **Probability of extinction** | **Extinct area (%)** |
|---|---|---|---|---|---|---|
| 45 | Area de Conservación Comunal | Peru | 9215 | 50-100 | 0.24 | 0 |
| 46 | Amacayacu | Peru | 7504 | 50-100 | 0.19 | 0 |
| 47 | Amazonas w | Brazil | 67306 | 50-100 | 0.27 | 0 |
| 48 | P.N Amazonia | Brazil | 38246 | >500 | 0.26 | 0 |
| 49 | Paragominas | Brazil | 20122 | 200-500 | 0.65 | 0 |
| 50 | Parauapebas | Brazil | 32045 | >500 | 0.65 | 6 |
| 51 | Maranhao | Brazil | 6225 | 100-200 | 0.77 | 0 |
| 52 | Manu | Peru | 43219 | 200-500 | 0.48 | 0 |
| 53 | Tambopata-Madidi | Peru - Bolivia | 58658 | >500 | 0.47 | 0 |
| 54 | Rondonia | Brazil | 53918 | - | 0.59 | 21 |
| 55 | P.N Campos Amazonicos | Brazil | 99175 | 100-200 | 0.58 | 1 |
| 56 | P.N Rio Novo | Brazil | 36627 | 50-100 | 0.52 | 3 |
| 57 | P.N Xingu | Brazil | 66555 | 200-500 | 0.60 | 46 |
| 58 | Araguacema | Brazil | 13323 | - | 0.71 | 30 |
| 59 | Araguaia | Brazil | 29728 | 50-100 | 0.60 | 0 |
| 60 | Paranaiba | Brazil | 45214 | 200-500 | 0.61 | 4 |
| 61 | Serra das Confusoes | Brazil | 7163 | <50 | 0.52 | 2 |
| 62 | Isiboro Securé | Bolivia | 20198 | - | 0.52 | 0 |
| 63 | Noel Kempff | Bolivia | 68229 | >500 | 0.51 | 0 |
| 64 | Chiapada dos Viadeiros | Brazil | 10243 | <50 | 0.61 | 0 |
| 65 | Grande Sertao | Brazil | 4618 | <50 | 0.61 | 0 |
| 66 | Cavernas do Peruaçu | Brazil | 2427 | <50 | 0.69 | 0 |
| 67 | Carrasco-Amboró | Bolivia | 8653 | 100-200 | 0.53 | 0 |
| 68 | Kaa Iya | Bolivia - Paraguay | 88852 | >500 | 0.49 | 0 |
| Id | **JCU Name** | **Country** | **Size (km²)** | **Population size** | **Probability of extinction** | **Extinct area (%)** |

| | | | | | | |
|---|---|---|---|---|---|---|
| 69 | Pantanal | Bolivia - Brazil | 86755 | >500 | 0.65 | 28 |
| 70 | Rio Doce | Brazil | 3505 | <50 | 0.70 | 87 |
| 71 | Tarija | Bolivia - Argentina | 12541 | 50-100 | 0.56 | 28 |
| 72 | Rio Paraná | Brazil | 17687 | 50-100 | 0.84 | 67 |
| 73 | Misiones | Argentina - Brazil | 36648 | 100-200 | 0.64 | 51 |
| 74 | P.N Copo | Brazil | 7139 | <50 | 0.56 | 14 |
| 75 | Mata Atlántica | Brazil | 30772 | 50-100 | 0.61 | 36 |

## Supplementary material 2.

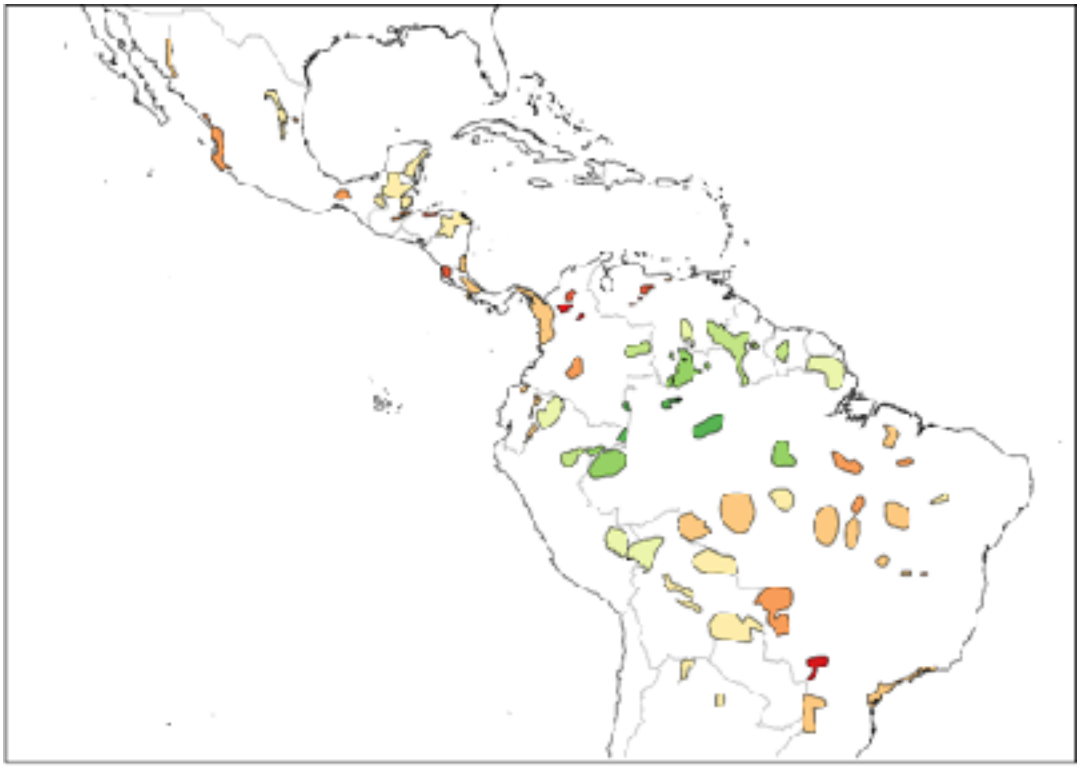


**Figure 1.** Map showing jaguar population endangerment based on the mean value of the model contained in each JCU. Color range represents level of endangerment; greens correspond to low endangerment while red corresponds to high endangered populations.

# Chapter 4

## Uneven tolerance to human disturbance interferes to dominance interactions of top predators

## Abstract

Anthropogenic activities may alter felids assemblage structure, facilitating the persistence of tolerant species (commonly meso-predators), excluding high-ecologically-demanding ones (top-predators) and, consequently, changing coexistences rules. We adopted a continental scale approach, using structural equation modelling, to investigate how habitat loss, livestock density, human pressure, and the presence of protected areas may modify intraguild relations of three Neotropical felids: jaguar, puma, and ocelot. All the investigated anthropogenic disturbance reduces jaguar occurrence probability; smaller livestock (sheep + goat) and jaguar presence have positive influence on pumas; meanwhile, puma presence and habitat loss negatively interfere on ocelots. The lack of negative effects of anthropogenic activities on pumas, in addition to the positive effect of sheep + goat, supports the established idea of pumas being more tolerant to habitat disturbance than jaguar and ocelot. Therefore, human disturbance seems to invert the hierarchical competition dominance between large felids and unbalancing community structure, disfavouring jaguar, and increasing pumas' position in the assemblage hierarchy, which pushes ocelots out, despite being less affected by anthropogenic disturbance. Moreover, the extension of forest cover is interfering in the felids' occurrence more than the level of protection, so conservation efforts should focus in the landscape – not only the protected areas, but in the surround areas where it is embedded – where issues are more complex and the potential for conflict is also higher. We urge an inexorable conciliation among environmental and livestock policies in order to achieve coexistence with wildlife.

**Key words:** coexistente, intragremial interactions, *Panthera onca, Puma concolor, Leopardus pardalis*, resource partitioning, human-wildlife conflict, structural equation modelling.

## INTRODUCTION

Anthropogenic activities have led to decline of high-ecologically-demanding species such as top predator carnivores, in name of tolerant species (Olden et al., 2018). When top predators are removed, mesopredator release may unbalance the underneath trophic levels (Soulé et al, 1988, Crooks & Soulé, 1999). This top-down regulation usually depends on a complex network of intraguild relationships, surpassing the overall idea of one single regulator and revealing how carnivore co-existence works on ecosystem maintenance (Monterroso, 2020). Despite the evidences of carnivores declining (Ripple et al., 2014), little is known about how anthropogenic activities impact intraguild relationships, which could either force or reduce co-existence by impeding, facilitating or unbalancing niche partitioning among species (Seveque et al, 2020).

Habitat loss and human-wildlife conflict are the main anthropogenic activities causing carnivores population declines and distribution constraining (Di Minin et al., 2016), besides a primary conservation concern in the Neotropics where agriculture and livestock farms are still expanding. There are over 400 million cattle heads in the Neotropics (FAO, 2021), occupying more than 60% of its surface (Gilbert et al., 2018). This widespread industry favours a global conflict scenario, firstly by reducing the species native habitats and after by making big cats to share territory with livestock (eg. Zimmermann et al., 2005, Amit et al., 2013, Michalski et al., 2006, Llanos et al., 2020, Villalva and Palomares, 2019). Protection of territory is the main instrument to minimise these threats (Coetzee et al., 2014; Gray et al., 2016) and has increased in recent decades through the promotion of protected areas (Watson et al., 2014). However, the effectiveness of this measure is controversial (Rodrigues et al., 2004; Craige et al., 2010; Laurence et al., 2012), especially for top carnivores whose populations require vast territories (Woodroffe and Ginsberg, 2008).

In summary, jaguars are dominant over pumas (Haines, 2006) and ocelots are subordinate to both species due to its smaller size (Elbroch and Kusler, 2018, Wallach et al., 2015). Jaguars and pumas exhibit different tolerance to habitat disturbance, in which jaguars seems to be prevalent in pristine habitats (Di Bitetti et al., 2010), so more sensitive to habitat degradation (i.e. Torres et al., 2017, but see Foster et al., 2010), while pumas can inhabit more degraded landscapes and be excluded from pristine habitat by jaguars (Sollman et al., 2002). In fact, in numerous regions where jaguars have been locally extinct, pumas still persist (Nielsen et al., 2015, Quigley et al., 2017). Ocelots also tolerates some level of habitat disturbance, being observed in degraded landscapes where they coexist with pumas (Lima Massara et al., 2018) and even where pumas are absent (Boron et al., 2020). Moreover, ocelots are not deeply threatened by human-livestock conflict that largely affect jaguars and pumas (Inskip & Zimmermann, 2009).

Despite this knowledge, we have a poor understanding of the mechanisms behind global co-existence patterns of these species (Linnell & Strand, 2000, Elmhagen & Rushton, 2007, Periquet et al., 2015). The lack of global comprehensive research is certainly due to the demanding effort of methods used for investigating coexistence (usually camera trapping or radio tracking) that restrains their use at broader scales. Therefore, a compiled dataset from broad research programs such as the Neocarnivore database (Nagys-reis et al., 2020) enables the investigation of distribution-scale patterns and other global data of socioeconomics and environmental variables allow to put human disturbance into account.

Our goal was to examine whether anthropogenic disturbance affects the co-existence patterns of Neotropical top predators, investigating how potential human persecution, habitat cover and quality, and livestock affect the intragremial relationships of jaguar, puma, and ocelot at a continental scale. Based on the co-existence theory, which assumes a competitive dominance hierarchy correlated with body size (Palomares & Caro, 1999, Donadio & Burskirk, 2006, Linnell & Strand, 2000), we predicted that pumas should avoid spatial overlap with jaguars while ocelot should avoid spatial overlap with jaguars and pumas. However, this dominance hierarchy could change accordingly to anthropogenic influence in human dominated areas, increasing occurrences of puma and ocelot due to their higher environmental tolerance. Therefore, jaguars' occurrence should be conditioned to larger extension of habitat amount than pumas and ocelots. Livestock ranching, in its turn, should reduce jaguar and puma's presence by promoting population depletion due to livestock predation and, consequently, retaliatory persecution. Protected areas could stabilise human-mediated pressure by ensuring the offer of a native habitat and a refugee to retaliatory hunting.

## METHODS

### 2.1. Data gathering

Neocarnivores database is a compilation of georeferenced data on carnivore distribution, obtained from studies conducted from 1818 to 2018, representing the largest data set on neotropical wild carnivores to date (Nagy-reis et al., 2020). From this database, we selected occurrences of jaguars, pumas, and ocelots since 2000, in order to discard the unwanted effect from old entries (such as the presence of jaguars in the Atlantic forest in the past century where the species is currently almost extirpated). To avoid data from casual encounters, we only kept data obtained by systematic sampling where methodology was equally capable of detecting the three species, i.e. camera trapping and genetic fecal sampling. We completed this dataset with 586 entries corresponding to new genetic samples, mostly from pumas and ocelots, collected by the authors. Using the species occurrence locations, a presence-absence layer was generated for each species at the resolution scale of 0.0833° decimal degree, around 100 km$^2$ in the equator, which is the average adult jaguar male home range (Gonzalez-Borrajo et al., 2017). This resolution scale was kept as spatial resolution for all variables.

Forest cover was included as a proxy for environmental quality outstanding as a principal component for the habitat of jaguar (Hoogesteijn and Mondolfi, 1992, De Angelo et al., 2013), puma (Regolin et al., 2017), and ocelot (Regolin et al., 2017). For this purpose, we used the Global Land Cover 2015 (Buchhorn et al., 2020), a 100 m-resolution layer classifying land uses and cover at 23 classes, from which forest cover areas were selected to obtain the coverage percentage in a resampling process at 100 km$^2$. We used the Global Human Influence Index as a proxy for human presence that may affect felids through direct persecution (i.e hunting) or through avoidance behaviours to humans. This dataset is created from nine global variables related to human population pressure, infrastructure, and access (WCS, 2005). Protected areas were obtained from the World Database on Protected Areas (UNEP - WCMC, 2015) corresponding to the IUCN categories. Any pixel containing a portion of a protected area took the value of its category while unprotected territories took value zero.

Livestock density accounts for the combined effect of habitat loss and retaliatory hunting related to livestock practices. We defined livestock pressure using the Gridded Livestock of the World (GLW) model (Gilbert et al., 2018), which compiles and harmonises the distribution of livestock cadaster data at a subnational level. In the ultimate version of this model (GLW3 areal-weighted), the distribution of livestock is free from the influence of any other variables, contrary to previous models based on RF algorithm that used a multiple layer approach (Robinson, 2014). This enhancement provides greater utility for ecological modelling by eliminating the effect of confounding variables, which could interfere in the interpretation of our study. The layers used in our study were goat and sheep densities, which were combined in a single layer (hereinafter goat + sheep), and bovine cattle density (hereinafter cattle). Goat and sheep densities were combined to avoid overloading the model with too many variables, keeping the interpretation simple, based on the difference in livestock size and husbandry practices.

