Patrones geográficos de distribución y abundancia de presas de los grandes carnívoros del Neotrópico

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PATRONES GEOGRÁFICOS DE DISTRIBUCIÓN Y ABUNDANCIA DE PRESAS DE LOS GRANDES CARNÍVOROS DEL NEOTRÓPICO

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TESIS DOCTORAL

Patrones geográficos de distribución y abundancia de presas de los grandes carnívoros del Neotrópico

Tesis Doctoral

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Palabras clave: *predicción de abundancia, presas de jaguares y pumas, identificación del depredador, Neotropical, modelado de nicho ecológico, distancia al centroide del nicho ecológico, influencia humana, Cuniculus paca, Myrmecophaga tridactyla, Pecari tajacu, Tayassu pecari*

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Quiero dedicar el tremendo esfuerzo de estos años a mi amado Héctor Zambrano y a nuestra pequeña hija Emilia

A mis primeras niñas, Ana Sofía y Natalia

A mi familia

Ustedes le dan sentido a mi existencia…

El único modo de superar una prueba es realizarla. Es inevitable.

El anciano Cisne Negro Real

Tabla de contenidos

Resumen

El objetivo general de esta tesis doctoral consistió en generar modelos espaciales de predicción de abundancia de presas de jaguares y pumas a escala biogeográfica. Dichos modelos se centraron en el Neotrópico por ser la región de mayor solapamiento en la distribución de estos carnívoros. Para alcanzar este objetivo general, en primer lugar identificamos a las principales especies presa de jaguares y pumas consumidas en la región Neotropical mediante una revisión bibliográfica. Pero con la finalidad de basarnos en información fiable, también evaluamos si el método tradicional de identificación del depredador a través de la apariencia de las excretas (el cual es propenso a errores de identificación) generaba un sesgo en la información disponible sobre la dieta de estos felinos. Como resultado de éste análisis encontramos que el método usado para identificar al depredador tuvo un efecto sobre la información disponible, por lo que decidimos basarnos únicamente en los estudios que usaron métodos altamente fiables de identificación. Así, elegimos cuatro especies de presa sobre las cuales generamos los modelos espaciales de predicción de abundancia: el pecarí de collar, el pecarí de labios blancos, el oso hormiguero gigante y la paca común.

Primeramente, usamos al pecarí de collar como especie modelo para probar si la posición de las poblaciones de la especie con respecto al centroide de su nicho ecológico describía las abundancias mejor que su posición en relación al centroide geográfico de su distribución. También evaluamos la forma de la relación entre la abundancia y la distancia al centroide del nicho (DCN), probando si ésta definía la abundancia máxima esperada en cada sitio mejor que la abundancia media, debido al efecto de factores limitantes no medidos. Además, evaluamos si la inclusión de la influencia humana (IH) al modelo ayudaba a explicar mejor la variación geográfica de la abundancia poblacional que la DCN por sí sola. Por último, seleccionamos el mejor modelo para generar un modelo

espacial de predicción de abundancia a lo largo de toda su área de distribución. Los resultados de estos análisis mostraron que la abundancia del pecarí de collar se relacionó negativamente con la DCN y con la IH, la cual contribuyó a explicar la variación no predicha por la DCN. En contraparte, no encontramos una relación significativa entre la abundancia y la distancia al centroide geográfico. Las relaciones analizadas presentaron una forma de cuña, en la que la abundancia máxima de pecarí de collar dependió de la DCN, mientras que la abundancia mediana dependió de la DCN más el nivel de IH.

Posteriormente, evaluamos la importancia de la IH no solamente para determinar los patrones de abundancia a gran escala, sino también como predictor de la distribución de las tres especies de presa restantes: el pecarí de labios blancos, el oso hormiguero gigante y la paca común. Específicamente, evaluamos si al añadir la IH al conjunto de variables ambientales mejoraban las predicciones de los modelos de nicho. Además, analizamos la relación entre la DCN y la IH con las abundancias poblacionales de las distintas especies, y evaluamos cuál era el mejor modelo para cada especie, si el que incluía ambos factores, o el que incluía solamente alguno de ellos. Finalmente, usamos el mejor modelo para generar la predicción espacial de abundancia de cada especie. Nuestros resultados mostraron que la adición de la IH al conjunto de variables ambientales contribuyó a mejorar el desempeño de los modelos de nicho, excepto para el oso hormiguero gigante. Sin embargo, su importancia relativa en la construcción del modelo fue alta solamente para la paca común. Por otro lado, encontramos una relación negativa entre la abundancia y la DCN (excepto para la paca común) y entre la abundancia y la IH (excepto para el oso hormiguero gigante). Dichas relaciones presentaron una forma de cuña en el caso del pecarí de labios blancos, cuya abundancia mediana respondió a la DCN, y la máxima respondió a la DCN más el nivel de IH.

En conclusión, las abundancias poblacionales de la mayoría de las especies estudiadas disminuyeron al alejarse del centroide de su nicho ecológico, donde las condiciones son las más favorables. La excepción encontrada a este patrón pudo deberse a que la especie se ve muy influenciada por factores locales no incluidos a escala espacial gruesa. También concluimos que más allá de las variables ambientales, la IH fue un factor muy relevante a considerar en los modelos de abundancia, ya que en la mayoría de las especies estudiadas ésta disminuyó al aumentar el nivel de IH. La excepción encontrada a este patrón pudo deberse al grado de tolerancia de la especie a la presión humana. Además, hay que tener en cuenta que en algunos casos la relación abundancia-DCN, así como la relación abundancia-IH pueden tener una forma de cuña, presentando tanto altas como bajas abundancias cerca de las condiciones óptimas y sólo bajas lejos de éstas. Este tipo de relaciones las pendientes varían según el cuantil de abundancia analizado. Las dos excepciones encontradas pudieron deberse a un bajo tamaño de muestra. Cuando la relación tuvo forma de cuña, el mejor modelo dependió del cuantil analizado y de la tolerancia de la especie a la presión humana. Finalmente, encontramos que las áreas en las que se espera una mayor abundancia de presas coinciden con zonas en las que se ha reportado una alta densidad de jaguares y pumas, así como una alta probabilidad de persistencia de jaguares a largo plazo. Dichas áreas se localizan principalmente en la subregión Amazónica de la región Neotropical, y en su mayoría corresponden a la ecorregión de los bosques húmedos del suroeste Amazónico.

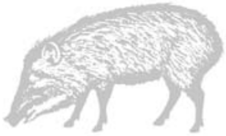
Abstract

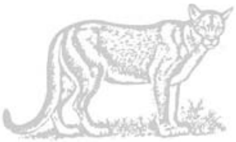
The general objective of this PhD thesis was to generate spatial models of abundance predictions of prey of jaguars and cougars at biogeographic extents. These models focused on the Neotropical region where cougars and jaguars largely overlap. To achieve this objective, first, we identified the main prey for both species in the Neotropical region through a literature review. We also assessed if the traditional method of predator identification in the field through faeces appearance (which is prone to misidentification) would bias the information available about the diet of these felids. As a result of this analysis, we found that the method employed for predator identification had an effect on the results available about diet. Therefore, we only used studies based on high-confidence identification methods. We selected four prey species to generate the spatial models of abundance predictions: the collared peccary, the white-lipped peccary, the giant anteater, and the spotted paca.

First, we used the collared peccary as a model species, to evaluate whether the geographic variation in the population abundance was related to the location with respect to the centroid of its ecological niche or to the centroid of its geographic range. Moreover, we assessed the shape of the abundance-niche centrality relationship, testing whether the distance to the niche centroid (DNC) defined the maximum expected abundance better than the mean abundance, due to the effect of unmeasured limiting factors. Furthermore, we tested whether including human influence (HI) improved the relationship between abundance and DNC. Finally, we created a spatial model of abundance predictions using the best model. Our results showed that the abundance of collared peccary was negatively related to DNC and HI, which partially explained the variation not predicted by DNC. On the other hand, we did not find a significant relation between the abundance of collared peccary and the distance to the geographic centroid. The relationships analyzed were wedge-shaped; maximum abundance of collared peccary was related to the DNC, while the median abundance was related to the DNC plus the level of HI.

Secondly, we assessed the importance of HI not only in determining the large-scale patterns of abundance, but also in determining the distribution of the other three prey species: the white-lipped peccary, the giant anteater, and the spotted paca. Specifically, we evaluated whether the addition of HI to the set of environmental variables improved the predictions of the niche models. In addition, we analyzed the relationships between abundance and DNC, abundance and HI, and abundance and both factors together. We used the best abundance model obtained for each species to generate spatial predictive maps of the population abundance. Our results showed that niche-model predictions improved with the inclusion of HI, except for the giant anteater. However, its relative importance was high only for the spotted paca. The relationships between abundance and DNC and between abundance and HI were negative, except for the spotted paca, and the giant anteater, respectively. Such relationships were wedge-shaped for the white-lipped peccary, thus the median abundance responded to DNC, while the maximum abundance responded to DNC plus the level of HI.

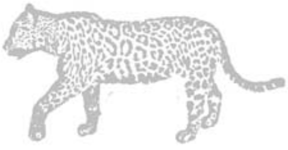
We concluded that the population abundance of most of the species studied decreased as the DNC increased, since the niche centroid harbors the most favorable conditions for the species. The exception found to this pattern might be related to a greater influence of local factors not included on broader scales. Moreover, we concluded that beyond the environmental variables, the HI was a very important factor to consider in abundance models, because in most of the species studied abundance decreased as HI increased. The exception found to this pattern might be related to the degree of tolerance to human pressures. Furthermore, it should be considered that in some cases the abundance-DNC, and the abundance-HI relationships can be wedge-shaped, in which both low and high abundances would be found towards the most favorable conditions, whereas the less favorable would be characterized only by low abundances. In wedge-shaped relationships slopes differ according to the abundance quantile analyzed. The two exceptions found to this pattern might be due to a small sample size. When the relationship was wedge-shaped, the best model depended on the quantile analyzed, and on the degree of tolerance to human pressures. Finally, we found that high predicted prey-abundance areas coincided with areas of high density of jaguars and cougars, as well as with areas of high probability for long-term jaguar persistence. They are located mainly in the Amazonian subregion of the Neotropical region, and mostly correspond to the southwest Amazon moist forest ecoregion.





CAPÍTULO 1

Introducción General



Los jaguares (*Panthera onca*) y los pumas (*Puma concolor*) son los felinos más grandes del continente americano y se les considera especies prioritarias en la conservación a nivel internacional (Caso *et al.* 2008, Nielsen *et al.* 2015). Al ser depredadores tope, el impacto que tienen sobre sus presas puede generar efectos de cascada a través de la cadena alimenticia, resultantes de la fuerte interacción entre los consumidores y su alimento (Paine 1980, Ripple *et al.* 2014). Por otra parte, estos carnívoros tienen también un fuerte impacto social, ya que por un lado amenazan la propiedad humana al consumir su ganado (o al ser acusados de consumirlo) (Crawshaw 2004, Michalski *et al.* 2006, Soto-Shoender y Giuliano 2011), y por otro, generan un atractivo emocional en ciertos sectores de la población. Esta contraposición de percepciones e intereses hace que su conservación sea una tarea compleja.

Ambas especies se consideran depredadores oportunistas, generalistas de hábitat y de presas (De Azevedo 2008, De Angelo et al. 2011), para los cuales la abundancia y distribución del alimento son los factores más importantes que condicionan su ocurrencia, estructura social, tamaño de su área de actividad, y grado de traslape de nicho y competencia (Gittleman y Harvey 1982, Sunquist y Sunquist 1989, Laundré et al. 2007). Se ha postulado que en estas especies la calidad del hábitat está más relacionada con la abundancia de presas que con la estructura de la vegetación *per se*, siendo la cantidad y la calidad de presas aspectos clave a considerar para la caracterización de sus hábitats (Sunquist y Sunquist 1989). Por este motivo, conocer la variabilidad geográfica de la abundancia de presas podría ser una herramienta de gran utilidad en la gestión y conservación de los grandes felinos americanos. Para ello, primeramente es necesario identificar cuáles son las presas principales de dichas especies, y desarrollar a continuación modelos que permitan predecir la heterogeneidad espacial en la distribución y abundancia de éstas. Además, es importante que dichos modelos incluyan la influencia humana, ya que si bien sus efectos sobre la abundancia de las especies son ampliamente conocidos y considerados en muchos estudios locales (e.g. Peres y Nascimento 2006, Urquiza-Haas *et al*. 2011, Flesher y Laufer 2013, Suarez *et al*. 2013), los efectos de la influencia humana son a menudo ignorados en estudios biogeográficos. Ello es probablemente debido a la dificultad de abordar la caracterización de las relaciones entre las especies y la influencia humana en grandes gradientes geográficos.

Identificación de las principales presas de jaguares y pumas

Los jaguares y los pumas tienen distribuciones muy amplias y pueden encontrarse en una gran variedad de hábitats, especialmente el puma (Seymour 1989, Sunquist y Sunquist 2002), el cual se distribuye prácticamente en todo el continente americano, por lo que es de esperar que su alimentación sea diversa y varíe espacialmente. La literatura sobre los hábitos alimenticios de estas especies a lo largo de sus rangos de distribución es medianamente abundante (e.g. Nuñez *et al.* 2000, Scognamillo *et al.* 2003, Rosas-Rosas *et al.* 2008, Oliveira *et al.* 2010, Zanon-Martínez *et al.* 2012). Sin embargo, la gran mayoría de los estudios se basan en análisis de excretas, las cuales a menudo son identificadas mediante métodos relativamente subjetivos y propensos a errores de identificación, tales como exámenes morfológicos, de localización, y eventualmente de los rastros que pudieran estar asociados a éstas, a partir de los cuales se infiere la especie que origina dichas excretas (Fernández *et al.* 1997, Farrel *et al.* 2000). Estos métodos de identificación en campo han demostrado ser menos fiables que otros de laboratorio basados en análisis de ácidos biliares (Taber *et al.* 1997, Ray y Sunquist 2001, Mukherjee *et al.* 2004) o en análisis genéticos (Posluszny *et al.* 2007, McVey *et al.* 2013, Sollman *et al.* 2013). Los errores de identificación son, de hecho, un problema de gran impacto que no solamente se limita a jaguares y pumas, sino que se presenta en todos los carnívoros en general para los cuales la identificación de sus excretas se ha basado tradicionalmente en exámenes visuales y no de laboratorio (Fedriani y Fuller 2000, Cunningham *et al.* 2006, Bustamante-Ho 2008).

Hipótesis sobre la heterogeneidad espacial en las abundancias

En cuanto la predicción de las abundancias poblacionales de presas, es bien sabido que la abundancia de las especies varía geográficamente a lo largo de sus áreas de distribución como resultado de las interacciones con los distintos ambientes a los que están expuestas, incluyendo diferentes factores bióticos y abióticos. Brown (1984) y Brown *et al.* (1995) mostraron tres propiedades relacionadas con la distribución desigual de la abundancia. Primero, que la mayoría de los sitios ocupados presentan relativamente pocos individuos, mientras que pocos sitios pueden mantener poblaciones grandes, lo que podría deberse a que en los últimos se cubren en mayor medida los requerimientos del nicho de la especie. Segundo, que existe una autocorrelación espacial de la abundancia poblacional, de forma que sitios cercanos tienden a tener abundancias similares. Tercero, que la abundancia sigue un patrón espacial de centralidad, que en lo sucesivo llamaremos la “hipótesis de la centralidad geográfica”: los sitios con mayores abundancias se encontrarían hacia el centroide del rango geográfico donde se distribuye la especie, mientras que en la periferia de la distribución geográfica la abundancia sería menor. Esta idea ha sido frecuentemente asumida en estudios ecológicos (e.g. Lawton 1993, Lesica y Allendorf 1995, Channell y Lomolino 2000), si bien la universalidad de la relación entre el centroide geográfico y la abundancia se ha puesto a prueba en un meta-análisis en el que se encontró que sólo en el 39% de 145 casos estudiados se cumplían los patrones predichos (Sagarin y Gaines 2002).

Como alternativa a la hipótesis de la centralidad geográfica, se ha propuesto que los patrones geográficos de la abundancia son principalmente el reflejo de la estructura interna del nicho ecológico de la especie (Martínez-Meyer *et al*. 2013). Por tanto, las abundancias poblacionales locales estarían determinadas por su posición en el espacio multivariado del nicho ecológico en lugar de por su posición geométrica, por lo que se esperarían altas abundancias cerca del centroide del nicho, definido por las condiciones ambientales. En lo sucesivo nos referiremos a ésta como la “hipótesis de la centralidad del nicho”.

La hipótesis de la centralidad del nicho toma sus bases de los conceptos planteados por Hutchinson y Maguire. Hutchinson (1957) definió el nicho ecológico como un hipervolúmen n-dimensional, en el que cada punto corresponde a un estado del ambiente que permitiría que la especie existiera indefinidamente. Posteriormente, Maguire (1973) propuso que ese hipervolúmen tiene una estructura interna en la cual las condiciones óptimas (i.e. donde la tasa intrínseca de crecimiento poblacional es más alta) están hacia el centroide del nicho ecológico y van decreciendo progresivamente hacía los bordes.

Existen algunos estudios empíricos previos que han evaluado la hipótesis de la relación abundancia-distancia al centroide del nicho, encontrando a menudo una relación inversa significativa (Yañez-Arenas *et al.* 2012, Martínez-Meyer *et al.* 2013, Jiménez-Cervantes 2015, Ureta *et al.* 2015, Ureña-Aranda *et al.* 2015). Dichos trabajos predicen que esta relación se define por una tendencia central multidimensional entre la abundancia y los factores ambientales. Sin embargo, las predicciones de la distancia al centroide del nicho basadas en datos ambientales podrían estar informándonos sobre las abundancias potenciales en lugar de las abundancias reales alcanzadas, ya que otros factores limitantes de diversa índole no considerados podrían estar limitando así mismo a las poblaciones locales (Cade *et al.* 1999, Cade y Noon 2003). Un excelente ejemplo lo constituye el impacto humano, que puede influir negativamente en las abundancias poblacionales de muchas especies animales silvestres, ya sea debido a la persecución directa asociada a la caza, control de pestes, etc. (Brashares *et al*. 2001, Peres 2001, Aquino *et al*. 2007, Peres y Palacios 2007, Urquiza-Haas *et al*. 2011), o indirectamente mediante los efectos de la pérdida y la fragmentación de sus hábitats naturales (Peres 2001, Barlow y Peres 2006, Fahring y Rytwinski 2009, Urquiza-Haas *et al*. 2011, Gutzwiller *et al*. 2015). Bajo este esquema de influencia humana negativa, podría esperarse que la relación entre abundancia y distancia al centroide del nicho estuviera modificada por la actividad humana, es decir, pudiéndose encontrar bajas abundancias locales en puntos que de otra manera están localizados en una posición cercana al centroide del nicho. De ser así, la relación entre la abundancia y la centralidad del nicho ecológico podría tener una forma de cuña, donde hacia el centroide se encuentren abundancias tanto altas como bajas, manteniéndose las abundancias bajas hacia la periferia (VanDerWal *et al.* 2009, Januchowski-Hartley *et al.* 2011, Tôrres *et al.* 2012, Thuiller *et al.* 2014, Carrascal et al. 2015).

Por otro lado, si la influencia humana tuviera un efecto determinante sobre la abundancia poblacional de una especie, también determinaría en última instancia su presencia. En un escenario contemporáneo donde los humanos dominan los ecosistemas globalmente (Dirzo *et.al.* 2014), el papel de las actividades humanas sobre la ecología de las especies debe ser considerado explícitamente. Se ha demostrado previamente que la influencia humana afecta el tamaño del rango geográfico de los mamíferos (Di Marco y Santini 2015), así como sus contracciones (Channell y Lomolino 2000, Murray y Dickman 2000, Laliberte y Ripple 2004, Woodroffe *et al.* 2004, Yackulic *et al.* 2011). Si bien la influencia humana sobre los ecosistemas acontece en todo el mundo, está aumentando rápidamente en las regiones tropicales (Venter *et al.* 2016), lo cual hace especialmente necesario evaluar su contribución relativa en los patrones de distribución y abundancia de especies neotropicales.

El nicho ecológico

Existe una variedad de conceptos producto del enfoque que distintas escuelas de pensamiento le han dado a la idea del nicho ecológico (Peterson *et al.* 2011). En la presente tesis nos basamos en el concepto de nicho Grineliano (Grinnell 1917) para modelar el nicho ecológico de las especies. El concepto de nicho Grineliano enfatiza variables no interactivas (i.e. no ligadas, que la especie no provoca un impacto en ellas) medidas principalmente a resoluciones espaciales gruesas, que son muy importantes a gran escala para determinar la distribución de las especies (i.e. variables scenopoéticas en Hutchinson 1978). Los nichos y sus distribuciones son estimados y visualizados en la asociación de los espacios geográfico y ambiental (Peterson *et al.* 2011). Estas dimensiones del nicho pueden medirse usando datos disponibles en grandes cantidades (Peterson *et al.* 2011).

Objetivos de la tesis

De acuerdo con lo expuesto anteriormente, el objetivo principal de la presente Tesis Doctoral consiste en generar modelos de abundancia de presas importantes de jaguares y pumas a escala biogeográfica, centrados en el Neotrópico. Dicha región representa además el área de mayor solapamiento entre las distribuciones de estos felinos (Zeller 2007, IUCN 2015). Este objetivo general fue abordado a través de una serie de objetivos particulares que se presentan a continuación y que se desarrollan en los capítulos 2, 3 y 4 de la tesis. En el capítulo 2, se identifican las principales especies de presa de jaguares y pumas consumidas en la región Neotropical. A fin de evaluar la fiabilidad de estudios previos, también evaluamos si el método tradicional de identificación de excretas generaba un sesgo en los resultados obtenidos en los estudios disponibles sobre la dieta de estos felinos, lo cual no había sido probado con anterioridad.

Como resultado de dichos análisis decidimos basarnos únicamente en los estudios que usaron métodos fiables de identificación del depredador a pesar de que estos fueron muy escasos. Los criterios que usamos para la selección de presas reportadas en tales estudios fueron los siguientes: que hubieran sido identificados a nivel de especie; que tuvieran un porcentaje de ocurrencia ≥10%; que se distribuyeran en el Neotrópico; y que hubieran datos disponibles de densidades poblacionales en distintos puntos de sus áreas de distribución. Así, elegimos cuatro especies para generar los modelos espaciales de predicción de abundancia: el pecarí de collar (*Pecari tajacu*), el pecarí de labios blancos (*Tayassu pecari*), la paca común (*Cuniculus paca*), y el oso hormiguero gigante (*Myrmecophaga tridactyla*).