### 2.2. Data Analysis

Structural equation modelling (SEM) is a collection of procedures whereby complex hypotheses, particularly those involving networks of path relations, are evaluated against multivariate data (Bollen 1989, Grace 2006). This multi-equational method of data analysis is capable of representing a wide array of complex hypotheses about how system components interrelate based on the analysis of covariance relations. SEM enables a broad set of scientific questions providing countless possibilities for quantitative research. In this sense, univariate models are suitable for studying individual processes or responses while SEMs are appropriate for studying multiple processes by controlling the behaviour of the system, allowing to quantify the relative importance of the interaction between species (or processes), as well as the cascade effects (Grace, 2010). However, the use of SEM is only suitable for testing causal models grounded in solid understanding of the system (Dunham & Niewiarowski, 1996, Hatcher, 1994), making essential the robust construction of *a priori* model at light of specific questions (Hoyle et al., 2012). Our SEM was built based on solid knowledge about felid species, their ecosystems, and the main human disturbance affecting them.

A basic causal model has endogenous and exogenous variables. A variable is endogenous if its value is determined or influenced by one or more independent variables (excluding itself) while an exogenous variable is a factor whose value is independent from other variables in the system. Intragremial relations among species (endogenous variables) constitute the core of the proposed model, once the effect of one species is investigated on others, which can be under influence of environmental variables (i.e. forest cover, human index, livestock, and protected areas, i.e. exogenous variables).

After testing correlation between exogenous variables, eliminating the risk of unpredicted causal relations among them (Supplementary Material S1), we adopted the follow equations as predictor models composing SEM: (1) jaguar occurrence, considering the effect of protected areas, human index, cattle, goat+sheep, and forest cover; (2) puma occurrence, considering the effect of jaguar occurrence, protected areas, human index, cattle, goat+sheep, and forest cover; (3) ocelot occurrence, considering jaguar and puma occurrences, protected areas, human index, and forest cover. Livestock rarely compose ocelot's prey base, so cattle and goat+sheep variables were excluded from ocelot equation.

We standardised the variable set to compare the effects among predictors. The magnitude of standardised coefficients indicates the degree to which the predictor directly affects the criterion variable if the rest of variables remain constant. This means that the variation of one standard deviation in the presence of jaguars would suppose the resulting coefficient value standard deviations in the presence of pumas if the rest of the model remain unaltered. Mediation (indirect effect) was determined by the coefficient product of the indirect structural path, which added to the direct effect corresponded to the total effect.

We performed statistical analysis using lavaan package (Rosseel, 2012), and transform data with raster (Hijmans & Van Etten, 2012), sp (Bivand et al., 2013) and spatial (Venables & Ripple, 2002) packages in R version 4.0.3 (R Development Core Team, 2021).

## RESULTS

We obtained 1459 independent presence-absence raster units distributed over the Neotropical region (Figure 1), covering most of the countries. No data were available for Suriname, Guyana, Nicaragua, Honduras, and El Salvador indicating lack of recent research in these countries. Ocelots (n = 1075) and pumas (n = 1005) occurrences covered the larger extent of study area, 73% and 68% respectively; jaguars (n = 506) were rarer, appearing in 35 % of the studied area. We found the three species

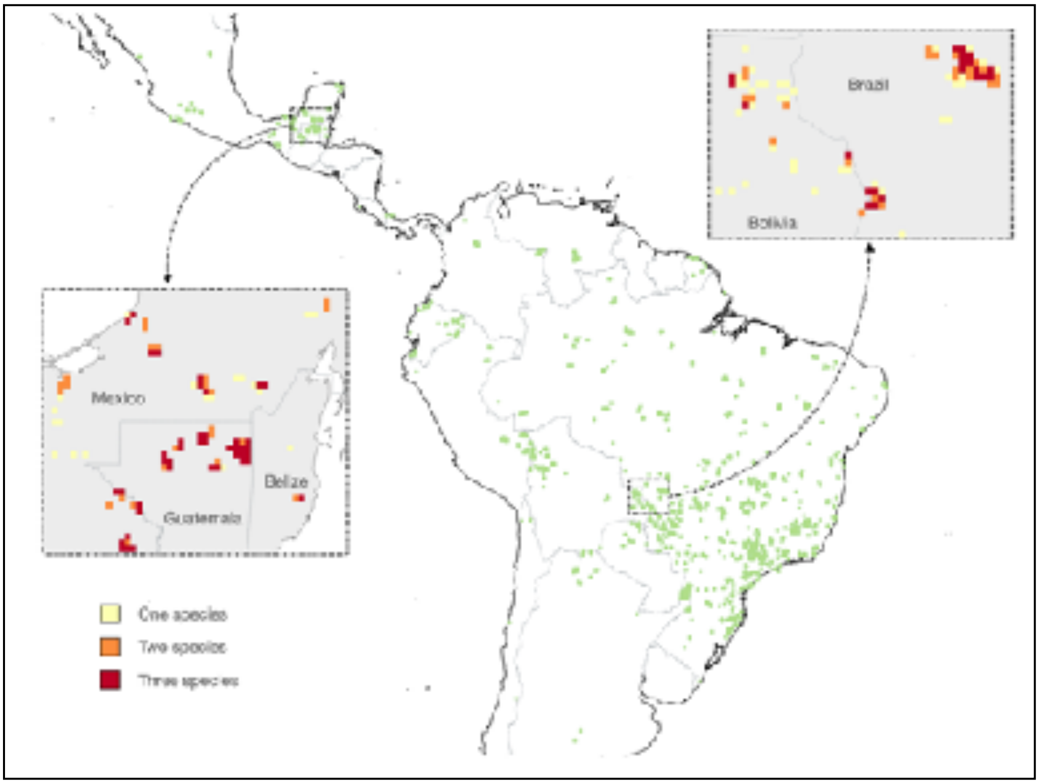


**Figure 1.** Study area map. Green dots represent a buffer zone of 10 km on rasterised presence data of jaguars, pumas and ocelots extracted from Neocarnivores dataset (Nagys Reis et al., 2020). Zoom spanning Yucatan and Pantanal regions as symbolical examples showing pixels of 100 Km$^2$. Colours indicate the number of species detected in each pixel.

co-existing in 21% of the studied area, two species coexisted in 35%, and only one species in 44 %.

SEM analysis showed a good fit (CFI = 1, RMSEA = 0.00, SRMR = 0.004), so the predictions of endogenous variables were robust. Jaguar presence was negatively related to human index, cattle, and goat + sheep and positively related to forest cover; pumas were positively influenced by jaguar and goat + sheep density; and ocelot, in its turn, were positively affected by forest cover, but showed negative association with puma presence (Table 1, Fig. 2).

| **Species** | **Variable** | **Estimate ± SE** | ***z value*** | **p value** |
|---|---|---|---|---|
| Jaguar | Cattle | -0.061 ± 0.028 | -2.163 | 0.031 |
| | Goat + Sheep | -0.060 ± 0.025 | -2.415 | 0.016 |
| | Forest | 0.233 ± 0.029 | 7.985 | < 0.001 |
| | Human index | -0.220 ± 0.027 | -8.117 | < 0.001 |
| | Protected areas | -0.024 ± 0.025 | -0.970 | 0.332 |
| Puma | Jaguar | 0.129 ± 0.029 | 4.476 | < 0.001 |
| | Cattle | -0.001 ± 0.031 | -0.013 | 0.990 |
| | Goat + Sheep | 0.080 ± 0.027 | 2.959 | 0.003 |
| | Forest | -0.025 ± 0.033 | -0.763 | 0.445 |
| | Human index | 0.037 ± 0.030 | 1.224 | 0.221 |
| | Protected areas | -0.004 ± 0.027 | -0.160 | 0.873 |
| Ocelot | Jaguar | 0.050 ± 0.028 | 1.805 | 0.071 |
| | Puma | -0.263 ± 0.025 | -10.387 | < 0.001 |
| | Forest | 0.118 ± 0.029 | 4.123 | < 0.001 |
| | Human index | -0.004 ± 0.029 | -0.130 | 0.897 |
| | Protected areas | -0.001 ± 0.026 | -0.051 | 0.959 |

**Table 1.** Summary of SEM regression model for endogenous variables explaining the relations among variables. Estimate ± Standard error, z value and *pvalue* are shown.

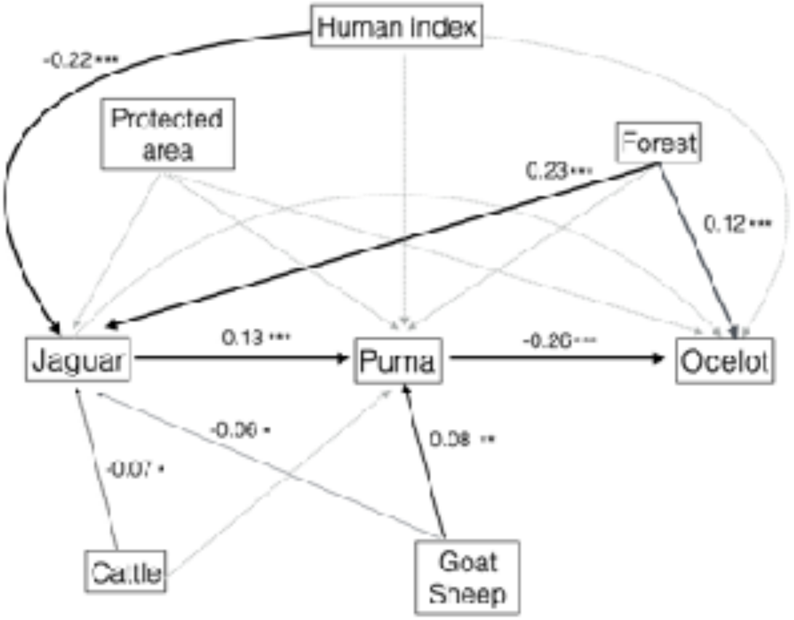


**Figure 2.** Structural Equation Model (SEM) showing the relations among variables. Solid lines denote significant relations, dotted lines denote non significant relations. Width of each line is proportional to the relative strength of relationship and the number indicates the path coeficiente values. Significance of relations are indicated by asterisks (*pvalue* < 0.001 ***, *pvalue* < 0.01 ** and *pvalue* < 0.05 *).

Contrary to our expectations, we observed a positive effect of jaguar on puma and no effect on ocelot, instead the negative effect predicted to both species. The prediction of the negative effect of puma on ocelot was corroborated and it is twice bigger than the effect of jaguar on puma. Total effect (direct + indirect effect) did not show any substantial change from direct effects in the relationships among species (Supplementary Material S2).

The effect of exogenous variables also shows the complexity of felids distribution and co-occurrence pattern: while both livestock variables adversely affected jaguar presence, cattle had no effect on puma and goat + sheep favoured them; human index negatively affect jaguar, having no effect on puma and ocelot; forest cover do not affect puma, but affect twice more jaguar than ocelot; and protected areas show no association to any feline presence.

## DISCUSSION

### *Anthropogenic activity's effects on interspecific relationships*

Anthropogenic activities negatively affected jaguar, unlike pumas and ocelots, suggesting a behaviour alteration of individuals in areas under human presence or livestock production. There are strong evidence of human activities influencing species behaviours, causing nocturnity (Gaynor et al., 2018), movement restrictions (Tucker et al., 2018), and anti-predatory behaviours (Tambiling et al., 2015; Laundré et al., 2001; Berger, 1999). On jaguar, anti-predatory behaviours may operate through direct avoidance human activities (Llaneza et al., 2012, Oriol-Cotterill et al., 2015); if not, by changes on prey-base behaviour (Taber et al., 2006, Scognamillo et al., 2006, Gutierrez et al., 2017, Azevedo et al., 2018).

The unexpected positive effect of jaguars on pumas may relay with local segregation – in any spatial, temporal, or trophic niche dimensions – promoting species coexistence. For jaguars and pumas, spatial segregation seems common at fine scale (Palomares et al., 2016), sometimes directly promoted by habitat selection (Foster et al., 2010, Sollman et al., 2012, Foster et al., 2013, Porfirio et al., 2017) and sometimes by synchromism with different prey base (Taber et al., 2006, Scognamillo et al., 2006, Gutierrez et al., 2017, Azevedo et al., 2018). Temporal segregation, in its turn, may rule when habitat availability is restricted by anthropogenic activities (Di Bitetti al., 2010, De la Torre et al., 2017), supporting our overall idea of human disturbances changing the structural rules of felids coexistence.

The lack of evidences of anthropogenic activities affecting pumas, in addition to the positive effect of sheep + goat, supports the established idea of pumas being more tolerant to habitat disturbance than jaguars (Sollmann et al., 2012, De Angelo et al., 2011, but see Foster et al., 2010). Under these circumstances, we can assume that human disturbance is inverting the hierarchical competition dominance between large felids, favouring puma and increasing its position in the assemblage hierarchy. The widespread facilitation of pumas would cause ocelots' distribution contraction, despite being less affected by anthropogenic disturbance. Therefore, pumas seem the key species mediating the unbalancing on community structure through their higher environmental tolerance and competitive dominance over other less tolerant felids.

### *Protected areas and habitat loss*

Jaguars and pumas are among the large mammals with greatest distribution contraction (Morrison et al., 2007) and, at least jaguars, with few viable populations in the long term (Zanin et al., 2015). Despite being a widespread conservation strategy worldwide (CBD, 2011), protected areas are not sufficient to increase felids occurrence probability, so breaking the distribution contraction. This revels the inefficiency of protected areas, despite being by insufficient extension (Zanin et al., 2021) or incapacity of guaranteeing a hunting-free refugee for felids population. For jaguars and ocelots, the extension of forest cover more than the level of protection is interfering in their presence. Therefore, to assure felids conservation, we need integrative strategies that consider not only protected areas, but any fragment and the anthropogenic matrix in the landscape where protected areas are embedded. In summary, our conclusions remark the need to focus conservation efforts at a landscape level, where issues are more complex and the potential for conflict is also higher.

### *Livestock*

The asymmetrical effect of livestock on big cats reveals that the link of livestock conflict and big cats is more complex than assumed (Inskip & Zimmermann, 2009). Pumas' higher tolerance to habitat disturbance allow greater withstand in areas under livestock pressure; moreover, goat and sheep can provide an increment of prey availability. This "minor" livestock farming, which positively influence pumas, is mostly located in dry regions (such as the Brazilian Caatinga, the Guajira - Barranquilla xerophytic scrub region in Colombia, or the Pre-Andean slopes) where prey availability is scarce due to the scant primary production. These areas also correspond to suboptimal habitats for jaguars where, with the exception of small patches in the Caatinga (Morato et al., 2014), the species have been locally extirpated (Quigley et al., 2017).