En el capítulo 3, usamos al pecarí de collar como especie modelo para probar si la posición de las poblaciones de la especie con respecto al centroide de su nicho ecológico explicaba mejor las abundancias que su posición en relación al centroide geográfico de la distribución. También probamos si la relación entre la abundancia y la distancia al centroide del nicho definía la abundancia máxima esperada en cada sitio mejor que la abundancia alcanzada, dado el efecto de factores limitantes no medidos. Por último, evaluamos si la inclusión de la influencia humana al modelo ayudaba a explicar mejor la variación geográfica de la abundancia poblacional que la distancia al centroide del nicho por sí sola, y generamos un modelo espacial de predicción de abundancia a escala biogeográfica.

En el capítulo 4, evaluamos la importancia de la influencia humana para determinar los patrones de distribución y abundancia a gran escala de las tres especies de presa restantes: el pecarí de labios blancos, la paca común y el oso hormiguero gigante. Específicamente, evaluamos si al añadir la influencia humana al conjunto de variables ambientales mejoraban las predicciones de los modelos de nicho. Además, analizamos la relación entre la distancia al centroide del nicho y la influencia humana con las abundancias poblacionales de las distintas especies, y evaluamos cuál era el mejor modelo predictivo para cada una de las especies: el que incluía ambos factores, o el que incluía solamente alguno de ellos. Finalmente, usamos el mejor modelo para generar la predicción espacial de abundancia de cada especie.

Aproximación metodológica general

Existen numerosos métodos para modelar los nichos y las distribuciones de las especies, una forma de clasificarlos es en cuanto al tipo de información biológica que requieren. En este sentido, en la presente tesis nos centramos en algoritmos que sólo requieren datos de presencia de la especie. Específicamente utilizamos MaxEnt (Phillips *et al.* 2006) y GARP (Stockwell y Noble 1992, Stockwell y Peters 1999). El primero es un algoritmo de presencia/fondo, el cual evalúa cómo el ambiente en el que la especie está presente se relaciona con el ambiente de toda el área de estudio ("el fondo") (Peterson *et al.* 2011). Por lo tanto, usa registros de presencia junto con datos ambientales tomados de toda el área de estudio (o al menos de una muestra grande de ésta), potencialmente incluyendo las localidades de presencia (Peterson *et al.* 2011). El segundo es un algoritmo de presencia/pseudoausencia, que muestrea pseudoausencias en el área de estudio con el propósito de comparar localidades donde la especie está presente contra un conjunto de localidades que tienen una probabilidad inferior a 1 de constituir localidades de presencia (Peterson *et al.* 2011). La sutil diferencia entre este método y el anterior es que los datos de pseudoausencias son tomados únicamente de sitios en los que no hay presencias (Peterson *et al.* 2011). Sin embargo, a menos de que una especie de amplia distribución esté muy bien muestreada, generalmente los resultados basados en fondo y pseudoausencias no difieren dramáticamente (Peterson *et al.* 2011).

Para calcular la distancia al centroide del nicho ecológico de cada especie, nos basamos en Martínez-Meyer *et al*. (2013). Después de modelar el nicho, se obtiene el modelo binario de distribución potencial, el cual es usado para calcular el centroide del nicho y la distancia euclidiana "en el espacio ambiental" que existe desde cada una de las celdas en las que se predice presencia al centroide del nicho.

Esto se lleva a cabo de la siguiente manera, se extraen los valores correspondientes a las celdas con predicción de presencia. Todas las variables usadas para modelar el nicho son estandarizadas con el fin de convertirlas a una escala común con media = 0 y desviación estándar = 1. Finalmente, se calcula la distancia euclidiana multidimensional desde cada celda con predicción de presencia al centroide del nicho como se muestra a continuación:

$$DCN = \sqrt{\Sigma(\mu_j - a_{ij})}^2$$

donde DCN = distancia al centroide del nicho, μ_j = media de la variable *j* (valor estandarizado = 0), and a_{ij} = valor de la variable *j* en la celda *i*.

Por otro lado, para evaluar la influencia humana a gran escala, utilizamos bases de datos globales que integran información sobre densidad de población humana, uso de suelo, infraestructura y acceso humano (WCS *et al*. 2005, Venter *et al.* 2016).

Importancia de las especies de estudio

Además de ser importantes en la dieta de jaguares y pumas, las cuatro especies presa seleccionadas son una fuente importante de alimento para los humanos (Bodmer *et al.* 2004a, Bodmer *et al.* 2004b, Gallina *et al.* 2012, Patton 2015), incluyendo, aunque en menor medida, al oso hormiguero gigante (Miranda *et al.* 2014). En el caso de los pecaríes, además su piel se comercia internacionalmente (Bodmer y Lozano 2001, Fang 2003). Como consecuencia de ello, la cacería es una de las amenazas principales de las cuatro especies presa estudiadas, junto con la destrucción de sus hábitats naturales (Gongora *et al.* 2011, Keuroghlian *et al.* 2013, Miranda *et al.* 2014, Emmons 2016). Las cuatro especies tienen áreas de distribución muy grandes (abarcando una amplia variedad de ambientes), que se solapan en el centro y sur del continente Americano (IUCN 2011, Reyna y WCS 2013, IUCN 2014, IUCN SSC 2016). Son principalmente consumidores primarios (Mayer y Wetzel 1987, Pérez 1992, Eisenberg y Redford 1999), a excepción del oso hormiguero gigante, que basa su dieta en hormigas y termitas (Eisenberg y Redford 1999). Estas especies juegan también un papel importante en la dispersión de semillas (Beck 2005, Keuroghlian y Eaton 2009). Tanto el pecarí de labios blancos como el oso hormiguero gigante están catalogados como especies “vulnerables” de acuerdo a la lista roja de especies amenazadas de la IUCN (versión 3.1, Keuroghlian *et al.* 2013, Miranda *et al.* 2014), considerándose además al oso hormiguero gigante como el mamífero más amenazado de Centro América. Todos estos factores realzan la importancia de predecir la abundancia de estas especies más allá del papel que juegan para determinar la calidad del hábitat de sus depredadores naturales. Sin embargo, el poder predecir la calidad del hábitat de estos depredadores sería de gran utilidad para preservar la biodiversidad en las áreas neotropicales, ya que se trata de especies clave (Noss *et al.* 1996) que requieren de áreas extensas para su conservación.

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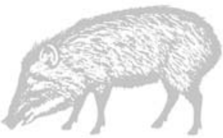

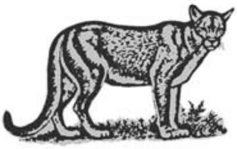

CAPÍTULO 2

Predator identification methods in diet studies: Uncertain assignment produces biased results?

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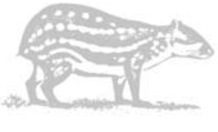

Abstract

Diet analyses are critical for understanding the ecology of animal species and designing management and conservation strategies. Nonetheless, diet studies of many mammalian carnivores are based on indirect analyses (mostly through their faeces) rather than on direct observations of their feeding behavior, introducing varying degrees of uncertainty into predator species identification. Here, we tested the hypothesis that trophic similarity between diet studies are associated with the predator identification method used by comparing results obtained in studies that used either *high confidence identification* (HCI; i. e. genetic or chemical analyses of faeces, or stomach or colon content) or *low confidence identification* methods (LCI; i. e. faeces appearance) for jaguars and cougars. We reviewed the literature on diet of these species and 1) assessed if similarity of the diet was related to the method used to identify the species, and 2) assessed the possible consequences that potential misidentification of faeces could have on diet descriptions (i. e. prey potentially included or omitted). For both aims we took into account the influence of geographical distance between study sites. Furthermore, we briefly summarized the most reliable knowledge currently available about the diets of both species. Our analyses indicated that the method used for predator identification significantly influences diet similarity, with HCI studies being more similar among them than LCI studies or HCI-LCI studies. Studies based on LCI methods apparently overemphasized the importance of reptiles, rodents, and some mesocarnivores in the diet of both predators, whereas other prey items were not detected. Although approaches for a reliable identification of predators are expensive and require specialized technicians and equipment, we highlight the need to invest in them in order to accomplish a better ecological understanding of the feeding ecology of carnivore species, which is a key factor to consider in conservation and management plans.

Introduction

Diet studies are of key importance for understanding predator-prey relationships and species interactions, since they provide information both on predators' fundamental resources and their potential impact on prey populations (e. g. Gittleman and Harvey 1982, Bekoff et al. 1984, Sunquist and Sunquist 1989). Additionally, comprehensive knowledge of predators' diets is valuable because it may provide information useful for managing human-predator conflicts over prey consumption or identifying prey populations that need to be supported for the conservation of endangered carnivores. However, reliable data on predators' diets is often difficult to obtain from direct observations, especially in rare or elusive species such as many mammalian carnivores (Thompson 2004). In these cases, most of the information available is gathered using indirect methods for the quantification of prey consumed, including the analysis of prey remains from stomach and colon contents and, more frequently, examination of faeces (Mills 1996).

Accurate identification of the predator species from their faeces is critical for obtaining reliable data on the composition of their diets. This identification is often achieved by one of two general methods: (1) inspection of the morphology and appearance of faeces in the field and, eventually, other associated evidence such as tracks, photographic captures, scrapes, hairs and radio locations (e. g. Fedriani et al. 2000, Cunningham et al. 2006, Bustamante-Ho 2008); or (2) laboratory chemical analyses such as the analysis of biliary acids (e. g. Taber et al. 1997, Ray and Sunquist 2001, Mukherjee et al. 2004) or genetic analyses (e. g. Posluszny et al. 2007, McVey et al. 2013, Sollman et al. 2013). Species identification from faeces in the field can be subjective and uncertain, resulting in high misclassification rates, because it depends on the experience of the observer, the degree of preservation of the faeces, the quantity and quality of associated evidence and the presence of other carnivore species that may deposit similar faeces (Fernández et al. 1997; Farrell et al. 2000, Davison et al. 2002, Chame 2003; Harrington et al. 2010). Despite these limitations, studies based on faeces identified in the field (hereafter referred to as “low confidence identification”, LCI) still constitute the main source of knowledge on the diet of many mammalian carnivore species (e. g. Fedriani et al. 2000, Rodríguez-Estrella et al. 2000, Carrillo et al. 2001, De Villa-Meza et al. 2002, Alves-Costa et al. 2004, Rosalino et al. 2005, Cunningham et al. 2006, Bustamante-Ho 2008, Krawczyk et al. 2013). In contrast, faeces identification using laboratory methods such as biliary acid and DNA analyses (hereafter “High confidence identification” HCI) have yielded more accurate results (e. g. Fernández et al. 1997, Palomares et al. 2002, Kohn and Wayne 1997, Hansen and Jacobsen 1999, Davison et al. 2002, Harrington et al. 2010, Roques et al. 2011), but their use is still restricted because they are costly and may require the development of highly specialized, species-specific laboratory protocols (e. g. Cazón-Narvaez and Sühring 1999, Palomares et al. 2002, Roques et al. 2011). Yet, there is still a lack of knowledge about how the uncertainty associated with the method of predator identification from faeces may affect inferences on species’ diets.