Persecution for livestock predation is potentially asymmetric as well, revealed by previous findings about the ranchers' inability to discriminate between felid species (Cavalcanti et al., 2010; Villalva & Palomares, 2019), making any livestock predation overturning on jaguars by being the most familiar species. Therefore, puma presence may exert an extra pressure on jaguars in locations of uninformed ranchers (e.g. Villalva & Palomares, 2019), which may be extending in the Neotropics, generating a systematic decrease in jaguar populations.

Although big cats are law-protected in many countries, few apply these laws in an efficient way to reduce the real impact on ecosystems, demonstrating the scarce capacity or interest to manage livestock effects on wildlife. This widespread problem finds its turning point in Brazil, where livestock policies have quadrupled their values since 1960 (FAO, 2020) whilst jaguars were extirpated from the largest area of their historical distribution (Quigley, 2017). These policies with obvious macroeconomic objectives in their early phases, but in search of reconciliation with poverty reduction later on (Guanziroli, 2014), have made Brazil the country with the world largest cattle herd (FAOstat, 2021) whereas still harbours half of the world's jaguar population (Jedrezewski et al., 2018). Therefore, Brazilian livestock policies may be the main shield not only for jaguars as iconic species, but from the rest of the Neotropical predator community.

Extensive ranching has been suggested as an important strategy for neotropical big cats' conservation because it maintain large low modified territories (Hoogesteijn and Hoogesteijn, 2010) and reduces hunting due to economic ranchers´ income provided by tourism (Tortato et al., 2017). Despite the potential benefits of this human activity, livestock industry has devastating effects on carnivore community at a continental scale. Our conclusions have important conservation implications especially in the current scenario where agribusiness predominate Neotropical landscapes and the uninformed farming, where the role of carnivores is not considered, becomes a worrying phenomenon in the increasing human-wildlife conflict context (Marchini & Crawshaw, 2015).

## CONCLUSIONS

With a traditional approach of co-existence research, applied with a novel perspective aided by continental scale data, we provide new insights on the importance of anthropogenic activities on carnivore communities and their potential cascading effects. The evidences of hierarchical relations of big carnivores being modulating, and potentially inverted, by anthropogenic disturbance question the hierarchy theory among jaguars and pumas; not by denying the evident supremacy of jaguars over pumas in natural conditions, but by including a new component that unfold particularities to be joined to the theory. This prospect is particularly important in the world facing higher rate of habitat conversion due to the increasing human demand by food.

We restate the asymmetric effect of livestock on big cats that could be acting as an ecological sink for jaguars while facilitating the presence of pumas, which highlights the consequences of livestock industry on neotropical carnivore community and, through top-down cascade effects, in the entire ecosystem. Therefore, the inexorable reconciliation of environmental and agricultural policies, at the global level, is mandatory. Enlightening the mechanisms underlying human impacts on carnivores by incorporating cultural values, local environmental conditions, and a policy design will lead to interesting research in the near future and should allow evidence-based conservation policies (Van Eaden et al., 2018).

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## Suplemmentary material

| | Jaguar | Puma | Ocelot | Cattle | Goat + Sheep | Protected Areas | Forest | Human Index |
|---|---|---|---|---|---|---|---|---|
| Jaguar | 1.00 | | | | | | | |
| Puma | 0.09 | 1.00 | | | | | | |
| Ocelot | 0.07 | -0.26 | 1.00 | | | | | |
| Cattle | -0.24 | 0.00 | -0.09 | 1.00 | | | | |
| Goat + Sheep | -0.16 | 0.07 | -0.07 | 0.05 | 1.00 | | | |
| Protected Areas | 0.09 | -0.01 | 0.03 | -0.25 | -0.08 | 1.00 | | |
| Forest | 0.36 | -0.01 | 0.14 | -0.49 | -0.20 | 0.19 | 1.00 | |
| Human Index | -0.34 | 0.02 | -0.08 | 0.33 | 0.22 | -0.23 | -0.42 | 1.00 |

**S1.** Correlation matrix (Pearson) showing the relation among each variable on the Structured Equation Model.

| | **Effects on Jaguars** | | **Effects on Pumas** | | **Effects on Ocelots** | |
|---|---|---|---|---|---|---|
| Variables | IE | TE | IE | TE | IE | TE |
| Jaguar | - | - | - | 0.130 | -0.034 | 0.016 |
| Cattle | - | -0.061 | -0.009 | -0.010 | 0.000 | - |
| Goat + Sheep | - | -0.060 | -0.078 | 0.002 | -0.021 | - |
| Protected Areas | - | -0.024 | -0.003 | -0.043 | 0.010 | 0.000 |
| Forest | - | 0.233 | 0.029 | 0.005 | 0.007 | 0.125 |
| Human Index | - | 0.220 | -0.028 | 0.009 | -0.009 | -0.014 |

**S2.** Indirect (IE) and total effects (TE) for Structural Equation Model in Fig.1. Values of direct effect can be found on Table 2.

# Chapter 5

## Perceptions and livestock predation by felids in extensive cattle ranching areas of two Bolivian ecoregion

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## Abstract

Human-carnivore conflicts arise as one of the most urgent carnivore conservation issues worldwide. Jaguars (Panthera onca) and pumas (Puma concolor) coexist with livestock in much of their range and have been historically blamed for livestock predation. At present, livestock landscapes are increasing enlarging the conflict scenario. Knowledge of perception of locals is vital to understand the context in which the conflict emerges and data of predation on livestock become an effective tool to plunge into it. We assess local perceptions about felids and identify the bases of the conflict in Bolivian pantanal and dry forest ecoregion using livestock predation data. We interviewed local ranchers and crossed information with the governmental livestock database achieving a comprehensive study on the conflict, based on descriptive statistics for local perceptions and generalized linear mixed models for analyzing cattle predation by felids. The conflict appeared to be widespread since most ranchers suffered predation on cattle, especially in the pantanal. Data suggested low percentage of annual loss (1.8 %) with the exception of some punctual cases that may magnify the generalized negative perception towards felids. Factors related to cattle husbandry explained better felid predation on livestock rather than the habitat quality of the ranch. We recommend local administrations to recover livestock predation data and highlight the importance that husbandry practices may have to reduce cattle losses by felids.

**Key words**: Apex felids; Livestock predation; Extensive ranching; Average modeling

## Introduction

Protected areas appear to be insufficient to protect large carnivores from extinction (Woodroffe, 1998), as healthy populations of these species require vast areas to persist due to their wide home ranges, territoriality and prey necessities (Ripple et al., 2014). Conservation policies usually rely on protected areas often creating a fragmented landscape with islands of protected territories. However conservation of big carnivores require more integrated conservation measures that ensure wide connected areas (Rabinowitz and Zeller, 2010; Sanderson et al., 2002). In this context, human dominated landscapes are considered a more realistic scenario for carnivore conservation (Athreya et al., 2013; Chapron et al., 2014; but see Gilroy et al., 2015). Extensive cattle ranching is globally practiced and is characterized by maintaining vast areas of moderately modified landscapes and very low human density where free-grazing domestic animals coexist with wildlife. However , such a situation recurrently, leads to a conflict (Treves and Karanth, 2003) as carnivores may damage livestock, compete for prey or induce risky situations for people (Kleiven et al., 2004; Woodroffe et al., 2005). Generally it resulted in hunting of the carnivore species causing the decline of natural populations and ultimately affecting the whole ecosystem by top-down cascade processes (Estes et al., 2011).

Felids are largely affected by human-carnivore conflict becoming an urgent conservation issue for these species (Woodroffe et al., 2005). Severity of the conflict tends to increase with body mass (Inskip and Zimmermann, 2009) reason why jaguars (*Panthera onca*) and pumas (*Puma concolor*), the biggest cats in South America, are positioned in a conflict hotspot. Both species have been intensively reported to kill livestock throughout South and Central America where they co-occur with humans in close proximity (Rabinowitz, 1986; Quigley and Crawshaw, 1992; Hoogesteijn, 1993; Mazolli et al., 2002; Saenz and Carrilo, 2002; Conforti and Azevedo, 2003; Polisar et al., 2003; Crawshaw, 2004; Graham et al., 2004; Azevedo & Murray, 2007; Rosas-Rosas et al., 2008; Cavalcanti and Gese, 2010; Kissling et al., 2009). In a systematic review of human-felid conflict worldwide, Inskip & Zimmermann (2009) reported that the proportion of livestock loss by jaguars may ranged 0.3-2.3% while pumas sometimes were attributed for a higher number of medium-size domestic animals (up to

26% of sheep in 15 ranches). On the other hand, even more than 50% of total prey killed by jaguar may correspond to cattle, whilst it may comprise 15-43% of puma diet. So that, estimates on cattle predation by jaguars and pumas are highly variable among study sites and also did not provide consistent data on which species is more likely to prey upon cattle probably as the conflict strongly depend on the ecological context. As an extreme case, there are areas where pumas scarcely consume domestic species but jaguar did supplement diet with cattle (Forester et al., 2010), and *vice versa* (Scognamillo et al., 2003).

Numerous potential factors influence the cost-benefit balance that encourage jaguar and puma predation on livestock including innate and learned behavior, health and status of individuals (Mondolfi and Hoogesteijn, 1986; Quigley and Crawshaw, 1992), space and resources competition among jaguars and pumas (Scognamillo et al., 2003; Forested et al., 2010), abundance and distribution of natural preys (Polisar et al., 2003, Zanin et al., 2015) and cattle management practices (Michalski et al., 2006, Palmeira et al., 2008). Some possibilities to reduce frequency of felid attacks on livestock arise by a correct management of human-felid coexisting areas. Frequency of cattle predation was inversely related to availability and vulnerability of natural prey and directly related to availability and vulnerability of livestock (Polisar et al. 2003). Ranches that possessed abundant and diverse natural prey experienced fewer felid problems (Mondolfi and Hoogesteijn, 1986; Hoogestein et al., 1993). Meanwhile, increasing availability of domestic preys in areas with large cattle herd size positively affected predation rates (Michalski et al., 2006, Zarco-González, 2013). Aditionally, measures that ensure monitoring and carefully control of livestock with special attention to maternities which are more affected by predation is strongly recomended (Palmeira et al., 2008). Identifying main factors that affect cattle predation by jaguars and pumas may contribute to reduce the frequency of large cat depredation on livestock which ultimately may go a long way towards maintaining cat populations.

However, an effective approach to felid conservation should also consider perception of people inhabiting conflicting territories. Studies on local perception of the conflict reveals that killing domestic animals by carnivores is not the only or most important reason why people kill them (Cavalcanti et al., 2010). People demonstrates a deeply rooted hostility to jaguar and pumas related to the perception of their negative impacts on human livelihoods (Inskip and Zimmermann, 2009). Also other motivations such as fear or social acceptance, can also be determinant to stimulate killing (Marchini and Macdonald, 2012). So that, integrating local perceptions with cattle predation data allow us to better understand the human-felid conflict (Cavalcanti et al., 2010; Inskip and Zimmermann, 2009) in order to: (1) reduce the gap between local perception and reality, (2) involve ranchers and local administrations in systematic data collection of cattle losses, and (3) work with ranchers and local administrations to develop husbandry practices that can mitigate losses by apex carnivores. This way patterns of cattle predation may be addressed and the human-wildlife conflict may be managed to minimize the negative impacts on species conservation, human livelihoods and human well-being (Redpath et al., 2013).

Here, we used standardized questionnaires to study the conflict between jaguars/pumas and humans over extensive cattle ranching areas that extend along two main ecoregions of South-Eastern Bolivia, the Pantanal wetland and Chiquitano Dry forest. Such moderately modified landscapes may offer a real scenario for carnivore conservation as they partially conserved an inte-connected vegetation matrix through the vast territory dedicated to cattle raising. A global perspective of the human-felid conflict was provided in this survey by combining data collected from an interview-based sampling protocol and the livestock cadaster data of the region. The specific objectives were to (1) assess local ranchers perception on big felids in the two different ecoregion (the pantanal and the Dry forest), (2) characterize patterns of predation on livestock by jaguar and puma, (3) test the hypothesis that the occurrence of such predation is influenced by ranch characteristics, habitat variables and human-related features. We predicted that predation of livestock would be associated with ranch size and number of cattle because we expected larger ranches and herds may harbor more disperse and less managed cattle, and with habitat features that describe prime carnivore habitat (i.e. forest cover). Our results provided the assessment of the impact of cattle predation in the study area and suggestion to ranchers to implement practices to reduce livestock predation.

## Methods

### *Study area*

The study was carried out in the department of Santa Cruz de la Sierra (370 000 Km$^2$), located in South-Eastern Bolivia, limiting with Brazil, Paraguay and Argentina (Fig. 1). More than 140 000 Km$^2$ (almost 40 % of the department) are exclusively devoted to extensive cattle business, harboring more than 28 000 ranches and almost 3 million cattle heads in 2011 (Dirección de Sanidad Agroalimentaria, 2011). The region has extremely low population densities distributed in small dispersed communities along the rural areas and scarce number of cities and villages (Fig. 1). The department counts with two main ecoregions: The Pantanal wetlands in the Far East and the Chiquitano Dry forest in the rest of the area, both of them cataloged as of greater biodiversity interest (e.g. Parker et al., 1993). The Dry forest (Chiquitania) expands over 181.405 Km$^2$ where more than 10.500 ranchers breeded and fatten 1.463.562 cattle heads in

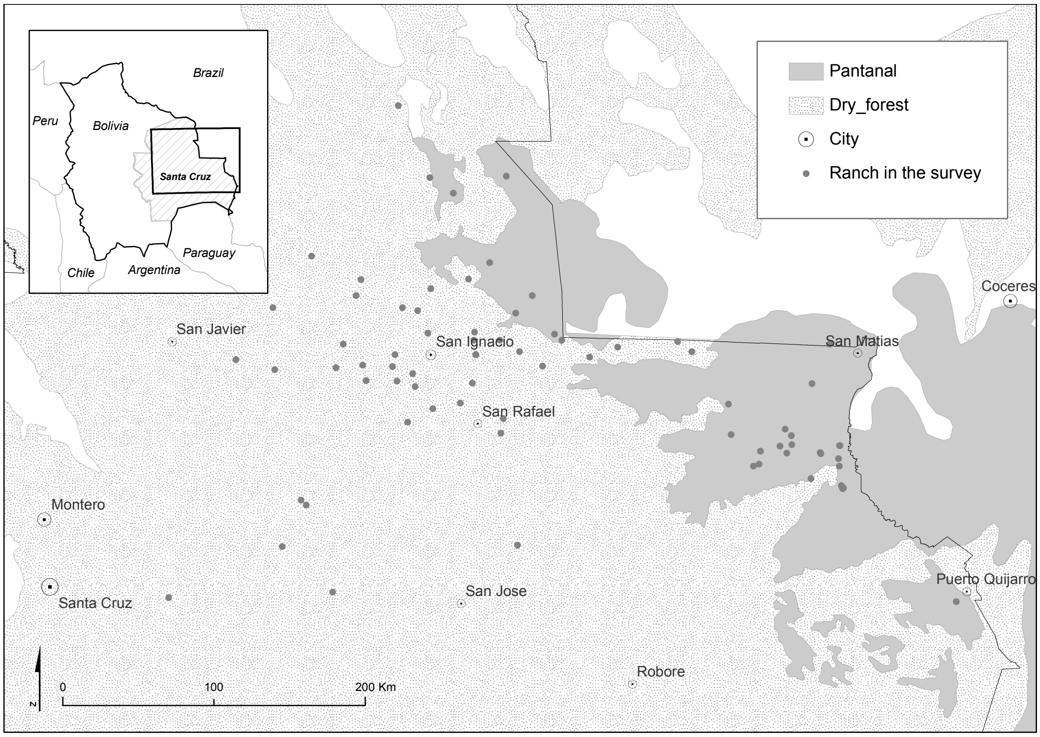

**Figure 1.** Study area. Grey dots correspond to location of the surveyed ranches in the Pantanal (grey background) and in the dry forest (gray dotted background). Main cities and villages are also represented.

2011, 18% being calves. The relation calve/cow was 0.47. The Pantanal expands over 51.330 Km$^2$ where almost 1.000 ranchers breeded 373.043 cattle heads in 2011, 17 % of them were calves. The relation calve/cow was 0.37. The climate is thermo-tropical, with a strong contrast between the rainy and Dry season. The pantanal landscape is a floodplain dominated by large pampas mixed with forests, while semi deciduous forests dominate the Dry forest. Most distinctive vegetation is sclerophilous shrublands (gr. Salvertia, gr. Caryocar), palm grooves (gr. Tabebuia gr. Copernicia), semidecidous forest (gr. Tabebuia gr. Anadenanthera) and wooden pampas (Tabebuia, gen. Callisthene). The department counts with important protected areas such as the Kaaiya National Park (34 000 Km$^2$) with a remarkable large jaguar population (Maffei et al., 2004) at the South of the study region, the Amboro national Park (6300 Km$^2$) at the West and the Area Natural de Manejo Integrado San Matías (29 000 Km$^2$) covering most of the studied Bolivian Pantanal which borders with Brazilian Pantanal. Questionnaires were carried out throughout the department rural areas covering to similar extent both ecoregions where conflict with felids is conceivable because of the presence of jaguars and pumas.

### *Data collection*

*Interviews*

We conducted structured questionnaires to ranchers in order to assess local perception on the human-felid conflict in the study area and collect data on livestock losses in ranches. Many of the interviews were performed at the anual cattle fair at San Ignacio de Velasco in July 2011. We take advantage of tis traditional event with a high affluence of ranchers coming from all regions of Santa Cruz de la Sierra department to buy and sell livestock, and thus possible bias associated with accessibility to ranches was avoided (Zimmermann et al., 2005). Besides, a fraction of questionnaires (n=44) were directly conducted in different properties between June-August 2011. As a result, a total of 86 questionnaires were undertaken from which 41 were located in the Pantanal and 45 in the Dry Forest. Ranches were widely distributed across both ecosystems which covered more than half of the Santa Cruz department including Velasco, Chiquitos, Nuflo de Chavez and Angel Sandoval provinces (Fig. 1).

Questionnaires were designed to provide information about (i) ranch characteristics including geographic localization, ranch size, cattle holdings, cattle density, (iii) felid occurrence (sightings, footprint detection) (iii) cattle loss by felid predation in a 24-month period before the interview date, and (ii) perception and attitude towards coexistence with felids (for further details see Appendix 1). Prior to conducting the interviews, a number of criteria should be strictly met by each local informant, preferentially the land-owner or the cattle manager of each ranch, to enhance reliability of collected data. We corroborated that this person (1) perfectly knew the rules for any activity within the ranch and details on cattle management practices, (2) was a resident in the ranch for at least 2 years, (3) worked with the cattle herd within the ranch, and (4) was willing to be interviewed. Reliability on predation data was based on the ability of all ranchers to identify kills by felids from other causes of cattle death such as desease, thirst or snake bite. Lost or stolen cattle was explicitly explained not to be included in the reported cattle loss number. We pooled together cattle loss by pumas and jaguars because not all interviewees were able to unambiguously distinguished the carcass predated by these two large felids and tracks of each species. Also, the interview-based sampling protocol was independently cross-validated by monitoring the presence and abundance of large felids as well as occurrence of predation events within 30 ranches (35% of all ranches interviewed). We performed a systematic sampling to record tracks and collect scats at these sites (P. Villalva et al., unpubl. data) and verified cattle kills by felids occurred during 3 months. On the basis of these field sampling data, we conclude that our interview data are reliable: respondents never falsely reported the presence of large felids and we verified all predation events reported by them. The long-term relationship with local land-owners for 3 years of fieldwork and research activity in the area (P.V) gives an extra confidence to the interview data obtained for this study.

*Cadaster and landscape data*

We extracted data on buildings (manager and cowboy houses) and cattle management structures (shed, ponds and wells) for each surveyed ranch from the Santa Cruz livestock cadaster data (Dirección de Sanidad Agroalimentaria, 2011). A semiquantitative variable based on numeric categories corresponding to the number of buildings in the ranch (0 no building, 1 manager house, 2 manager and cowboy house) was used as proxy of human presence. Ranches were also described in terms of habitat features such as net primary productivity (NPP) that was calculated from NDVI and EVI indexes and percentage of forest cover within a buffer of 5 Km radius around the ranch paddock based on satellite imaginary from Digital Globe 2011. Selection of this radius buffer (i.e. an area of 79 km$^2$) was based on the average jaguar home range in similar ecosystems (Soisalo & Cavalcanti, 2006; Maffei et al., 2004). All spatial data were conducted in QGIS v.6.2.1 (QGIS Development Team, 20…).

Also, ranch size or livestock holdings provided in the cadaster were used to cross-validate same data obtained from interviews. To increase confidence in our interview data we only retained study cases that had coincident data from both source of information for cattle loss modeling (n = 56).

### Data analyses

#### *Perceptions and attitude to felids*

Differences in local perception of ranchers about felids between both surveyed ecoregion (pantanal and Dry forest) were examined by Chi-square test or Fisher's exact test when any of the value of the contingency table were below 5. Non-parametric Wilcoxon test was employed to compare number of losses and ranch size between ecoregion.

#### *Cattle loss model*

We investigated the effect of ranch characteristics (ranch size, cattle holdings and cattle density), landscape attributes (forest cover and npp) and human-related features (human presence and attitude to attacks) on cattle loss by felids. Prior to modeling, we searched for confounding effects among variables using Spearman's correlation (Zar, 1999) in order to reduce the effects of multicollinearity. From any pair of independent variables that reported $r > |0.5|$ we removed the independent variable less correlated with the response variable, i.e. net primary productivity and forest cover in the ranch were highly correlated ($r = 0.82$). Only forest cover was retained for further analyses due to the importance that it has increasing vulnerability of cattle to felid predation (Quigley and Crawshaw, 1992; Zarco-González, 2013).

Model design was guided by four general hypothesis: 1) ranch features (relative to their size and abundance of domestic prey) influence cattle predation by felids; 2) cattle predation is explained by the surrounding landscape; 3) human presence and attitude to felids affect cattle predation. We constructed Generalized Linear Mixed Models (GLMM) with cattle loss as response variable, the above described explanatory variables (ranch, landscape and human-related features except the npp), negative binomial error distributions to avoid overdispersion and ecoregion as random effect to control for differences among pantanal and Dry forest. The set of candidate models included all possible combination of the saturated model, plus a null model with no explanatory variable. Model selection was then performed by ranking each model according to a bias-adjusted Akaike Information Criterion ($AIC_c$). This statistic rewards parsimony by penalizing the maximum likelihood for the number of model parameters. Last, we assessed uncertainty on model selection by weighting all AICc scores by the score of the best model (wi) (Burnham and Anderson, 2004). As non best approximating fitted model had DAIC < 3, we performed model averaging using the coefficients from the models that constituted a cumulative Akaike weight of 0.95 (Appendix 2) following the same subsampling procedure (Anderson, 2008).

Finally, we performed univariate GLMM for the three main explanatory variables revealed by model averaging (i.e. ranch size, cattle holdings and cattle density; see results) to estimate probability of cattle predation (yes or not) using a logistic link. All statistical analyses were performed using MASS (Venables and Ripley, 2002) and MuMIn (Burnham and Anderson, 2002) packages in R version 3.01 (R Development Core Team, 2013).

## Results

### *People interviewed*

All respondents (n=86) were men and most (91%) exclusively devoted to livestock. On average they were 41 years old (range: 18-72) and most of them had a medium education level (6% with no studies, 25 % primary, 41% secondary and 28% superior studies). Ranch owners or managers were 54% of people interviewed, whereas 46% were cowboys.

| | Pantanal | Dry forest |
|---|---|---|
| **People in the ranch** | Mean (range) / % /categories | Mean (range) / % /categories |
| Age | 40.6 (18-68) | 41.5 (19-72) |
| Education level | 2/15/13/6 | 4/6/20/19 |
| Owner/cowboy | 10/12 | 27/18 |
| **Perceptions** | | |
| Felids threat humans | 54 % | 43 % |
| Felids threat cattle | 91 % | 93 % |
| Cite cattle as prey | 84 % | 87 % |
| Puma population trend | 11/14/11 | 8/12/25 |
| Jaguar population trend | 10/8/13 | 7/11/29 |
| Puma footprint presence | 94 % | 51 % |
| Jaguar footprint presence | 88 % | 73 % |
| Identify footprints | 46 % | 33 % |
| Identify predated carcass | 20 % | 15 % |
| Cattle loss | 16.9 % | 8.5 % |
| **Attitude** | | |
| Response to cattle predation | 8/6/21 | 9/4/33 |
| Felid extirpation | 65 % | 33 % |
| **Ranch characteristics** | | |
| Ranch size (ha) | 4,064 (100-14,000) | 2,062 (120-7,000) |
| Cattle holdings | 1,429 (2-8,000) | 1,337 (200 - 6,000) |
| Cattle density* | 0.37 (0.2 - 0.4) | 1.19 (0.08 - 4) |
| Human presence | 0/11/16 | 1/9/20 |
| **Habitat features** | | |
| Forest cover (%) | 0.39 (0.1 - 0.9) | 0.6 (0.1 - 0.9) |
| npp (g/m$^2$) | 14,744 (11,754 - 18,989) | 16,211 (12,000 - 21,200) |

**Table 1.** Summary of local perception and attitude to felids, ranch characteristics and habitat features for each ecoregion surveyed. Mean, % of respondents or categories are shown for the different variables. Education level is reported as the number of respondents with no studies/primary/secondary/superior studies. Population trend of both felids is shown as increasing/stable/declining. Response to cattle predation correspond to ranchers that had no response/try to banish the felid/kill the felid. Only positive presence is shown regarding to percentage data (i.e. presence of footprints, identifying predated carcass and footprints). Felid extirpation is referred to the percentage of ranchers that consider felid extinction as positive.Human presence is reported as numeric categories corresponding to no buildings/manager house/manager and cowboy house.

### *Perception and attitude towards jaguars and pumas*

Most respondents considered felids a threat to cattle (93 %) and almost half as well as a threat to humans. Regarding to perception on felid preys, cattle was cited as the most common prey for both predators (91%) while rarely wild animals were referred as exclusive preys (9%).

Perceptions varied between ecoregion (pantanal vs. Dry forest) in many aspects. Ranchers in the Dry forest considered puma population in decline, while in the pantanal they affirmed that population is stable ($X^2 = 5.8983$, $P = 0.05239$). Decline of jaguars was a general perception and did not varied between ecoregion ($X^2 = 3.2228$, $P = 0.1996$). Regarding to perception of footprint presence, in the pantanal pumas were significantly ($\theta$=0.3998, $P = 0.1677$) more encountered than in the Dry forest, unlike jaguars prints that were common in both regions. However when we ask ranchers to identify felid footprints there were no difference among region ($X^2 = 0.975$, $P = 0.3234$). Only 38 % of all ranchers identified correctly both species even though most of them (74 %) believed that they knew. Interestingly, only 17 % of all ranchers were able to distinguish between carcasses predated by either felid species.

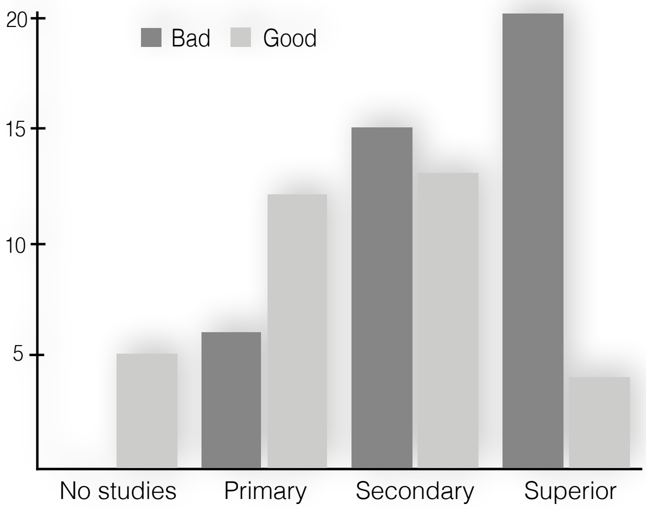

**Figure 2.** Relation between ranchers education level and opinion about local extinction of big felids. Dark bars represent ranchers against local extinction while light bars represent ranchers in favor of local extinction. Fisher's exact test: P < 0.001.

Attending to attitude of ranchers towards felids, poaching appeared to be the first response to cattle predation (70%) regardless of ecoregion ($X^2 = 2.4552$, $P = 0.293$). However, felid extirpation was more accepted by ranchers in the pantanal than those in the Dry forest ($X^2 = 5.9837$, $P = 0.01444$). The opinion about local extinction also varied between education level (Fig. 2) and number of losses. Those ranchers that stayed in school for longer considered negative the effects of local extinction (Fisher's test: $P = 0.0003$), while those with higher number of loss were in favor of it ($X^2 = 5.7799$, $P = 0.0162$). Most respondents in favor of local extinction cited the reduction of cattle predation as main motivation.