Our main objective was to assess the potential for bias resulting from the use of low confidence methods for identifying carnivore species by their faeces in diet studies. We analyzed the results of published studies on the diets of two large carnivore species, the jaguar (*Panthera onca*) and the cougar (*Puma concolor*). Cougars and jaguars are excellent study models because distinguishing their faeces in the field is not straightforward, they coexist over much of their range (the jaguar’s distribution is mostly nested with the larger cougar distribution) and both are generalist predators (Seymour 1989, López-González and González-Romero 1998, Laundré and Hernández 2010). Faeces from jaguars and cougars can be confused with each other (Fernández et al. 1997) and also with the faeces of several other sympatric, medium-sized generalist carnivores such as coyotes (*Canis latrans*), bobcats (*Lynx rufus*), wolves (*Canis lupus*), ocelots (*Leopardus* *pardalis)*, jaguarundis (*Puma yagouaroundi)*, and several fox species (e. g. Farrell et al. 2000). To achieve this general objective we address two specific aims.

First, we evaluated whether the similarity between studies of reported diets for jaguars and cougars was associated with the species identification method used in each study, assuming that diet similarity between studies of the same species should decrease with increasing inclusion of misidentified faeces. Thus, we expected that the similarity of diets reported would depend on the accuracy of the predator identification method (i.e. LCI vs. HCI), with more similar results among studies using HCI methods than among studies using different methods or studies using LCI methods. Alternatively, if the predator identification method did not affect diet results, we would expect that diet similarity was independent from the method employed.

Secondly, we identified possible biases in determined diet composition resulting from predator misidentification by accounting for the potentially erroneous omission or inclusion of some prey taxa in LCI studies. We expected that potentially erroneous inclusion of prey would occur more frequently than omission due to the inclusion of prey consumed by other predator species as a result of faeces misclassification.

We used geographic distance as a proxy of prey availability to control for potential differences between prey communities between study sites in both of our specific aims. For the second aim, we also included in analyses the ecoregion and distribution of representative prey.

Methods

Data collection and standardization

We reviewed diet studies for jaguars and cougars by searching the bibliographic databases “Scopus”, “Google Scholar” and “Web of Science” using different combinations of the terms cougar, diet, food habits, jaguar, *Panthera onca*, and *Puma concolor*. We ignored studies focusing on a single prey species or with poor discrimination and quantification of different food items. We included all diet studies that both provided information on the predator identification method and data necessary to calculate the percentage of prey occurrence (PO) from the analyses of faeces, stomach and/or colon contents. Studies were assigned either to HCI or LCI methods according to the origin of the samples: HCI for stomach and colon contents and for faeces where the predator species was identified using biliary acids or DNA analyses; and LCI for studies using other identification methods. The geographical location of each study was digitized using Geographic Information Systems (ARC/INFO v10.0, ESRI 2011). Studies from the same site and using the same kind of sample and predator identification method were pooled, as were data for items of the same prey species differing in size (e.g. “small” vs. “large”). Whenever possible we standardized the taxonomic resolution for the identified prey at the genus level.

Data analysis

Effect of predator identification method on diet similarity

We tested whether trophic similarity between pairs of studies was associated with the predator identification method using linear mixed models (LMM). Diet similarity for each pair was calculated using the Simplified Morisita index (Horn 1966), which ranges from 0 (completely distinct diets) to 1 (identical diets). We eliminated cases with a 0 index value, since complete lack of diet similarity is more likely to represent completely different available prey than methods-based differences, making these cases non-informative for our research question. We transformed remaining similarity values using the arcsin-transformation in order to comply with normality assumptions. Trophic similarity between pairs of studies was modeled as a function of the predator identification method (i.e. HCI vs. LCI) used in each study of the pair, resulting in three possible combinations (i.e. factor levels): HCI-HCI, HCI-LCI and LCI-LCI. In addition, the distance between study sites and the interaction between the distance and the predator identification method were both included as model predictors in order to account for potential differences in the community composition of potential prey that may result from the geographic separation between study areas. Distances were measured as the nearest distance between the centroids of each study area. Study was included as a random term to avoid pseudoreplication from repeated measurements in the similarity calculations and account for possible effects of other non-evaluated aspects of each study, such as sampling effort. Thus we included two random terms, one for each “study” of the pair. The significance of each fixed effect in the fitted LMM was assessed using Markov Chain Monte Carlo sampling (Bolker et al. 2008). Although the number of LCI studies was higher than HCI, preliminary analyses based on a randomization procedure showed that mean similarity values were not significantly affected by this difference (see Supplementary material Appendix 2 and Table A2).

Prey mismatches between predator identification methods

We compared the prey items obtained using LCI methods with those obtained using HCI methods to evaluate the potentially erroneous inclusion and omission of specific prey taxa as a result of predator misidentification. If HCI studies were indeed reporting more accurate results than LCI studies, we expected to find a significant difference between results obtained in HCI-LCI comparisons from those obtain in HCI-HCI comparisons. To evaluate this prediction, we compared each LCI study with all available HCI studies, obtaining the percentages of prey taxa that resulted from potential inclusion errors (i. e. found only using LCI methods) and omission errors (i. e. found only using HCI methods). We carried out the same procedure for all pairs of HCI studies, but generated two values per pair (equivalent to non-matching prey), rather than a single inclusion or omission value. We tested if there was a difference between the percentage of prey potentially included and omitted (obtained from HCI-LCI comparisons), and the percentage of non-matching prey (obtained from HCI-HCI comparisons) using the Mann-Whitney U test (Sokal and Rohlf 1981). The analyses of prey mismatches were performed for each ecoregion separately (Nearctic and Neotropic) because prey communities were expected to be more similar between studies within the same ecoregion. In addition, we tested whether differences in percentages of exclusive prey items between pairs of studies (arcsin-transformed to comply with normality assumptions) were associated with geographical distance between them using linear models. The analyses on the Jaguar included only the Neotropical region due to the scarcity of HCI studies in the Nearctic (we only found one). We assigned the ecoregion to each study site using the digital map of Terrestrial Ecoregions of the World (Olson et al. 2001).

Additionally, using the Mann-Whitney U test (Sokal and Rohlf 1981) we tested for differences in the number of samples collected (i.e. number of faeces, stomachs or colons) between HCI and LCI studies, since this could also affect the average frequencies of prey occurrence; there was no significant difference between study types in number of samples collected for jaguars (in the Neotropic) (U = 98.5, p = 0.98), or for cougars in the Nearctic (U = 29, p = 0.21) or Neotropic (U = 141, p = 0.87).

In order to further control for the effects of prey distributions, we also analyzed differences between diet studies undertaken within the distributional areas of each prey taxon considered representative of the diet of jaguars and cougars. We first identified the set of “representative prey” for each predator (PO ≥ 10% of the total diet in any study, excluding domestic prey), and then we identified their distribution using IUCN digital distribution maps (IUCN 2012). We assigned a potential inclusion error when a prey was considered a “representative prey” in at least one LCI study but it was not in any HCI study within the prey’s geographic range. Similarly, we assigned a potential omission error when a “representative prey” according to at least one HCI study was not “representative” in any LCI study. The number of LCI and HCI studies overlapping the distribution of each representative prey species was obtained using Geographic Information Systems (ARC/INFO v10.0, ESRI 2011). For each predator, we calculated the percentage of prey potentially included and omitted in LCI studies, and tested for the differences between inclusion and omission errors using a Z test (Sokal and Rohlf 1981). Finally, we provided a conservative estimate of the diet composition of the jaguar and the cougar throughout their distribution ranges by analyzing prey items from HCI studies with PO ≥ 10%.

Results

Data compilation and standardization

We found 61 studies on diet composition of jaguars and cougars meeting our criteria, from which we compiled a total of 32 data for jaguars (71.9% based on LCI, and 28.1% on HCI) and 61 for cougars (73.8% based on LCI, and 26.2% on HCI). Data based on a HCI of the predator were located in the Nearctic and Neotropic for cougars, but only in the Neotropic for jaguars (Fig. 1). For information about studies used and their complete references see Supplementary material Appendix 1, Table A1. In most cases prey items were identified to the genus level.

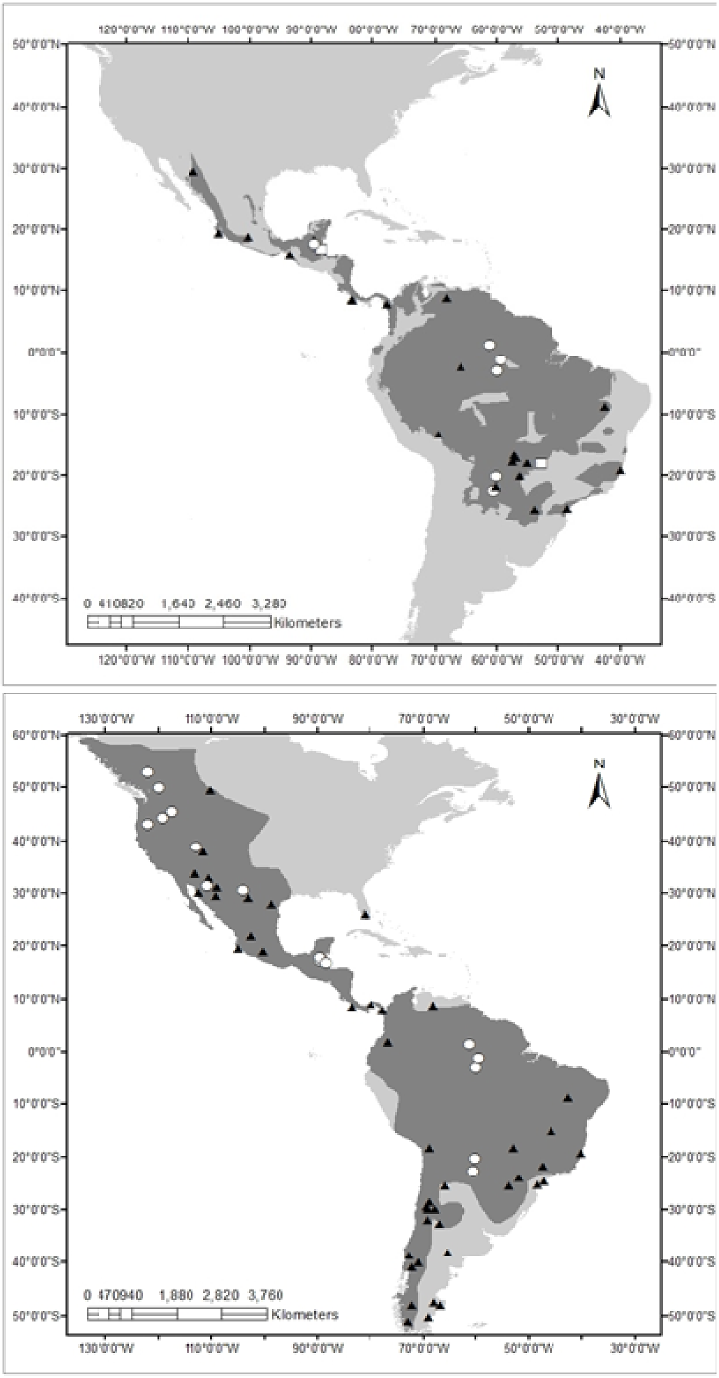

Figure 1. Geographical distribution of diet studies of jaguars (a) and cougars (b). Darkest areas are the current distribution ranges according to Zeller (2007) for jaguar and IUCN (2012) for cougar. White points represent sites of studies using high confidence identification methods, black triangles represent sites of low confidence identification studies, and white squares represent sites with both high and low confidence identification studies.