### *Livestock predation and factors affecting it*

Overall we recorded 913 cattle killed by big felids during the previous year in all the surveyed ranches. In general, most of them (77%) loss a moderate amount of

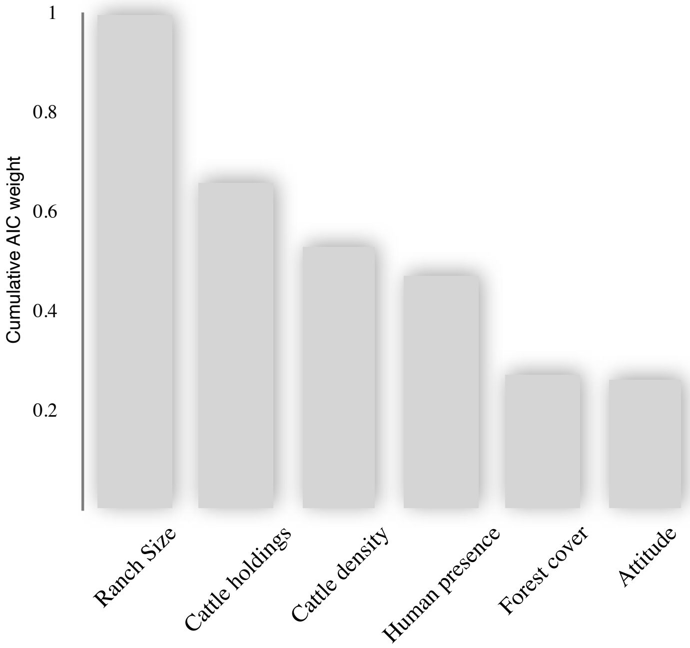

**Figure 3.** Cumulative AIC weight of covariates used in cattle loss models. Ranch size was the most influential variable, followed by other ranch features related to the abundance of domestic prey.

cattle (12.2 ± 2.8 cattle heads loss per ranch). Losses were significantly greater in the pantanal than in Dry forest (average 16.9 and 8.5 cattle heads per ranch, respectively; $X^2 = 10.634$, $P = 0.004908$). Felid predation represented 1.8 % of the total holdings (range= 0-26%) in surveyed ranches for the whole study area. In many ranches (47 %) felid predation represented less than 1 % of total holdings.

Model averaging evidenced the importance of ranch characteristics over ranchers attitudes, human presence and habitat features (Fig. 3). As expected, ranch size showed the greater significance to explain cattle loss, while cattle holdings and cattle density (interaction between both previous variables) were also of great importance, followed by human presence, forest cover and attitude, that was the less explicative in the set of tested variables. Regarding to the model, parameters showed a positive relation between cattle loss and ranch size alike cattle holdings (Table 2), meaning that larger ranches and greater holdings resulted in greater cattle loss. Cattle density and human presence relation was negative, prompting that greater cattle density and more residents in the ranch resulted in fewer cattle loss.

| **Variables** | **Estimate** | **S.E.** | ***P*** |
|---|---|---|---|
| *(Intercept)* | 0.996 | 0.950 | ns |
| *Ranch size* | 0.001 | 0.000 | *** |
| *Cattle holdings* | 0.001 | 0.000 | ** |
| *Cattle density* | 0.000 | 0.000 | *** |
| *Human presence* | -0.988 | 0.432 | * |
| *Response* | 0.229 | 0.206 | ns |
| *Forest cover* | 0.908 | 0.770 | ns |

**Table 2.** Parameters estimates for the generalized linear mixed-effects model explaining cattle loss by felids. Coefficient estimate, standard error (S.E.) and test z significance (*P*) are shown. ns $P < 0.1$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

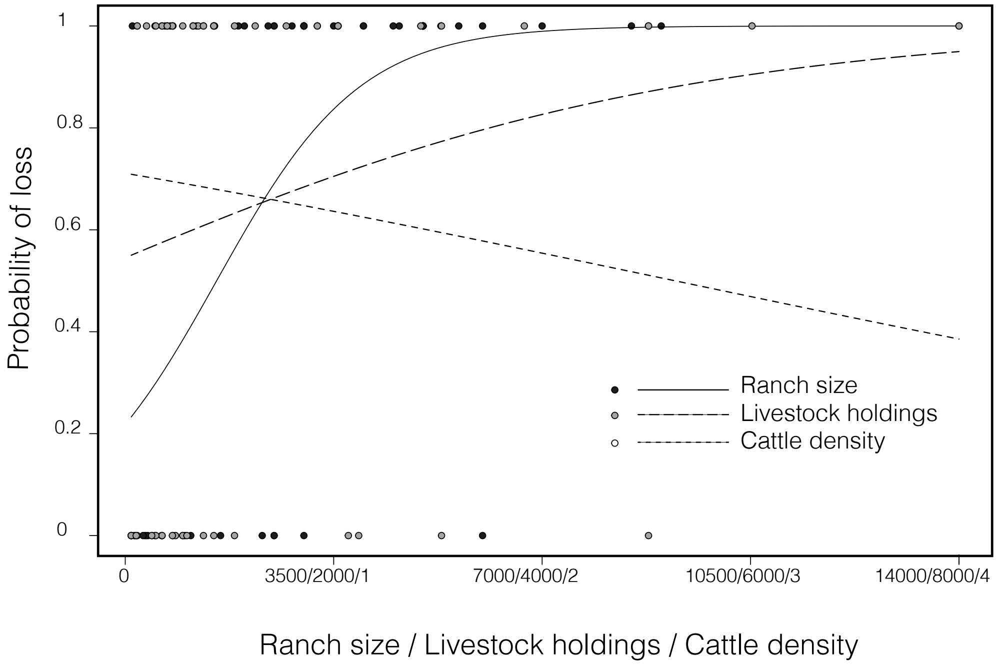

**Figure 4.** Probability of cattle loss in relation to three main variables of the best model. Dots represent empiric data (0 = no loss, 1 = at least 1 loss). Black dots and continuous line represent ranch size, grey dots and long dashed line represent livestock holdings and empty dots and short dashed line represent cattle density.

Meanwhile, probability of loss (Fig. 4) supported the previous result showing a marked slope of ranch size that quickly reached the upper limit. Ranches over 4000 ha had a 90 % probability of losing cattle.Livestock holdings curve showed a softer slope, while cattle density increase reduced the probability of loss.

## Discussion

Large carnivores interfere with human business becoming a serious problem for long term viability of their populations due to hunting (Woodroffe and Redpath, 2015). Extensive ranching areas preserve part of the natural landscape allowing apex carnivores to coexist with humans (Hoogesteijn and Hoogesteijn, 2011), thus to find strategies to minimize the conflict between ranchers and carnivores becomes vital to achieve the goal of conservation of large predators in exploited landscapes.

Our results suggest that felid-human conflict is widespread in the study region. Most ranchers assured that felids are a threat to cattle and many considered them a threat to humans what evidence the basis of the conflict. Moreover, the perception that both apex felids diet is mostly cattle illustrates the generalized negative attitude towards them. Previous poaching data in the area supported our findings by reporting a total of 347 jaguars and 230 pumas killed in 85 ranches in four years (Arispe, 2008; Arispe et al., 2006). On average, annual predated cattle was 1.8 % in the total sampled ranches, which is consistent with the reported 0.1 - 3% range for predation rate of felids worldwide (Jackson and Nowell, 1996). Maximum and minimum values corresponded to studies on livestock predation by jaguars and pumas, with annual losses of 0.1% in Los Llanos, Venezuela (Polisar et al., 2003) and 3.0 % in Sao Paulo, Brazil (Palmeira et al., 2008). In a similar Pantanal area predation rate was 2.3 % (Zimmerman et al., 2005).

We find marked differences among ecoregions not only in cattle loss but in many other aspects. Regarding to the characteristics of respondents, the level of studies was notably higher in the Dry forest than in the Pantanal. Also, education level appeared to be important for the perception of felids (Fig. 2), according to results of Cavalcanti et al. (2010) that found a negative correlation between attitude towards jaguars and the number of years attending school. We found that level of studies was notably higher in the Dry forest compared to the Pantanal, which explains the better attitude towards big cats in the Dry forest when they were asked about felid local extinction. The fact that ranchers in the Pantanal were more often pro-extinction of felids highlight the importance of this ecoregion for conservation efforts. On the other hand, perceived felids population trend revealed the decline of pumas in the Dry forest, while jaguar population remain stable. Supporting this result, presence of puma footprints were very low in the Dry forest (51%) compared to those cited in the Pantanal (94%), but we must be aware of the lack of credibility of this data due to the inability to differentiate tracks of both species. Also, predation impact on livestock markedly varied among ecoregion. Cattle loss was greater in the Pantanal than in the dry forest what can be explained by differences in cattle husbandry characteristics between regions. From this scope, ranch sizes were in average six times larger in the Pantanal than those in the Dry forest (see Table 1), factor that is pointed as the most important effect on cattle loss in this and previos studies (Zimmermann et al., 2005, Zarco-González, 2013). Despite type of cattle system had not been able to be tested due to scarce data, entire dataset from the livestock cadaster showed that the Pantanal is basically characterized by a cattle breeding system while the dry forest by a breeding-fattening system where proportion of calves/cow was 0.37 and 0.47 respectively (DSA, 2011). This information may have important implications for the higher number of cattle losses found in the Pantanal besides ranch size.

In general, the percentage of predated cattle might be low as compared with cattle deaths due to disease or drought (Azevedo and Murray, 2007, but see Tortato et al. 2015). Even though we did not measure other death causes, we found exceptional high predation rates in some of the surveyed ranches (up to 26 % of total holdings) which were personally visited by the authors to corroborate veracity of these data. These particular cases occurred in ranches located in the edge with agricultural areas, where poaching levels on wild preys may be very high and hence densities of wild prey extremely low. Usually ranchers of the area are aware of these dramatic cases which may skew their perception of the conflict and magnify the magnitud of the conflict (Chavez and Gese, 2006; Chavez et al., 2005; Conover, 2002; Sillero-Zubiri et al., 2007).

Modeling of cattle loss evidenced ranch size as the variable that contributed the most to explain cattle predation by felids. Similar effect was found in studies of jaguar and puma predation (Zimmermann et al., 2005, Zarco-González, 2013), even in other carnivores as suggested wolf predation on cattle in northern US (Treves and Karanth, 2003). Large ranches often harbor more disperse cattle which becomes certainly more difficult to handle compared to small ranches where cattle is more controlled. Moreover, large ranches may shelter higher amount of felids that may facilitate the encounter of cattle with eater cats. The amount of livestock (stockholdings) also affected predation on cattle. Greater amounts of cattle increase availability of potential prey which may promote opportunistic predation on cattle . Moreover high amounts of cattle in extensive systems turn the herd more difficult to handle. Both features, wide ranches and numerous herds usually lead to unmanaged cattle which has been highlighted as a key piece for cattle predation (Bagchi and Mishra, 2006; Hoogesteijn and Hoogesteijn, 2011). Cattle density (interaction between ranch size and total stockholdings) also standed out as an important factor explaining cattle predation, but with an inverse relationship (Fig. 4). High herd densities, especially when high proportion of adults exist, may increase the probability of defensive behavior (Tortato et al., 2015). Also, it may be related again to cattle management practices with high densities being readily handled in comparison to low densities that usually maintain cattle more disperse (Jori et al., 2006, Zarco-González, 2013).

Human presence in the ranch also contributes to explain cattle losses as showed the model averaging ranking (see Fig.3), although the predictor for cattle loss was only marginally significant (see Table 2). We expected a positive relation between human presence and predation, due to more people in the ranch will reduce natural prey thus increasing predation on cattle (Foster et al., 2014). Instead of this, we found a negative relationship. This unexpected result suggest that more people in the ranch tend to have a dissuasive effect on probability of felid attacks by direct persecution or avoidance behavior of cats. Besides, more people may assure more accurate cattle handling that may reduce the number of loss as already mentioned (Palmeira et al., 2008). Interestingly, the response of ranchers to predation events apparently did not affect cattle loss (Fig. 3 and Table 2). This is at odds with the popular belief that the extirpation of the individual predator could lead to the extirpation of the conflict. A more satisfactory way to minimize predation on cattle should be focused on improving management practices that might allow a real reduction of carnivore damage. However, the response of killing the felid before cattle predation is very common in both ecoregions, suggesting that the conflict is widespread and deeply rooted in the culture of the people inhabiting the whole study area.

We believe that extensive ranching can become an ally for big cat conservation. In order to mitigate the conflict we suggest two main recommendations: 1) To focus mitigation efforts in those ranches that have actually show high predation rates. This will locally attenuate the number of losses while, simultaneously, may help to start changing the general negative perception about predators, and 2) to encourage further investigation in determining which cattle management practices may reduce cattle predation. For this purpose a greater dataset than used in this study would be desirable. Thus, we suggest a systematic data recovery that could be easily handled by the institutions in charge of cattle cadaster. The new dataset should contain the actual large amount of ranch characteristics plus data on livestock predation in each ranch. Analysis of these data will help to locate conflict hotspots where focus strategies to conflict mitigation and to determine those management practices that affect cattle predation.

In conclusion, we believe that there is an urgent need in further investigation to implement those improved cattle husbandry practices that might mitigate predation by felids to contribute to the conservation and recovery of big felids in extensive systems. This approach should be along with the implementation of appropriate education programs of inhabitants in rural areas to build a positive baseline of conservation values within the ranching community, increasing their knowledge on those ranch features and measures that may reduce cattle loss consequently. We also encourage to rise awareness about the apex carnivores intrinsic value and role in ecosystems.

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# Chapter 6

## Selling jaguars as Tiger: impacts of asian medicine on American big cats

## Tiger trade threatens big cats worldwide

*Science letters 2019*

## Abstract

Unsustainable wildlife trade is one of the main global conservation challenges driving human-exploited species to extinction. High demand of traditional Chinese medicine for animal-based products has strongly contributed to illegal trade on diverse threatened species as tiger. The recent reversion of Chinese policy that forbidden the commerce of tiger parts together with the spread of their population worldwide impose a new context that favours illegal trade not just of the nearly extinct natural tiger populations, but also of most big cat species worldwide. Illegal trade of jaguars intended for traditional Chinese medicine has recently been evidenced in South America appearing as a severe threat to wild populations of the species in some countries. The magnitude of this conflict and impact on natural populations are still scarcely known but we believe it could be greater than it appears due to its difficult detection. We recommend the implementation of a genetic approach to gather information about the conflict by local authorities not only to effectively control tiger trade in Asian countries but also to manage jaguar illegal trade while is still at an initial stage.

**Key words:** Allee effect, apex felids, illegal trade, poaching, traditional medicine

Illegal wildlife trade is a major threat to biodiversity worldwide (Maxwell et al. 2016; Milner-Gulland 2018) and heavily contributes to the Anthropocene extinction crisis (Nijman 2010). Intense hunting pressure can result in Anthropogenic Allee effect on natural populations (Stephens et al. 1999) where severe reduction of population density ends up collapsing the biological effectiveness of a species. Continuous harvesting creates feedback loops in which a species become rare, and therefore increase its value, then stimulating further harvesting (Courchamp et al. 2006). This overexploitation may lead a species into an extinction vortex that is accelerated because of economic interests (Clavero 2016). There is a high-value illegal wildlife market worth an estimated USD 8-10 billion per year that is recognized as one of the largest global illicit businesses of transnational criminal organizations (Haken 2011). Mammals stand out as the dominant exploited group (Rosen & Smith 2010; Mc. Clenachan et al. 2016) primarily for consumption as bushmeat (Riple et al. 2016), but also there is an international luxury market of non-perishable products for medicinal (i.e. the traditional Chinese medicine) and decorative purposes that represents a high extinction threat to wild mammal populations. The disproportionate impact on these species is due not only to the extraordinary value that some animal parts reach, but also because they can be stockpiled and distributed globally, so that poaching occurs continuously (Webb 2016). Large-sized mammals are affected the most by illegal trade due to both intensive international demand and their intrinsic sensibility related to great spatial requirements and low population growth rates (McClenachan et al. 2016). Some widely known examples of transcontinental trade include tiger products (Mills & Jackson 1994; Nowell & Ling 2007), rhinoceros horns (Milner-Gulland & Leader-Williams 1992), and elephant ivory (Milner-Gulland & Beddington 1993; Scriber 2014). During the past half century, the intensively trade of these species bounded for Asian market has driven them to the actual endangered (tiger and Asian elephant) and critically endangered status (black rhino) (IUCN 2018). Main causes of their ongoing extinction process are not just the excessive reduction of population density, but also particularities of each species trade such as poaching preference on males that result in a strong biased sex ratio seriously affecting reproduction effectiveness, as it has already occurred in Asian elephant populations. The ecological impact of illegal trade on these species warns of the potential threat that similar species may face in a near future. Despite of the huge efforts to control and mitigate illegal trade, the extremely profitable luxury market explains why it is still currently in force.

Traditional Chinese medicine is a high-demand medical practice widely used in China and surrounding countries that has strong influence on illegal wildlife trade. Animal-based preparations may include parts of endangered species such as tiger bones. Tiger parts are highly quoted in traditional Chinese medicine in relation to disparate medical uses (Ellis 2005). For example, McClenachan et al. (2016) reported that the tiger penis worth up to USD 470,000 kg-1 and a complete individual could reach USD 350,000, placing the species among the most expensive animals (along with black rhino) traded. Demand for tiger-derived products has never slowed down; even it may increase as traditional Chinese medicine is becoming more popular and recognized worldwide (OMS 2013). Both are the causes -high value and great demand- of tiger overexploitation that has rapidly accelerated its decline over the last decades. Protective regulation that Chinese government approved in 1993 banning any trade of tiger parts has not contributed to effectively safeguard the species (EIA 2013). Actually, sale of tiger products has notably increased in the following years, especially since 2010, being China and Vietnam the main countries of origin and destination (Nowell 2014). Furthermore, a rapidly growing of captive facilities for tiger breeding (with nearly 260 establishments) has emerged during the last decade in Asia (especially China and Thailand) and South Africa (EIA 2017), where the number of captive tigers (7000-8000 individuals) almost doubles that of natural populations (3000-4000 individuals). Far from protecting the species, tiger farms have been involved in illegal trade of their parts and its derivatives (Nowell 2014). Lack of regulation to release captive-bred tigers has recently motivated (October 2018) Chinese government to reverse the ban, so today the trade of captive tigers (and rhinos) for medicinal, scientific and educational purposes has been legalized. This measure is likely to reactivate tiger illegal trade in the short term (but see Conrad 2012 or Biggs et al. 2013) due to the greater ease of laundering in the legal market. It should be noted the difficulty to differentiate between captive and wild animals especially when they are sold as derivatives (Stoner 2014), complicating analysis and monitoring.

Insatiable demand of tiger parts under the new context of legal tiger trade entails that poaching threatens not just the world's few remaining wild tigers but also other big cat species worldwide which may be marketed to consumers as tiger (Williams et al. 2015). Diverse felid species have been used as tiger substitutes in traditional medicine preparations being sold as tiger fakes; otherwise the market value drops drastically compared to authentic tiger products (Nowell 2014) making it affordable to another economic sector of society. Other Asian cats such as snow leopards, leopards, cloud leopards and Asian lions are also threatened as a result of the illegal trade of their parts (EIA 2017). Out from Asia, the transcontinental trade of African lions represents a clear and well-documented example that sheds light on tiger substitution by other felids (Koshoo 1997). Lion bones have intensively been trafficked from South Africa to East-Southeast Asia under a government agreement that allowed its use for wine preparations that traditionally containing tiger bones (Bahuer 2016). Since then, legal trade of lion bones has increased progressively, with about 6000 skeletons being sent during the last decade (Williams et al. 2017). This fact gives support to Koshoo´s predictions (1997), which declared "It is also clear that when tiger is decimated, the next target will be lion, followed by leopard and all other felines from Asia and Africa". However, it is possible that twenty years ago, the belief that strong demand for tiger parts could also threaten American big cat species was still unrealistic. Exponential growth of Chinese population generates an unprecedented demand for natural resources (see Bai et al. 2018) whose exploitation could trigger cascading effects through entire ecosystems even at tens of thousands of kilometres (Luque-Larena et al. 2018). In addition, Chinese expansion throughout the world creates an opportunity to explore new resources while preserves its deeply rooted culture and traditions in new places. South America has become the destination for a wide expatriate Chinese population as a consequence of the great economic investment of this country in the continent during the last 10 years (Perez 2017). Their economic activities, usually operating under low environmental and social standards, have raised the concern of critical observers for nature conservation. In this context jaguars (*Panthera onca*) are placed at the spotlight due to the new business opportunity of selling jaguar as tiger substitute in the traditional Chinese medicine market. This new tiger substitute has still not been well documented, probably because it is a recent phenomenon. First evidences of the emerging transcontinental jaguar trade comes from Bolivia and Surinam (Bale 2017; Bale 2018) and have been related to establishment of Chinese companies in the region. Specifically, Bolivian authorities seized more than 380 jaguar teeth between 2013-2016 and 11 different shipments containing up to 185 big cat fangs were sent from Santa Cruz de la Sierra destined to China in just one year (Rumiz & Rivero 2018). We believe that these evidences represent just the tip of the iceberg of an emerging phenomenon that seriously threatens America's largest cats. Lack of detection in other countries can be explained due to the difficulty of uncovering it, especially when dealing with derivatives. High price that tiger derivatives reach for traditional medicine (exceeding indeed the actual price of gold, diamonds or cocaine) (Biggs et al. 2013; McClenachan et al. 2016) is a claim for drug trafficking mafias whose decades of expertise in illegal business make detection even more complicated. The emergent threat of illegal trade on jaguars for Chinese medical purposes is added to the historic hunting pressure that the species has suffered through the extensive conflict with cattle. These two factors may drive jaguars to an overexploitation situation that can lead it to an extinction vortex in a short time. Increasing knowledge on the impact of illegal trade and developing intelligent-aid management tools are especially important in early stages of the process and ultimately could allow that jaguar and other felid species follow a different path from that of the tiger.

Great advances in molecular biology have been developed for big cats, providing new insights to diverse biological questions that would otherwise be unapproachable. New techniques that have been positively tested are actually ready-for-service for its application to illegal trade (Shina 2017) i.e. for the challenging tiger trade in China or the emergent increase of jaguar trade in Bolivia. A genetic approach has already been strongly recommended by many involved actors in illegal wildlife trade such as Interpol that proposed the development of intelligent platforms to allow the prosecution, investigation and forensic capacity of local authorities (Interpol 2014). Furthermore, the economic limitation has been exceeded allowing wide application opportunities at an affordable economic cost. As example, a very useful approach has already been proposed for field management of Rhinos illegal trade from South Africa to China (Biggs et al. 2013), based on horn harvesting and genetic profiling to control the legal market. Also genetic approaches have been recently implemented to aid management of Bengal tiger trade by geo-locating seizure samples in Nepal (Karmacharya et al. 2018). The new Chinese law should promote establishing a regulatory non-governmental institution to differentiate between captive and wild tigers based on DNA profiling, but we also must pay special attention on the impact that the new regulation have on long-distance populations of other big cats. We underscore the need for a close genetic approach also in those Latin American countries where the conflict has already been detected, allowing information and management tools to enforce intelligence-aid measures at the yet initial stage.

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Wildlife trafficking has become a billion-euro criminal industry supporting an international luxury market of medicinal and decorative animal-based products (*1*). Endangered species are disproportionately affected; continuous harvesting of their populations creates feedback loops in which a species become rare, which increases its value and stimulates further harvesting (*2*). The overexploitation of Asian tigers over centuries is a clear example of this phenomenon, which has led the species to its current endangered status (*3*). Some of the insatiable demand for tigers is now met by tigers raised and bred in captivity (*4*). In 1993, the Chinese government banned any trade of tigers, but in October 2018, the commerce of captive tigers was legalized for scientific, educational, and medicinal purposes (*5*). This measure may reactivate the illegal tiger trade, because a legal market provides sellers an outlet to traffic illegal products.

China's decision threatens not only the world's few remaining wild tigers, but also most big cat species worldwide, which may be marketed to consumers as tiger or as a substitute for tiger. For example, more than 6000 lion skeletons were legally moved from Africa to Asia during the past decade, marketed as a legal alternative to tiger bones (*6*). Recently, employees of construction companies with access to jaguars in Bolivia and Suriname attempted to send them illegally to China to serve as tiger substitutes in traditional medicine (*7*, *8*). Since 2013, more than 380 jaguar teeth have been seized by Bolivian authorities (*9*), and in 2016 alone, up to 185 big cat fangs were delivered to China (*10*). These data suggest a growing illegal trade that seriously threatens the world's largest cats.

Current molecular techniques can help stem the tide of illegal trade (*11*). The Chinese government should promote the establishment of a regulatory institution to differentiate between captive and wild tigers based on DNA profiling. If a product appears to be illegal, it should be seized and the seller should be penalized. Meanwhile, governments worldwide should pay special attention to the impact that tiger trade regulations have on the populations of other big cats that may be used as substitutes for tiger products.

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# Chapter 7

## General Discussion

Los ecosistemas terrestres están cada vez más humanizados (Radwan *et al*. 2021), suponiendo una amenaza para las especies de grandes carnívoros a través de la competencia por los recursos (Ripple *et al*. 2014). Por ello la coexistencia con el ser humano es imprescindible para la conservación de los grandes carnívoros (Frank *et al*. 2019) que, por su papel regulador en la cadena trófica, son fundamentales para el correcto funcionamiento de los ecosistemas (Estes 2011). El objetivo de esta tesis es profundizar en la ecología de los grandes felinos neotropicales en paisajes humanizados haciendo un especial esfuerzo para comprender el efecto de las actividades humanas sobre estas especies, así como sobre sus interacciones, con la idea de ofrecer una visión actualizada de las amenazas a las que se enfrentan.

## Amenazas de los grandes carnívoros neotropicales

Como resaltamos en la introducción de esta tesis, las amenazas de los grandes felinos neotropicales han cambiado con el tiempo. Las amenazas actuales son distintas de las históricas (y prehistóricas), si bien la causa última de todas las amenazas actuales corresponde a presiones de origen antrópico. Evidencias genéticas y fósiles apuntan a que las poblaciones de grandes felinos neotropicales sufrieron una importante reducción en su distribución debido a los cambios paleoclimáticos. El impacto del cambio climático glacial en las poblaciones de felinos fue la principal causa de extinción de estas especies en tiempos prehistóricos obligando a los felinos a permanecer recluidos en refugios del sur del continente americano. Estas especies pudieron recolonizar el norte del continente al final de la última era glacial (Eizirik et al. 2001, Rodriguez et al. 2008). En tiempos modernos la cacería comercial de gatos pintados fue la principal amenaza de los felinos neotropicales. La demanda del mercado peletero norteamericano y europeo afectó a gran parte de sus poblaciones hasta mediados del siglo XX. Sin embargo, esta amenaza fue minimizada gracias a la organización y compromiso internacional a través del convenio CITES (1975) que consiguió frenar drásticamente la presión de cacería. En la actualidad las amenazas a las que se enfrentan los grandes felinos neotropicales son más diversas. El cambio climático (Zanin et al. 2021), la pérdida y fragmentación de hábitat (Medellín *et al*. 2002, Paviolo *et al*. 2008, Foster *et al*. 2010a, Bernal-Escobar *et al*. 2015, Medellín *et* *al*. 2016), la cacería comercial (trofeos o tráfico de partes) y la cacería por depredación de ganado (Zimmermann *et al*. 2005, Hoogesteijn & Hoogesteijn 2008) destacan como las amenazas más importantes de las poblaciones de estas especies (Quigley *et al*. 2015).

## Cambio climático

Los cambios climáticos pasados han afectado a las distribuciones de distintas especies de felinos incluyendo a jaguares y pumas generando contracciones en sus rangos de distribución, aislamiento genético y extinciones locales (Arias-Alzate et al. 2017, 2020; Zanin et al. 2020). Debido a que el cambio climático actual es notablemente más rápido que los cambios climáticos pasados (Allen et al. 2018) es muy probable que los felinos neotropicales se vean afectados nuevamente, esta vez de manera más drástica. En el Capítulo 1 de esta tesis encontramos que los paisajes climáticos pasados explican los patrones genéticos actuales de jaguares y pumas. Los dos felinos muestran un patrón de aislamiento genético que se relaciona con el escenario climático del último máximo glacial (LGM) sugiriendo que dichas áreas han actuado como refugios alélicos. Ambas especies se enfrentarán de manera diferente a los escenarios de cambio climático futuro. El jaguar parece ser más vulnerable a los cambios climáticos al mostrar una menor variación genética mientras que el puma parece ser menos vulnerable. A pesar de las diferencias en la magnitud de la respuesta a los cambios climáticos pasados ambas especies son vulnerables al cambio climático, especialmente si - como se prevé - los cambios modernos sean más intensos y rápidos que los pasados.

El jaguar muestra además una relación con el paisaje climático actual, sugiriendo cierto grado de estructuración genética reciente. Sin embargo, el puma no parece haber experimentado cambios genéticos sustanciales entre las regiones de estudio en el pasado reciente. Probablemente este resultado se deba al amplio nicho climático que caracteriza a los pumas, que es el mayor de todos los felinos (Zanin & Neves 2019) y les permite habitar desde los fríos climas montañosos de las Montañas Rocosas hasta los climas semiáridos de la Caatinga brasileña (Zanin et al, 2021). Nuestros resultados apuntan a que los cambios climáticos futuros derivarán en cierto grado de aislamiento genético y pérdida de diversidad en los pumas y en un incremento notable de la ya alarmante situación de los jaguares.