Effect of the predator identification method on diet similarity

Linear mixed models showed that diet similarities between pairs of studies were significantly affected by the method used to identify the predator, the distance between study sites and the interaction of these two factors for both cougars and jaguars (Fig. 2, Table 1). Trophic similarity was highest between pairs of HCI studies (Fig. 2) and decreased with increasing distance between study sites (Table 1).

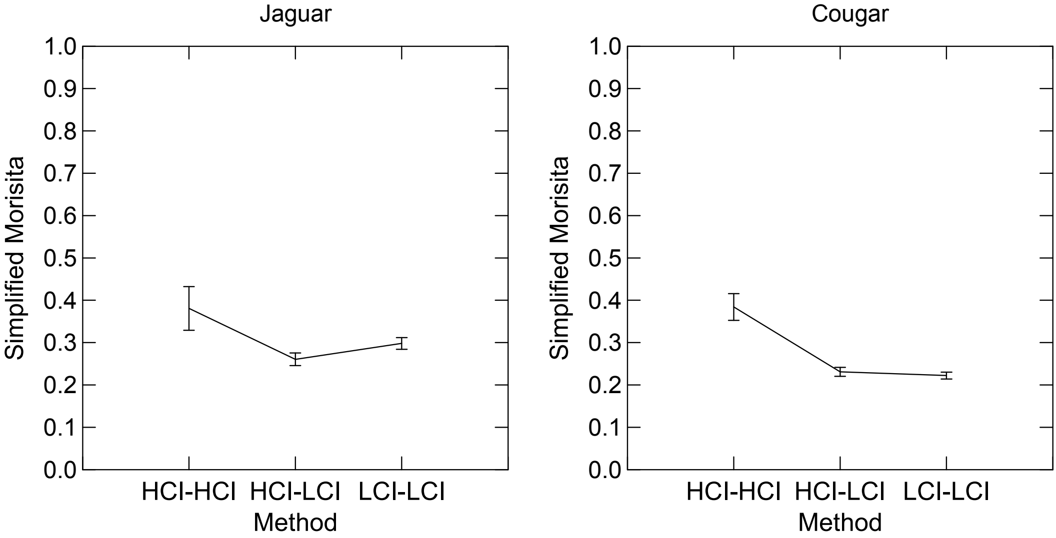

Figure 2. Mean and standard error of diet similarity (simplified Morisita index) between pairs of studies with similarity >0 according to the identification method employed for jaguars and cougars. HCI: high confidence identification; LCI: low confidence identification. Sample sizes (pairs of studies): HCI-HCI= 36 and 98; HCI-LCI= 200 and 563; LCI-LCI= 245 and 847, for jaguar and cougar, respectively.

Table 1. Linear Mixed Model results for the effect of predator identification method, distance between study sites, and their interaction, on the trophic similarity (simplified Morisita index) found between pairs of diet studies. Only pairs with similarity >0 were included in this analysis. Sample sizes (pairs of studies): HCI-HCI = 36 and 98; HCI-LCI = 200 and 563; LCI-LCI = 245 and 847, for jaguars and cougars, respectively.

Effect	Jaguar			Cougar		
	Estimate	SE	pMCMC	Estimate	SE	pMCMC
Intercept HCI-HCI	7.668e-01	7.530e-	0.0001	8.994e-01	5.052e-	0.0001
Distance	-5.844e-05	1.529e-	0.0004	-6.936e-05	6.902e-	0.0001
HCI-LCI	-2.456e-01	6.594e-	0.0001	-1.790e-01	4.158e-	0.0001
LCI-LCI	-1.975e-01	8.394e-	0.0156	-2.436e-01	5.658e-	0.0001
Interaction	4.571e-05	1.639e-	0.0084	1.867e-05	7.418e-	0.0086
Interaction	4.229e-05	1.614e-	0.0128	2.169e-05	7.167e-	0.0016

HCI: high confidence identification; LCI: low confidence identification; pMCMC, p value based on Markov Chain Monte Carlo sampling.

Prey mismatch between predator identification methods

The mean percentage of prey mismatch between studies was always lower for HCI-HCI comparisons than for HCI-LCI comparisons (Table 2). This difference was significant only for studies from the Neotropic, specifically for potentially erroneous inclusion of prey in LCI-based studies of jaguars, and for both potentially erroneous inclusion and omission of prey in LCI-based studies of cougars (Table 2). Prey mismatch increased significantly with distance between study sites in all HCI-HCI comparisons, except for cougar studies in the Nearctic (Supplementary material Appendix 3, Table A3). In HCI-LCI comparisons, the potentially erroneous inclusion of prey in LCI-based cougar studies increased with increasing distance in both ecoregions, and also on the omission of prey in the Nearctic (Supplementary material Appendix 3, Table A3).

Table 2. Mean percentage (±SE) of exclusive prey when comparing each pair of diet studies for jaguars and cougars in Neotropic and Nearctic regions with respect to predator identification method (i. e. HCI-HCI and HCI-LCH). For each pair of studies compared we obtained two values (one from each study of the pair). In the case of HCI-LCI comparisons, results are shown in different columns, with the study of reference indicated in bold. When the HCI study is used as the reference, the percentage of exclusive prey represents potentially erroneous omission of prey; when the LCI study is used as reference, the percentage of exclusive prey represents potentially erroneous inclusion of prey. Asterisks indicate when Mann-Whitney U tests detected significant differences for the comparison of **HCI**-LCI and HCI-**LCI** data with those obtained in HCI-HCI for jaguars and cougars separately.

	Percentage of exclusive prey					
	Jaguar			Cougar		
	HCI-HCI	**HCI**-LCI	HCI-**LCI**	HCI-HCI	**HCI**-LCI	HCI-**LCI**
Neotropic	55.6±2.67 N=72	59.5±1.60 N=198	65.1±1.33* *U*=5569.5 p=0.006 N=198	50.4±2.87 N=56	59.9±1.98* *U*=5826.5 p=0.005 N=272	73.8±1.28* *U*=3402 p=0 N=272
Nearctic	-	-	-	52.7±2.61 N=56	55.4±2.01 N=88	56.1±2.32 N=88

Analyses of prey mismatches between predator identification methods accounting for distributional ranges of the representative prey showed that almost half of the representative taxa in LCI studies were not representative in HCI studies (42.1%; N = 19 for jaguars; and 44.8%; N = 29 for cougars). On the other hand, we found that 15.8% (N = 19) of the representative prey in cougars according to HCI studies were not recognized as such in LCI studies. No potential omission errors were detected for jaguars (N = 11). The percentage of potential inclusion of representative prey was significantly greater than potential omission for jaguars (*Z* = 2.085, p = 0.037), but not for cougars (*Z* = 1.771, p = 0.076). For a complete list of representative prey see Supplementary material Appendix 4, Table A4.

Brief overview of the main prey consumed by jaguars and cougars in HCI studies

In the Neotropical region, mammalian prey such as anteaters, sloths, pacas, agoutis, peccaries, brocket deer, armadillos, and lagomorphs were frequently present in the diet of both jaguars and cougars. Coatis were a representative prey only in the jaguar's diet, whereas deer, opossums, and monkeys were representative only in the cougar's diet. For cougars in the Nearctic, the most important prey were deer, peccaries, moose, lagomorphs, porcupines, skunks, and carrion, but also domestic prey such as sheep and cattle. More details are provided in Supplementary material Appendix 5 and Table A5.

Discussion

The study of the diet in carnivore species through the analysis of faeces introduces uncertainty in predator identification that may cause serious biases in the identification and quantification of consumed prey. For cougars and jaguars, Fernández et al. (1997) showed that only 38% of jaguar and 30% of cougar faeces were correctly identified using subjective criteria as compared with identification through bile acid analyses. Furthermore, Farrel et al. (2000) found that 83% of faeces classified as jaguar or cougar based on their morphology were actually produced by ocelots (*Leopardus pardalis*) or crab-eating foxes (*Cerdocyon thous*). Our results show that diet similarity among existing studies was significantly affected by predator identification method, which demonstrates the serious implications of misidentifying predator species from faeces in trophic ecology studies.

We found that for both jaguars and cougars, the similarity between diet studies was higher between pairs of HCI studies than between LCI study pairs or between studies using different identification methods, once the effect of the geographical distance was accounted for. This result was consistent with our prediction that LCI methods would include a significant number of prey items from other predator species. Furthermore, prey mismatch analyses in the Neotropical region indicated that LCI studies included prey species that may actually have not been consumed by either cougars or jaguars and omitted prey species that may actually have been consumed by cougars. Additionally, we also found potentially erroneous inclusion and omission of "representative" prey items in the cougar's diet reported in LCI studies, as well as potentially erroneous inclusion in the jaguar's diet.

Potentially erroneous inclusion of prey was significant in LCI studies for both cougars and jaguars (though only in the Neotropic), as was the omission of prey for cougars. Faeces from these two species are especially difficult to distinguish without the aid of molecular methods (Fernández et al. 1997; Farrel et al. 2000). Since cougars and jaguars largely overlap in the Neotropical region, it seems plausible that prey inclusion and omission errors could be due to a greater difficulty in discriminating these two predator species in this region. Mammalian carnivore diversity is also higher in the Neotropic than in the Nearctic, which could have also contributed to the apparent increase in identification errors.

Our study cautions the use of low-confidence predator identification studies for synthetizing the current knowledge on species trophic ecology. Reviews on jaguar and cougar diets have largely ignored the uncertainties associated with species identification errors and they have assumed equal confidence in results even when studies differ greatly in their methods (e.g. see Iriarte et al. 1990, López-González and González-Romero 1998, De Oliveira 2002 and Laundré and Hernández 2010). Analyses of the most representative prey species indicate that studies using LCI methods may have overestimated the contribution of reptiles, rodents and some mesocarnivores in the diet of jaguars and cougars as compared with results from HCI studies (Supplementary material Appendix 4,

Table A4). On the contrary, the importance of porcupines in the cougar diet was not detected in LCI studies (Supplementary material Appendix 4, Table A4). More importantly, misleading results about the contribution of game species or domestic livestock in the diet of top predators can generate negative human attitudes toward them. According to our results, the proportion of deer (*Odocoileus* sp.) and sheep (*Ovis* sp.) in the diets of jaguars and cougars, respectively, may have been overestimated in LCI studies; while the importance of moose (*Alces* sp.) in the cougar's diet was underestimated (Supplementary material Appendix 4, Table A4). In addition, studies on the jaguar's diet carried out in the same study area but using different predator identification methods have reported contrasting results for the percentage of the diet composed of game species such as peccaries and species of conservation interest such as the pampas deer and the giant anteater (see Silveira 2004 vs. Sollmann et al. 2013; and Rabinowitz and Nottingham 1986 vs. Foster et al. 2010).