Hay que añadir que los cambios en el uso de suelo son actualmente la más notoria amenaza de los felinos (ver siguiente epígrafe de esta discusión) sin embargo, clima y cambio de uso de suelo no son eventos independientes y mantienen una estrecha relación que va más allá de sus efectos independientes sobre las especies (Jia et al. 2019). Por ejemplo, las pérdidas de producción agrícola debidas a los efectos del cambio climático se compensan a través de la expansión de nuevas tierras agrícolas, reduciendo la vegetación nativa y creando ciclos de retroalimentación positiva que aceleran el cambio climático (Feddema et al. 2005; Jia et al. 2019). Por ello el crítico estado de conservación de los felinos causado por cambios en el uso de suelo probablemente empeore de forma no lineal a causa de la interacción entre cambio climático y pérdida de hábitat (Zanin et al., 2021).

### Pérdida y fragmentación del hábitat

La pérdida y fragmentación del hábitat como consecuencia del cambio de usos del suelo causa severas reducciones en las poblaciones animales del todo el mundo (Ripple et al. 2017). La modificación del hábitat y su consiguiente pérdida desemboca en el denominado síndrome de los "bosques vacíos" (Redford 1992), donde la mermada biodiversidad provoca una pérdida de funciones ecológicas imprescindibles para el equilibrio de un ecosistema (Benítez-Lopez et al. 2021; Magioli et al., 2021). La extirpación (extinción local) de grandes mamíferos ya sean herbívoros o depredadores causa efectos en cascada en el ecosistema (Kurten 2013) afectando al reclutamiento vegetal y favoreciendo explosiones demográficas de roedores y mesocarnívoros (Terbourgh et al. 2001; Estes et al. 2011). Los grandes carnívoros, por sus características intrínsecas, son especialmente susceptibles a la pérdida y fragmentación de hábitat y en concreto los grandes felinos encuentran en la pérdida de hábitat su más notoria amenaza actual (Morrison et al. 2007; IUCN 2015; Zanin et al. 2015). Algunos ejemplos de grandes felinos que han sufrido importantes contracciones de rango son los tigres asiáticos, *Panthera tigris* (Tian et al. 2011 o Sharma et al. 2013), leones africanos

*Panthera leo* (Dolrenry et al. 2014), pumas, *Puma concolor* (Sweanor et al. 2000, Balkenhol et al. 2014) o jaguares, *Panthera onca* (Haag et al. 2010, Zanin et al 2015a).

Una drástica reducción de una población de carnívoro no sólo conduce a la extinción *per se* por la falta de efectivos poblacionales, sino que tiene además implicaciones genéticas que retroalimentan su grado de amenaza. La reducción de la diversidad genética tiene consecuencias sobre el potencial adaptativo de una población (o especie) pudiendo convertirse en un componente trascendental para su viabilidad (Casas-Marce et al. 2017). La fragmentación (pérdida de hábitat parcial) provoca aislamiento entre poblaciones de carnívoros (y/o sus presas) que quedan recluidos en los parches de vegetación nativa restantes impidiendo, en muchos casos, el intercambio genético entre poblaciones y reduciendo por tanto la diversidad genética. En poblaciones mermadas genes ventajosos pueden perderse mientras que genes deletéreos pueden comportarse como neutros (Kimura, 1962), resultando en una acumulación de características genéticas negativas (Charlesworth et al. 1993). En casos extremos como pueden ser los cuellos de botella (en los que ocurre una drástica reducción del tamaño poblacional) la acción de la deriva genética provoca una pérdida de diversidad cuya magnitud se relaciona con su severidad y duración (Garza & Williamson. 2001, Lucena-perez et al. 2021). Por tanto, el descenso poblacional severo producido por la pérdida de hábitat puede ser cíclicamente retroalimentado por la erosión genética característica de poblaciones reducidas o aisladas aumentando consecuentemente su riesgo de extinción y trascendiendo más allá de la diversidad de una especie, conectando con la resiliencia de todo un ecosistema (Allendorf et al. 2013).

Las tasas de deforestación en el Neotrópico son las más elevadas junto con las del África Tropical siendo la agroindustria su motor principal, responsable de un 70% de la deforestación de América Latina (FAO 2020). Las plantaciones de soja, palma y la ganadería despuntan como principales actividades agroindustriales (FAOstat, 2022) cuya principal finalidad es la de abastecer a los países desarrollados de materias primas. Es bien conocido que la expansión de actividades humanas en ecosistemas tropicales representa la principal causa de pérdida de especies y es responsable de reducciones en los niveles de biodiversidad (Gibbs et al., 2010, Newbold et al., 2020), afectando especialmente a los grandes carnívoros. Pero ciertas cuestiones siguen sin resolverse:

¿Hasta qué punto la pérdida de hábitat es el motor principal de la extinción de estas especies? ¿Cuál de las distintas actividades antrópicas afectan más a los grandes carnívoros? Si es así, ¿se pueden medir estas diferencias? En el Capítulo 3 de esta tesis respondemos a estas cuestiones a través de un modelado ecológico a escala continental tomando el jaguar como especie de estudio. Encontramos que la ganadería destaca entre las principales causas del patrón de extinción de la especie, resultando ser el motor principal de su extinción a escala continental. Los efectos de la agricultura y el urbanismo, a pesar de haber sido destacados como factores que limitan el uso del espacio de grandes felinos (Petraca 2014, De Angelo *et al*. 2013), parecen tener un importante efecto a escala regional pero no tanto a escala continental. Estos resultados sugieren que la ganadería extensiva, a pesar de su aparente limitado impacto sobre la pérdida de hábitat (ya que mantiene grandes superficies naturales poco alteradas), tienen un impacto profundo sobre las poblaciones de jaguares. La persecución y cacería de grandes felinos a causa del conflicto ganadero parece ser la explicación más plausible, ya que el conflicto está ampliamente distribuido y se encuentra en todas las regiones en las que la ganadería coexiste con los grandes felinos como veremos más adelante en esta discusión.

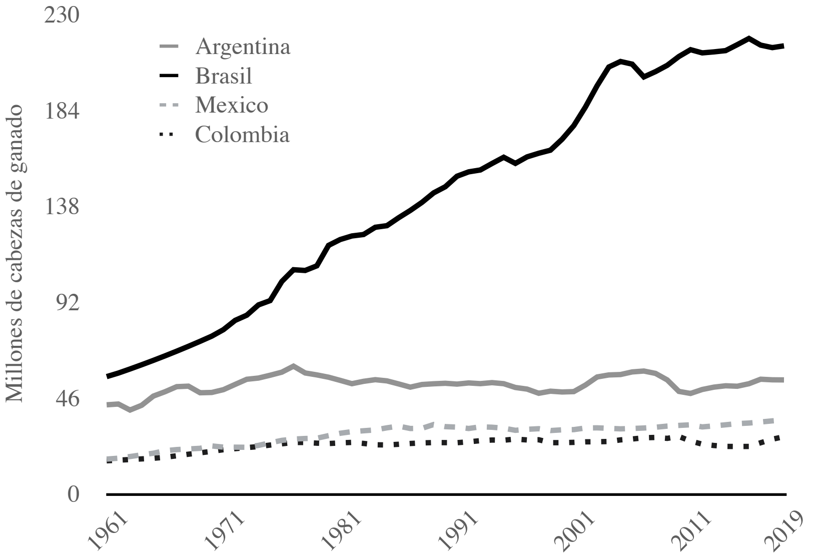
Por otro lado, en el mismo capítulo respondemos a otra pregunta importante para comprender el estado actual de las poblaciones de grandes carnívoros: ¿A qué nivel de amenaza antropogénica se enfrentan sus poblaciones? En este caso nuestros resultados apuntan a que el jaguar ha perdido (o pronto lo hará) el 60 % de su rango de distribución histórica. Esta estima se encuentra en línea con las últimas estimas basadas en opiniones de expertos (Quigley et al. 2017) pero muestran un notable aumento respecto de los estudios de los últimos 20 años (Sanderson et al. 2002; Zeller, 2007; Zeller et al. 2013), apuntando a que la reducción de la especie avanza implacablemente hacia su extinción. Los resultados obtenidos en el modelado son claros, las distintas presiones antrópicas afectan de manera diferente a la especie. Sin embargo, se conoce que diferentes especies de carnívoros, incluso siendo muy similares, toleran de forma diferente las presiones antrópicas, por lo que cabría esperar que las mismas presiones afecten de manera diferente a especies diferentes. Pero ¿afectan las presiones antrópicas también a las relaciones entre los felinos? Si es así ¿cómo lo hacen? En el capítulo 4 respondemos estas preguntas estudiando cómo las relaciones intragremiales entre felinos se ven afectadas por las presiones antrópicas. En un contexto natural los jaguares son la especie dominante pero menos tolerante a las presiones humanas, mientras que los pumas son la especie subordinada, pero más tolerante a esas mismas presiones (Palomares et al. 2016). Encontramos que las relaciones intragremiales de estos grandes carnívoros se ven moduladas por las perturbaciones humanas y que su efecto asimétrico modifica la estructura de la comunidad de carnívoros a escala continental. También observamos que el impacto de la ganadería es mayor sobre jaguares que sobre pumas, por lo que los primeros parecen ser más sensibles a esta perturbación humana. Estos resultados sugieren que los jaguares se ven sistemáticamente desfavorecidos frente a los pumas en los sistemas humanizados y que esto puede tener efectos en cadena sobre toda la comunidad de carnívoros y por tanto sobre todo el ecosistema a una escala continental.

### Ganadería: extinción o conservación

Como hemos comentado brevemente en el epígrafe anterior la ganadería extensiva mantiene grandes superficies de hábitat relativamente inalteradas. La densidad de población humana en estos sistemas es muy baja y los grandes depredadores pueden encontrar espacio suficiente para habitar. La ganadería extensiva ha demostrado ser un potencial aliado para la conservación de los grandes felinos -así como para los ecosistemas en que habitan- generalmente a través de combinar una explotación ganadera respetuosa con la naturaleza y el ecoturismo (Hoogesteijn *et al*. 2015, Tortato and Izzo 2017, Nassar *et al*. 2013). Si bien es cierto que existen excepciones a la regla como las recién citadas, en esta tesis evidenciamos el penetrante efecto que la industria ganadera ejerce sobre los grandes carnívoros a escala continental. Esta conclusión no es excepcional, encontrando el crónico conflicto de la ganadería extendido por el neotrópico, sin duda con serias implicaciones sobre la dinámica poblacional de los felinos (Loveridge *et al*. 2010). La extensa bibliografía del conflicto ganadero (ver apartado "*Percepción: conflicto o coexistencia*") corrobora esta visión para la gran mayoría de países neotropicales.

La ganadería no sólo afecta a nivel de especie, como hemos comprobado con el caso del jaguar, sino que también tiene implicaciones desde el punto de vista de la comunidad de carnívoros. Como hemos resaltado en el apartado anterior la coexistencia entre felinos en sistemas humanizados no depende tanto de sus relaciones naturales de dominancia sino más bien de las presiones externas a las que se ven sometidas. Es por ello que la ganadería extensiva, ampliamente distribuida por el Neotrópico, tiene un efecto sumidero para jaguares y un efecto facilitador para los pumas suponiendo una desestructuración del gremio de carnívoros. La facilitación de los pumas reduce la competencia intragremial con los jaguares, favoreciendo su coexistencia, efecto que ya se ha encontrado en múltiples especies de carnívoros (Seveque *et al*. 2020). Cuando el depredador top es degradado a una posición relegada en la cadena trófica, resulta difícil su ubicación ecológica (Orilo-Cotterilli *et al*. 2015), por lo que las consecuencias sobre la reducción de su población son evidentes. La facilitación de los pumas en los sistemas ganaderos también afecta a los ocelotes, incrementando la competencia intragremial, evidenciando potenciales efectos en cascada con consecuencias sobre el ecosistema completo (Terborgh & Winter 1980, Soulé *et al*. 1988).

Los grandes felinos están protegidos por ley en la mayor parte de los países, pero muy pocos de éstos aplican la ley de manera efectiva para reducir el impacto en los ecosistemas. Nuestros resultados manifiestan la escasa capacidad o interés por manejar el efecto de la ganadería sobre los ecosistemas a una escala supranacional. Se impone una vez más la economía a la salud ambiental. Este problema generalizado en los países neotropicales tiene su caso más extremo en Brasil, donde la cabaña ganadera se ha cuadruplicado desde 1960. La agresiva política agropecuaria engendrada con evidentes objetivos macroeconómicos fue reconducida a través de objetivos sociales (Guanziroli, 2014) haciendo de Brasil la mayor cabaña ganadera del mundo. Existen en Brasil 214 Millones de cabezas de ganado bovino, mientras que habitan 211 millones de personas (FAOstat, 2019); este hecho unido a que Brasil alberga más de la mitad de la población de jaguares (Jedrezewski *et al*. 2018) apunta a que la política agropecuaria brasileña serán el principal motor para la conservación (o no) de las comunidades de carnívoros del Neotrópico.



Histórico de los mayores productores de ganado bovino del neotrópico.
Fuente: *Faostat, 2022*

**Percepción: conflicto o coexistencia**

Existen razones científicas de peso para pensar que el conflicto con la fauna salvaje debería ser cada vez menos frecuente ya que la fauna peligrosa se restringe cada vez más a áreas más pequeñas y se reemplaza por animales de menor tamaño que son menos peligrosas (Naughton-Treves 1999, Ripple *et al*. 2014, 2016, 2017). Además, la tecnología permite al ser humano ser más eficiente en la búsqueda y caza de fauna. Por ello se ha postulado recientemente que el conflicto con la fauna salvaje es cada vez menor por la ausencia de grandes depredadores (Treves & Santiago-Avila 2020). Esta teoría parece acertada cuando es aplicada a regiones donde los grandes carnívoros han sido reducidos a niveles casi anecdóticos o a zonas muy despobladas. Así ocurre en muchos países europeos donde incluso existen ambiciosos planes de reintroducción (Samojlik *et al*. 2018, Sarmento *et al*. 2017). Sin embargo, éste no parece ser el caso de los países neotropicales (*sensu* Sclater 1858), donde aún se comparte gran parte del espacio con los grandes felinos y el conflicto se encuentra generalizado. Parece claro que la intensidad (tanto en frecuencia como en severidad) de los conflictos es creciente y seguirá aumentando en relación a la necesidad de compartir espacios cada vez más abarrotados (Abrahams 2020). En este contexto cabe señalar que, como vimos en el Capítulo 3, la extinción aparece ligada al histórico conflicto ganadero a escala global. La compilación bibliográfica en relación a los conflictos con grandes felinos (revisión en Castaño Uribe *et al.* 2016 o Medellin *et al.* 2017) sugiere que el conflicto se encuentra generalizado por todo el Neotrópico no estando tan solo restringido a reductos donde se hallan desplazados los depredadores, sino más bien expandiéndose por grandes extensiones de territorio. Por otro lado, encontramos que las presiones humanas y entre ellas la ganadería, motor del conflicto, modifican la estructura de la comunidad de carnívoros. El reemplazo de jaguares por pumas en sistemas ganaderos puede suponer un incremento del conflicto debido a una mayor tolerancia del último al hombre, que le permite estar más cerca y desenvolverse mejor en estos ambientes.