Although a comprehensive description of jaguar and cougar diets is beyond the scope of this study, we can highlight some general findings focusing exclusively on HCI-based studies. First of all, the high variability of prey taxa found in the diets of both species confirms the generalist predatory behavior for both felids, although mammal species were preferred according to their percentage of occurrence. We also found that representative prey species were similar in jaguars and cougars, though they were consumed in different proportions. Armadillos were consumed in most of jaguar studies, and pacas and brocket deer in most of cougar studies. Sloths and pacas were more important for cougars than for jaguars, while anteaters, armadillos, agoutis, peccaries, brocket deer, lagomorphs and birds were more important for jaguars than for cougars. With respect to mammals that could be identified at the species level, *Tamandua tetradactyla*, *Choloepus didactylus*, *Cuniculus paca* and *Mazama gouazoubira* occurred in both predators' diets in the Neotropical region, which could imply some degree of niche overlap in those areas where they are sympatric. In the

Nearctic region, cervids (mainly *Odocoileus* sp.) were the most consumed prey by cougars in most studies.

Final considerations

Jaguars and cougars are considered to be threatened by habitat loss, fragmentation, poaching and the depletion of their prey (Sanderson et al. 2002, Negri and Quigley 2010). In this context, conservation and management programs based on accurate knowledge on their trophic ecology are urgently needed. Though we found a relatively high number of diet studies for both predators, the number of studies using predator identification methods that yield consistently reliable data was much lower than expected and covered a small fraction of each predator's distribution area (9 study sites distributed in 4 countries, and 16 sites in 6 countries for jaguars and cougars, respectively). Because estimates such as niche breadth and/or overlap, mean prey weight, and biomass consumed depend on the number, kind and proportion of the items in the diet (e. g. Levins 1968, Colwell and Futuyma 1971, Hurlbert 1978, Ackerman et al. 1984, Iriarte et al. 1990), inaccurate diet assessments could have far-reaching implications, especially when used to understand species coexistence, competition and human-wildlife conflicts (e. g. Núñez et al. 2000, De Azevedo 2008, Rosas-Rosas et al. 2008). Therefore, we make a case for increasing the effort to use more accurate predator identification methods in diet studies and caution against making generalizations based on studies where the inadvertent inclusion of other predator samples is uncertain.

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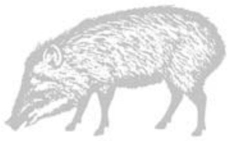
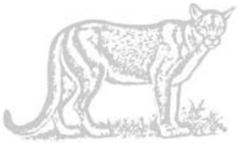
Supplementary material (Appendix EXXXXX at www.oikosoffice.lu.se/appendix). Appendix 1-5.

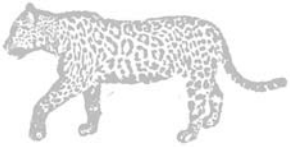




CAPÍTULO 3

Niche centrality and human influence predict rangewidevariation in population abundance of a widespread mammal (*Pecari tajacu*)

Martínez-Gutiérrez, P.G., Martínez-Meyer, E., Palomares, F.
& Fernández, N. (under review) Diversity and Distributions



Abstract

Aim

To evaluate whether geographic variation in population abundance of a widespread mammal (*Pecari tajacu*) is related to its location with respect to the centroid of its ecological niche, or to the centroid of its geographic range. Moreover, to assess the shape of the abundance-niche centrality relationship, since it could be influenced by unmeasured factors limiting abundance below its potential (producing both low and high abundances near the centroid). Furthermore, to test whether including human impacts improves the abundance-niche centrality relationship, and therefore the prediction of geographic variation in population abundance. In addition, to generate a predictive map of population abundance across the species range.

Location

The Americas.

Methods

We modeled the ecological niche of the species using occurrence and environmental data, and created a spatial model of distance to the niche centroid (DNC). We tested the relationships between abundance and DNC and abundance and distance to the geographic centroid (DGC). We evaluated whether the rate of change in the abundance-DNC relationship was steeper near the upper boundary than on the median abundance. We tested whether the human influence index (HII) improved predictions based on DNC. Finally, we generated a broad-scale predictive map of population abundance.

Results

We found a negative relationship between abundance and DNC; relationship to DGC was not significant. The abundance-DNC relationship was wedge-shaped, steeper for the 0.90 than for the 0.50 quantile of abundance. The HII had a negative effect in both quantiles; the model that included DNC and HII was the best for the 0.50 quantile, while DNC alone was the best for the 0.90.

Main Conclusions

Population abundances are related to the structure of the ecological niche, especially the maximum abundance expected in an area; thus the DNC approach can be useful in obtaining a spatial approximation of potential abundance patterns at biogeographic extents. Nonetheless, to achieve a better prediction of realized abundances it is important that human impacts also be considered.

Introduction

Geographic patterns in population abundance are the result of interactions between species and the different environmental characteristics (biotic and abiotic) that they experience across their ranges. Understanding these patterns has important practical conservation implications, such as for identifying critical habitats to protect threatened species, setting priority areas for protection, forecasting future changes, and for managing conflicts between humans and wildlife (e.g. Rodríguez *et al*. 2007, Franklin 2010, Guisan *et al*. 2013, Miller 2015). Understanding geographic patterns of abundance is also important for determining which environmental factors may potentially limit species' populations, since spatial variation in abundance may reflect the extent to which local conditions meet species' niche requirements (Brown *et al*. 1995). However, the availability of abundance data required to address these questions is poor for most species, and shows strong geographic and taxonomic biases (Newbold 2010). Population data are especially limited for tropical areas, as compared to higher latitudes (Collen *et al*. 2008), and availability is also related to characteristics such as rarity, detectability, or popular appeal. This lack of abundance data challenges assessments of species' responses to anthropogenic threats, as well as evaluating the effectiveness of conservation efforts.

Spatial modeling of abundance derived from distribution models could offer a practical solution to this problem in theory requiring only occurrence and environmental covariates as inputs (Peterson *et al*. 2011). In this regard, different hypotheses have been proposed to describe relationships between species' distributions and geographic variations in abundance. Brown (1984) proposed that the uneven distribution of population abundances follows a centrality pattern across distribution ranges with abundance greatest towards the geographic center of each species' range and declining towards the edges. This hypothesis implies that the geometry of species' distributions informs about environmental conditions affecting population processes. However, questions were raised about the universality of this relationship in a meta-analysis that included plants, birds, mammals, fish, and invertebrates, showing that only 39% of 145 separate tests actually followed that pattern (Sagarin & Gaines 2002).

A recent alternative hypothesis has emerged, proposing that geographic patterns of abundance are mostly the spatial reflection of the internal structure of the Hutchinsonian ecological niche of species (Martínez-Meyer *et al*. 2013). This hypothesis proposes that local population abundances are determined by the position in the multivariate cloud of the ecological niche, with higher abundances expected to occur towards the center of the niche, as defined by environmental conditions (Maguire 1973). This hypothesis has been supported by a series of empirical studies showing inverse relationships between population abundance and distance to the ecological niche centroids (DNCs); (Yañez-Arenas *et al*. 2012, Martínez-Meyer *et al*. 2013, Jiménez-Cervantes 2015, Ureta *et al*. 2015, Ureña-

Aranda *et al*. 2015). They assume that this association is defined by a multi-dimensional central-tendency relationship between abundance and environmental determinants. However, the DNC predictions based on environmental data might inform about potential abundances expected at each location instead of realized abundances; even assuming that a relevant subset of environmental limiting factors can be identified and quantified to define the niche, other environmental, ecological, and demographic factors may impose additional constraints on population abundances (Cade *et al*. 1999, Cade & Noon 2003). Therefore, a wedge-shaped relationship might be expected in which, both low and high abundances would be found towards the niche centroid (i.e. highest suitability), whereas marginal niche regions (i.e. lowest suitability) would be characterized only by low abundances (VanDerWal *et al*. 2009, Januchowski-Hartley *et al*. 2011, Torres *et al*. 2012, Thuiller *et al*. 14, Carrascal *et al*. 2015). An important example of such a variable would be the effects of human influence on abundances.

Here, we analyzed broad-scale patterns in population abundance in relation to the niche-centrality hypothesis in the context of different levels of human influence, using the collared peccary (*Pecari tajacu*) as a model species. The collared peccary is a broadly-distributed mammal in America that can be found in diverse habitats, from tropical forests to deserts (Gongora *et al*. 2011), therefore covering a wide range of climatic conditions and intensities of human pressure. It is also an important species for conservation, since it is a key prey species for the largest carnivore predators of the continent (Martínez-Gutiérrez *et al*. 2015); at the same time, it suffers from the pressure of over-hunting in some areas due to its importance as a source of protein and hides (Gongora *et al*. 2011). First, we tested the hypothesis that the position of species' populations in relation to the niche centroid (calculated following Martínez-Meyer *et al*. 2013) describes abundances better than the position in relation to the geographic centroid. Second, we tested the hypothesis that the abundance-niche centrality relationship defines the maximum expected abundance at any location, rather than the realized abundance owing to the unmeasured factors. Third, we evaluated whether accounting for human influence as well as DNC explains geographic variation in population abundance better than DNC alone. At last, we generated a spatial predictive map of population abundance across the species range.

Methods

Species data

We compiled occurrence data for the collared peccary from the following digital public databases: VertNet beta (http://portal.vertnet.org/search), UNIBIO (http://unibio.unam.mx/), REMIB (http://www.conabio.gob.mx/remib/doctos/remib_esp.html), SpeciesLink (http://splink.cria.org.br), ArctosDatabase (http://arctos.database.museum/SpecimenSearch.cfm), Global Biodiversity Information Facility (http://www.gbif.org/), and Mammal Species of the World, Smithsonian Institution (http://collections.nmnh.si.edu/search/mammals/). We reviewed the geographic coordinates of each observation based on the descriptions of localities in the original databases, and only used observations from the period 1940-2013, which resulted in 402 occurrence records. Finally, we translated point data into a grid of 0.02° spatial resolution to match the resolution of environmental layers (see below), resulting in 372 unique grid cells known to hold collared peccary, see Table S1, and Fig. S1 in Supporting Information (where ‘S’ indicates Supporting).

We collected independent population abundance data from across the species’ range by systematically searching publications in research journals and theses, using the bibliographic databases Scopus (https://www.scopus.com/), Google Scholar (https://scholar.google.com/) and Web of Science (http://www.webofknowledge.com). From each publication, we georeferenced the study location and recorded population density estimates (ind/km^2), based on line transect methods (Buckland *et al*. 2005); we obtained 75 density observations, and again we assigned georeferenced locations to a 0.02° grid (as with the occurrence data). For grid cells with more than one density estimate, we randomly chose one, for a total of 72 unique grid cells (see Table S2, and Appendix S1).

Environmental variables

To characterize the species' niche, we selected 13 environmental variables: 9 bioclimatic, 3 topographic and one of primary productivity. Climate variables were drawn from the WorldClim database, version 1.4, which provides monthly average information for the period 1950-2000 at spatial resolution of 30'' (approx. 1 km) (Hijmans *et al*. 2005). Bioclimatic variables included isothermality, temperature annual range, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of wettest month, precipitation seasonality, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. We did not use the other 10 bioclimatic layers from WorldClim to characterize the species niche owing to high correlation with all the selected variables (at least one Pearson's $r > 0.85$). Topographic variables included elevation, aspect, and slope, all calculated from the digital elevation model of the shuttle radar topography mission (STRM), also at a spatial resolution of 30'' (Farr *et al*. 2007). Mean annual net primary production was calculated from the Global Production Efficiency Model product, derived from the Advanced Very High Resolution Radiometer for the period 1981-2000 at a spatial resolution of 8 km (Prince and Goward 1995, Prince & Small 2003). Finally, for computational tractability, all layers were resampled to a grid size of 0.02° resolution (approx. 2 km in the study region). This size is roughly comparable to the average home range size of herds of the collared peccary (mean = 1.5 km^2; range = 0.24 - 8.00 km^2; Gongora *et al*. 2011).

Human impact

For analyzing human impacts on landscapes, we used the Global Human Influence Index (HII) dataset of the Last of the Wild Project, version 2 (Wildlife Conservation Society *et al*. 2005). This dataset integrates information from eight layers related to human population densities, land use, infrastructure, and human access. As with previous layers, we resampled the data to match the 0.02° grid resolution.

Ecological niche modeling

We modeled the ecological niche of the collared peccary using GARP (Genetic Algorithm for Rule-set Production; Kumara & Suganthasakthivel 2011, Sobek-Swant *et al*. 2012, Peterson *et al*. 2014, Gentry *et al*. 2016). GARP detects nonrandom relationships between species' occurrences and pseudo-absences in relation to environmental variables; model results can be projected into geographic space to generate potential distribution maps (Stockwell & Noble 1992, Stockwell & Peters 1999). A strength of GARP is that it uses 4 algorithms to calculate species-environment relationships to generate prediction rules. These rules result from an iterative process of rule construction and evaluation, in which each prediction is used to improve the next iteration (Stockwell & Noble 1992, Stockwell & Peters 1999). GARP models were fit using Desktop GARP v.1.1.6 (Scachetti-Pereira 2002).

We specifically used the following modeling protocol. First, we delimited the study area by generating a 100-km buffer around the distributional range of the collared peccary based on the IUCN distribution map (IUCN 2011) and around observations from the present study that felt outside the IUCN distribution map. We took the union of these two layers to generate the study area (see Fig. S1). We assumed that this area reflects the geographic region that has been accessible to the species over relevant time periods (M in the BAM framework;

Peterson *et al*. 2011). We iteratively fit 100 GARP models through splitting the original sample into two subsets: 70% of occurrences (i.e. 260) for calibrating the model, and the remaining 30% (i.e. 112) for evaluating the model. In each iteration, we produced a binary model, and compared it with testing observations. We retained the 20 models with the lowest omission error according to these tests, which we reduced to the 10 models closest to the median predicted area (Anderson *et al*. 2003). In this way, we ruled out potentially overfit models and models that present overly large predicted areas (Pearson *et al*. 2007). The predictions of these 10 binary models were combined (summed) to produce a final consensus model with values ranging between 0 and 10. Finally, we produced a binary potential distribution map by thresholding the consensus map at E = 5% omission error, i.e. a threshold value at which 95% of calibration occurrence points were included in the prediction.

Geographic variation in local population abundance

We calculated the geographic centroid of the potential distribution map, and the geographic distance from each of the 72 population density observation sites to the geographic centroid. We tested the relationship between local population densities and distance to the geographic centroid (DGC) using a generalized least squares regression analysis (GLS) with a power variance function structure (Pinheiro & Bates 2000).

To calculate distance to the niche centroid (DNC), we followed Martínez-Meyer *et al*. (2013). We used the binary distribution map to calculate the niche centroid and calculated the Euclidian distance in “environmental space” from each pixel with predicted presence to that centroid. We extracted the values of the 13 environmental characteristics of each grid cell with predicted presence, and standardized these variables to convert them to a common scale with mean = 0 and standard deviation = 1. Finally, we calculated multidimensional Euclidean distance from each grid cell to the niche centroid as follows:

$$DNC = \sqrt{\Sigma(\mu_j - a_{ij})^2}$$

where DNC = distance to the niche centroid, μ_j = mean of variable *j* (standardized value = 0), and a_{ij} = value of the variable *j* in grid cell *i*.

We represented DNC in a raster map, and rescaled the values between 0 and 1, with 0 representing the niche centroid and 1 the largest distance to this centroid. We analyzed relationships between DNC and the 72 local population densities of collared peccary using a GLS with power variance-function structure (Pinheiro & Bates 2000). In addition, we evaluated whether the rate of change in local abundance was steeper near the upper boundary of the conditional distribution using quantile regression analyses (Koenker & Bassett 1978). Quantile regression is a method for estimating functional relationships between variables at any portion of the probability distribution of the relationship between the response and the predictor, instead of only in the mean response (Cade & Noon 2003). The significance of the regression at each quantile was assessed by constructing confidence intervals through a Huber sandwich estimate of the covariance (Koenker & Machado 1999). We evaluated the 50th and 90th percentiles representing the central response in population abundance and the upper limit of abundance, respectively. We compared the results using an ANOVA test of equality of slopes (Koenker 2005).

We tested effects of the human influence on the population-abundance niche-centrality relationship with two different analyses. First, we tested whether the deviation in the observed abundance from the abundance predicted by the quantile regression models could be explained by the human influence index (HII). For this purpose, we fit a linear regression model with the residuals of the quantile regressions as the response variable and the HII as predictor (i.e. one model for the 50th and one for the 90th percentile). Second, we evaluated a

quantile regression model including both DNC and HII. To compare the relative contributions of the two factors, we standardized the variables to convert them to a common scale with mean = 0 and standard deviation = 1. Then, we selected the best model at each quantile between three competing models: a model with DNC exclusively; a model including DNC and HII; and a null model of no effect. Model selection was performed calculating the Akaike Information Criterion (AIC) and Akaike weights (w_i) (Burnham & Anderson 2002). Finally, we used the coefficients of the best model selected for each quantile to generate spatial predictions of local abundances. We only extrapolated spatial predictions for the observed rank of abundance.
All the analyses were conducted in R (R Core Team 2014), using the package *nlme* for estimation of generalized least square linear models (Pinheiro & Bates 2000) and the *quantreg* package for quantile regressions (Koenker 2015).

Results

Ecological niche modeling

Ecological niche models were highly significant for all 10 best subset models (all $\chi^2 > 6.690$, *d.f.* = 1, all $P < 0.01$), which indicates that the distribution predicted by all of these models was more coincident with independent testing data than expected by random. The threshold value of consensus to produce the binary model (of presence/absence) was 4. The resulting potential distributional area extended from the southern USA to northern Argentina (Fig. 1).

Large areas presenting environments closer to the niche centroid were located in central Brazil, extending to eastern Bolivia and Peru, Paraguay, and northern Argentina. Such conditions are also in southeastern Mexico, northern Guatemala, and Belize (Fig. 1). On the other hand, large areas with environments far from the niche centroid were located from the southern USA to central Mexico; and from western Colombia to Ecuador (Fig. 1).

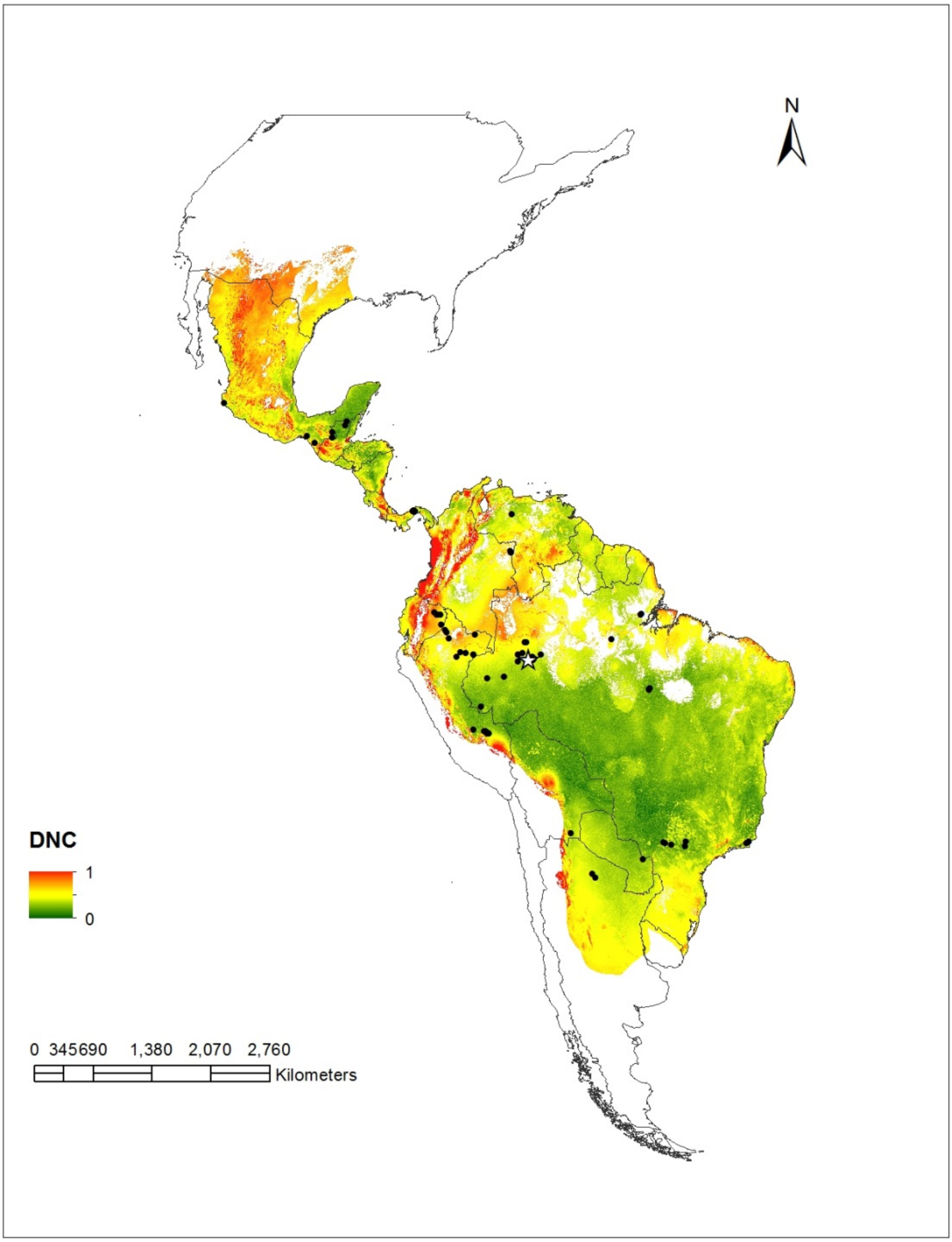


Figure 1 Model of the ecological niche of *Pecari tajacu* representing the distance to the niche centroid (DNC), with values from 0 = niche centroid (green) to 1 (red) = farthest from niche centroid. Black points represent 72 abundance data of the species (ind/km^2). White star represents the geographic centroid. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Geographic variation in local population abundance

GLS models showed that the local population abundance was significantly negatively associated with DNC (regression coefficient = -30.51 ± 7.07 SE; *P* < 0.001), (Fig. 2). The alternative model, relating population abundance to DGC, was not supported (regression coefficient = -0.0006 ± 0.0003 SE; *P* = 0.07; AIC = 356.3 vs. 383.3, respectively).