A escala local, en el Capítulo 5, encontramos el conflicto generalizado en dos grandes ecoregiones: el Pantanal y la Chiquitanía. La pérdida media de ganado bovino por ataques de felinos en estas regiones (1.8 %) se encuentran dentro del rango de depredación de ganado por otros grandes carnívoros - inferior al 3 % - (Jackson & Nowell 1996). No obstante, el conflicto tiene un profundo arraigo en la cultura de la región. Es común que los vaqueros persigan a los felinos cuando encuentran una mínima evidencia de paso, incluso sin haber sufrido ataques a ganado propio. Hemos observado que, en general, los rancheros basan sus percepciones y actitudes en las experiencias sociales más que en las suyas propias. En ocasiones la experiencia social se erige en base a los casos más extremos de su entorno, tomando como ideario los casos más graves de depredación puntual, como puede ser un ataque a un potrero desatendido utilizado por una madre felina enseñando a cazar a sus crías. Los factores sociales pueden desempeñar un papel extremadamente importante en los conflictos, aunque raramente se consideran en los estudios científicos (Dickman 2010). Un ejemplo sencillo y conocido es la mitología relacionada con el vampirismo que se relaciona con actitudes negativas hacia los murciélagos (Prokop *et al.* 2009). De manera similar la gran mayoría de los rancheros no toleran la presencia de felinos en sus tierras (Capítulo 5 y datos sin publicar) no por haber sufrido gran cantidad de ataques, sino más bien motivados por información de terceros que aseguraron tener una gran cantidad de pérdidas en algún momento. En este contexto, he podido detectar cómo las ferias de ganado del oeste boliviano, donde acuden los ganaderos de toda una región, sirven de punto clave para diseminar historias que, alentadas por el furor de la fiesta, pronto se convierten en mitos regionales que llegan a los parajes ganaderos más recónditos. La falta de capacidad de muchos rancheros para discriminar entre huellas de felinos o carcasas consumidas por distintos felinos - Capítulo 5 - magnifican potencialmente tanto la presencia de felinos como las pérdidas de ganado. Por ello se atribuyen pérdidas de ganado por otros motivos y se magnifican las depredaciones de jaguar frente a las de puma por ser el primero el más conocido por los rancheros menos profesionales. La mayor parte de los rancheros respondieron a los ataques de felinos con la persecución y cacería, comportamiento que muy probablemente esté generalizado en el neotrópico y sea clave para explicar porqué la ganadería funciona como el principal motor de extinción de estas especies.

## Detalle de la historia natural y comportamiento depredatorio

Los jaguares y pumas comparten rasgos históricos y comportamentales (Sunquist & Sunquist, 2002) que, junto a su gran tamaño desencadena el conflicto ganadero (Inskip & Zimmermann, 2009). Aunque las dos especies son esquivas y evitan al hombre, encontramos en su comportamiento depredatorio diferencias que podrían ser el detonante del efecto asimétrico que la ganadería ejerce sobre estas especies. En los sucesos de depredación de ganado es común que, una vez depredada la presa, el jaguar ronde su carcasa durante días incluso sin perderla de vista (es común encontrarlo encaramado a un árbol para controlar su alrededor). El puma, sin embargo, suele arrastrarla hacia un lugar protegido abandonando el lugar de la caza tras alimentarse. Los pumas depredan sobre presas más pequeñas que pueden desplazar con mayor facilidad y es común que las escondan bajo hojarasca o tierra para evitar llamar la atención de carroñeros y oportunistas. Además presas de menor tamaño pueden ser consumidas en menos tiempo. Los jaguares, en cambio, suelen cazar presas más grandes que no esconden ni tapan (aunque sí suelen intentar subirla a un árbol) por lo que son fácilmente localizadas por carroñeros y oportunistas obligando al jaguar a merodear por la zona durante varios días para proteger su alimento.

Los vaqueros detectan los eventos de depredación observando la columna de buitres que suelen sobrevolar más temprano que tarde una carcasa. Cuando se visita el lugar de la depredación si el depredador fue un puma es muy probable que éste haya abandonado el lugar. Sin embargo, si el depredador fue un jaguar es posible encontrarlo encaramado al árbol más cercano o merodeando por la zona con el estómago lleno, donde será fácilmente cazado por los vaqueros. Ya Darwin en *Los viajes del Beagle* (1845) comentaba: "*Es decepcionantemente fácil localizar a un jaguar*" y - añado- especialmente si ha depredado ganado. En cambio, el puma es más difícil de localizar y sólo se encontrará fortuitamente o persiguiéndolo de forma dirigida. Esta diferencia comportamental hace que el jaguar sea más vulnerable que el puma frente a los ganaderos.

### El tráfico de especies

Los decomisos de partes de felino con destino a países asiáticos han sido encontrados en su mayoría en Bolivia y Surinam (Bale 2017, Bale 2018) sin embargo, es muy probable que este negocio esté operando en otros países neotropicales y pase inadvertido por su naturaleza ilícita. Parece obvio que los casos encontrados sean tan sólo la punta del iceberg de un problema de mayor envergadura con implicaciones internacionales. La potencial implicación de redes del crimen organizado con conexión directa con el lavado de dinero y el tráfico de drogas, armas u otros productos hace que el potencial crecimiento de este negocio sea desconocido. Además, el elevado valor que alcanzan los derivados de felino en el mercado ilegal puede incentivar su caza. El abastecimiento del mercado asiático podría tener consecuencias importantes para la conservación de las poblaciones de felinos salvajes sin embargo, el número de decomisos de partes de felino con este fin parece irrisorio en relación con el número de felinos cazados en las estancias ganaderas (Morcatty *et al*. 2020, Villalva & Palomares 2019) por lo que su amenaza parece ser relativa. Sin embargo, si este negocio ilícito se concentra en regiones concretas o incentiva la cacería por cazadores y ganaderos, esto puede suponer un incremento en la presión de cacería con importantes repercusiones en las poblaciones locales de felinos.

Los actores del tráfico de felinos pueden ser, en Bolivia, más diversos de lo que sugieren los decomisos y además del tráfico internacional existe un tráfico nacional de partes de felino que es común en el país andino (Arias *et al*. 2021). Con facilidad se encuentran enseres derivados de felinos (especialmente pieles) en casas de cualquier estrato social, desde las casas más humildes de una comunidad rural a las casas más pudientes en las grandes ciudades (observación personal). Otro foco de tráfico ilegal de felinos es el turismo; artesanos que viajan en una ruta circular anual por varios países neotropicales (principalmente Ecuador, Perú, Bolivia, Brasil) venden a los turistas baratijas elaboradas con *productos naturales*, entre los cuales es común encontrar productos procedentes de felinos salvajes. Estos artesanos durante su viaje anual cruzan áreas naturales donde adquieren estos productos que transportan a otros países convirtiéndose, generalmente sin saberlo, en traficantes de fauna internacionales. El impacto del turismo urbano sobre los felinos no ha sido cuantificado, pero podría suponer un impacto incluso mayor que el tráfico para el mercado asiático. Parece existir un arraigo profundo hacia este tipo de productos en la sociedad boliviana y un íntimo vínculo con el conflicto ganadero.

## Áreas protegidas y conservación

La eficacia de las áreas protegidas ha sido reiteradamente cuestionada y sus beneficios no siempre son claros o suficientes para la protección de la biodiversidad (Adam et al., 2008). Sin embargo ésta sigue siendo la estrategia de conservación principal adoptada por la mayoría de las administraciones y estados. De hecho, durante la pasada década (2010 - 2020), se ha incrementado un 42 % la superficie protegida del planeta afectando a un 16.6 % de la superficie terrestre (UNEP WCMC 2021). Sin embargo, esta estrategia de conservación no protege de forma efectiva a las especies que viven en bajas densidades y/o tienen amplias áreas de campeo como son los grandes carnívoros; por ello la mortalidad de grandes carnívoros suele ser mayor por causas antrópicas que por procesos estocásticos incluso dentro de Areas Protegidas (Woodrooffe & Gingsberg, 1998), probablemente debido a la intensa presión humana a su alrededor (Jones *et al*. 2018). Nuestros resultados apoyan esta hipótesis. Por un lado, cabe señalar que la mayor parte de la distribución de grandes felinos neotropicales corresponde a tierras privadas donde el grado de protección depende sólo de las posibilidades o intereses del propietario. Los resultados del Capítulo 3 muestran que parte de las *Unidades de Conservación del Jaguar* se encuentran amenazadas por las presiones antrópicas que las circundan incluso habiendo penetrado ya profundamente en algunas de ellas. Este es el caso del Pantanal o de las ya (casi) extirpadas poblaciones del norte de México y la Mata Atlántica Brasileña a pesar de contar con Áreas Protegidas de tamaño notable (Material suplementario 2. Capítulo 3). También el modelo de ecuaciones estructurales del Capítulo 4 muestra que el grado de protección no afecta de manera significativa ni a la presencia de grandes felinos ni a sus relaciones intragremiales. A la escala continental de nuestra aproximación no encontramos indicio alguno de la efectividad de las áreas protegidas para los grandes felinos, por lo que consideramos que éstas no son suficientes para proteger de manera efectiva a los grandes felinos. Por ello parece lógico sugerir que un escenario más realista para la conservación de grandes carnívoros debería tener en cuenta los paisajes humanizados (Athreya *et al*. 2013; Chapron *et al*. 2014), en su mayoría propiedad privada, que además aseguren la conexión de las extensas áreas necesarias para su supervivencia a largo plazo (Rabinowitz and Zeller 2010; Sanderson *et al*. 2002).

### Políticas ambientales

Existe un alineamiento de los países neotropicales para mejorar las leyes de protección medioambiental y su aplicación incluso mostrando un especial interés por aliviar los conflictos de la coexistencia con la fauna salvaje y el tráfico internacional de especies (por ejemplo, la Declaración de Lima 2019). A pesar de las intenciones firmadas, es necesario un liderazgo nacional (y en muchos casos regional) para conseguir resultados reales. Es vital incorporar los valores socio-culturales, ecológicos y legales de cada región sin olvidar que el diseño de las estrategias debe permitir la evaluación de sus efectos (Van Evaden *et al*. 2018 a). Es inexorable la reconciliación, al más alto nivel, de las políticas ambientales y las agropecuarias, urgiendo especialmente en el caso de los felinos la implementación de políticas pecuarias en las que se ponga en valor el servicio ecosistémico de los depredadores. Para conseguirlo sería necesario contar con un plan educativo que permita sustituir la información infundada sobre el conflicto ganadero por información fidedigna, basada en hechos. Esto podría ayudar a reducir el conflicto a través de cambios en la percepción local. Para que las políticas conciliatorias mencionadas fuesen efectivas, deben incorporar la realidad social de cada región por lo que es necesario reiterar la necesidad de un liderazgo regional.

Por último, cabe enfatizar la necesidad de un serio replanteamiento de las actuales políticas, leyes y prácticas en materia de conservación, donde se mantiene el histórico enfoque de protección de la fauna enfocado (o mejor dicho restringido) a las áreas protegidas. Las políticas en materia de conservación no deberían repetir compulsivamente los enfoques históricos sino basarse en las evidencias actualizadas (Van Eaden *et al.* 2018 b) que ya han probado ser claves para la reducción de los conflictos del ser humano con la fauna (Melzehimer *et al.* 2020). Sugiero por tanto el uso de una aproximación interdisciplinar, con un foco especial en la dimensión social, que ha demostrado su efectividad a escala continental mediante la aprobación de leyes de protección en sinergia con estrategias de apoyo a la opinión pública (Chapron *et al.* 2014).

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# CONCLUSIONES

## *Capítulo 2.* ***El cambio climático amenaza a jaguares y pumas.***

*1.* Jaguares y pumas exhiben patrones de aislamiento genético correlacionados por el último máximo glacial, sugiriendo que estas áreas actuaron como refugios alélicos.

*2.* Los jaguares son más vulnerables a los cambios climáticos que los pumas.

## *Capitulo 3.* ***La ganadería es la mayor causa de extinción actual de los jaguares.***

*3.* La ganadería extensiva se revela como la mayor amenaza antrópica de los jaguares, sugiriendo que la persecución y caza de estos felinos está generalizada a escala global.

*4.* En la actualidad el rango histórico de los jaguares se ve potencialmente reducido un 60 %, suponiendo una notable contracción respecto a la década anterior.

## *Capitulo 4.* ***La estructura de la comunidad de carnívoros se desestabilizan con las perturbaciones humanas.***

*5.* Las perturbaciones humanas modulan las relaciones de dominancia de los grandes carnívoros. Los felinos neotropicales manifiestan un efecto asimétrico a dichas perturbaciones a escala continental.

*6.* Los pumas son menos sensibles a las perturbaciones que los jaguares, que se ven sistemáticamente desfavorecidos en sistemas humanizados. Los ocelotes se ven afectados indirectamente por su especial competencia con los pumas.

*7.* Es inexorable la conciliación entre políticas pecuarias y ambientales para que la industria humana sea viable con la vida salvaje. Ambas nos sustentan a corto y largo plazo respectivamente.

## *Capitulo 5.* ***La ganadería extensiva amenaza la conservación de los grandes felinos en el Este boliviano.***

*8.* La actitud de los ganaderos hacia los grandes felinos se basan en información no contrastada y poco fiable, creando una percepción irreal del conflicto.

***9.*** Es urgente la implementación de políticas pecuarias en las que se ponga en valor el papel de los depredadores en el ecosistemas así como un plan educativo que permita sustituir la información infundada sobre el conflicto por información fidedigna (basada en hechos).

***10.*** Es necesario incorporar la realidad social de cada región para que las políticas conciliatorias mencionadas arriba sean efectivas.

### ***Capitulo 6. La medicina tradicional asiática supone una nueva amenaza a las poblaciones de felinos neotropicales***

***11.*** La demanda de productos derivados del tigre, usados en medicina tradicional asiática, supone una amenaza a las poblaciones de grandes felinos de todo el mundo, incluyendo a los felinos neotropicales que habitan a miles de kilómetros.

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