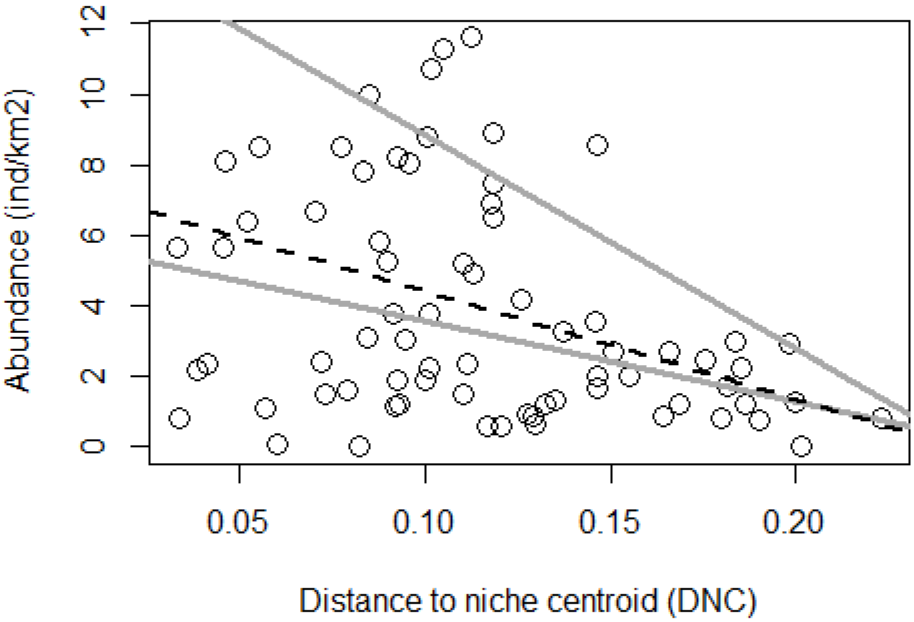


Figure 2 Relationship between local population abundance of *Pecari tajacu* and niche centrality (from 0 = niche centroid to 1 = farthest from niche centroid). Gray lines represent the quantile regressions for the 90th (upper line) and 50th percentiles. The dashed line represents the linear regression (GLS) with power variance function structure.

Quantile regression analyses indicated a steeper relationship between abundance and DNC for the 90th percentile (quantile regression coefficient = -60.33 ± 16.63 SE; *P* < 0.001) than for the 50th percentile (quantile regression coefficient = -22.65 ± 5.09, *P* < 0.001), (Fig. 2). The ANOVA test of equality of slopes showed that this difference was significant ($F_{1,\ 143} = 5.50$, $P = 0.02$). These results suggest that local population abundances were lower at longer distances to the niche centroid, and that this effect was steeper at the upper limit of the abundance distribution.

We found that the residuals of the 0.50 and 0.90 quantile regressions based on DNC were significantly negatively associated with HII (regression coefficient for quantile 0.50 = -0.09 ± 0.03; $P < 0.01$; regression coefficient for quantile 0.90 = -0.12 ± 0.04; $P < 0.01$), (Fig. 3).

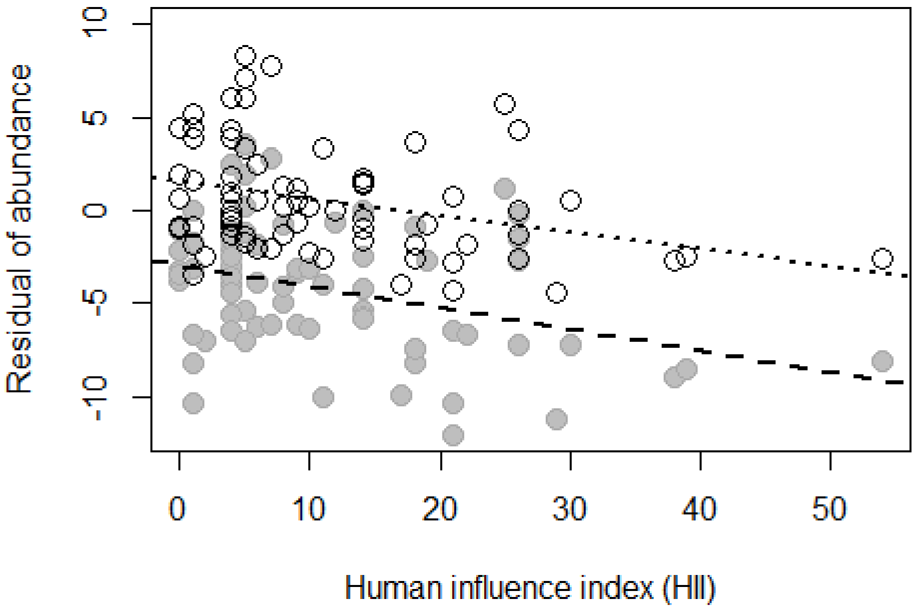


Figure 3 Regression of the human influence index on the residuals obtained from the relationship between local population abundance of *Pecari tajacu* (ind/km^2) and distance to the niche centroid. The upper line represents the regression on the residuals of the 0.50 quantile regression (white dots) and the lower line is the regression on the residuals of the 0.90 quantile regression (gray dots).

This result indicates that lower population abundances than expected from the DNC model are associated with higher human influence. Quantile regression analyses also showed significant negative effects of HII on population abundance (Table 1); this effect was stronger at the 90th percentile (ANOVA test of equality of slopes: $F_{2, 142} = 3.25$, $P = 0.04$). The effect of DNC was comparatively stronger than the effect of HII at both percentiles (Table 1).

Table 1. Quantile regression model results for the effects of distance to niche centroid (DNC) and the human influence index (HII), on the median (0.50 quantile) and upper limit (0.90 quantile) of abundance of *Pecari tajacu* (ind/km^2). The standardized coefficients (Stand. Coeff.) are also shown to compare the two predictors.

Quantile (τ)	Predictor	Coefficient	SE	*P*	Stand. Coeff.
0.50	DNC	-22.62	5.59	< 0.001	-1.04
	HII	-0.09	0.02	< 0.001	-0.94
0.90	DNC	-54.74	15.72	< 0.001	-2.51
	HII	-0.10	0.04	< 0.05	-1.08

Model selection results between all models tested are shown in Table 2: for the 50th percentile, the best model included both DNC and HII as predictors; for the 90th percentile, the best model considered only DNC. Based on these results, we built spatial models of expected abundances for the 50th and 90th percentile, which ranked 0.0004 - 6.61 ind/km^2 for the 50th, and up to 11.60 ind/km^2 for the 90th percentile (Figs. 4 and 5, respectively).

Table 2. Model selection between quantile regression models (Akaike Information Criterion - AIC, and the Akaike weights - w_i) on the median (0.50 quantile) and upper limit (0.90 quantile) of abundance of *Pecari tajacu* (ind/km^2). Y ~ 1 = null model of no effect. Y ~ DNC = abundance as a function of distance to the niche centroid. Y ~ DNC + HII = abundance as a function of distance to the niche centroid and the human influence index. The best model for each quantile according to the Akaike weights is indicated in bold.

	Quantile (τ) 0.50		Quantile (τ) 0.90	
Model	AIC	w_i	AIC	w_i
Y ~ 1	375	0.00	423	0.04
Y ~ DNC	369	0.02	418	**0.61**
Y ~ DNC + HII	361	**0.98**	419	0.35

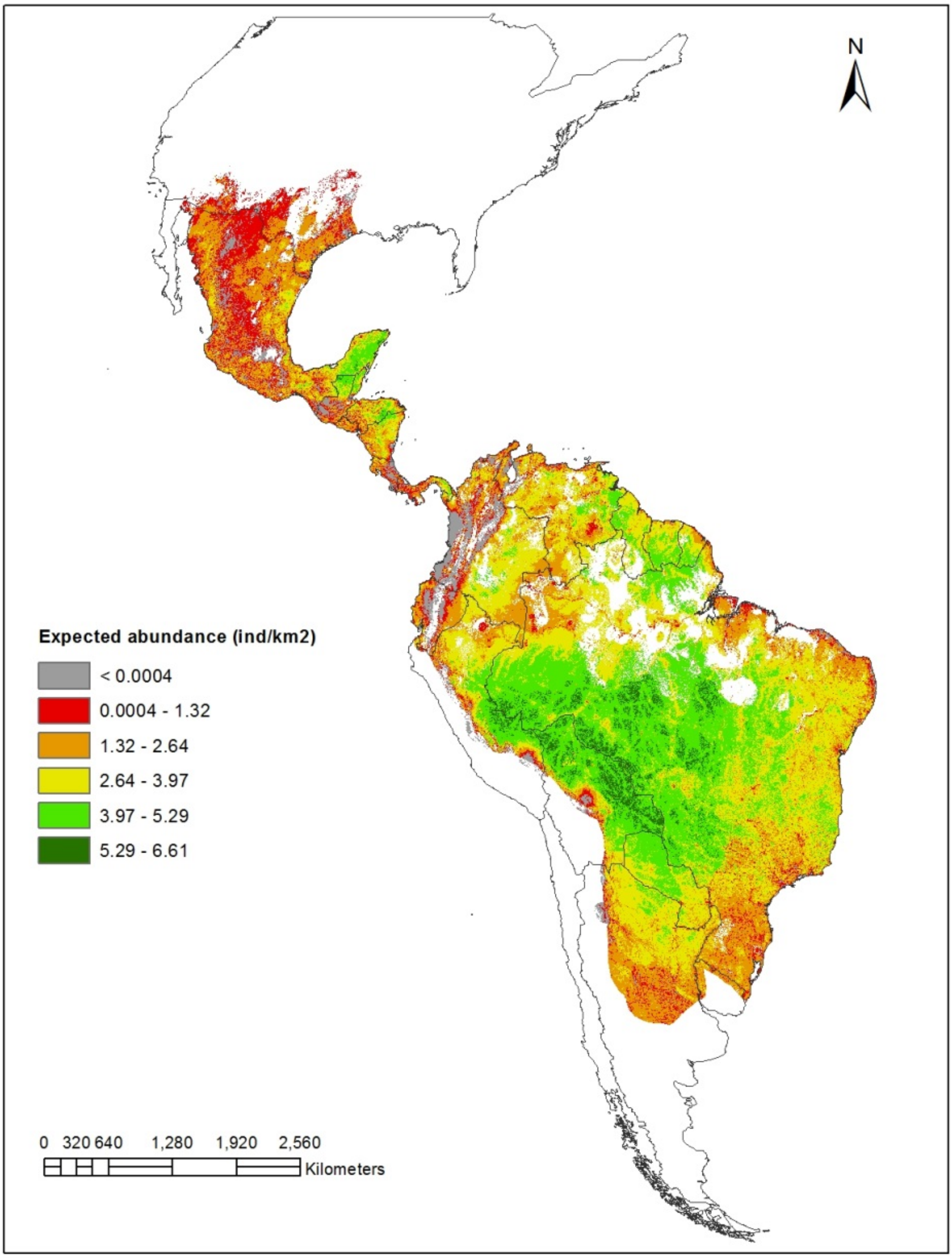


Figure 4. Abundance prediction of *Pecari tajacu* along its potential geographic range based on the effect of distance to the niche centroid and the human influence index on the observed median density (50th percentile). We only extrapolated spatial predictions for the observed rank of abundances, therefore in gray we represent areas with an abundance prediction below the minimum observed. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

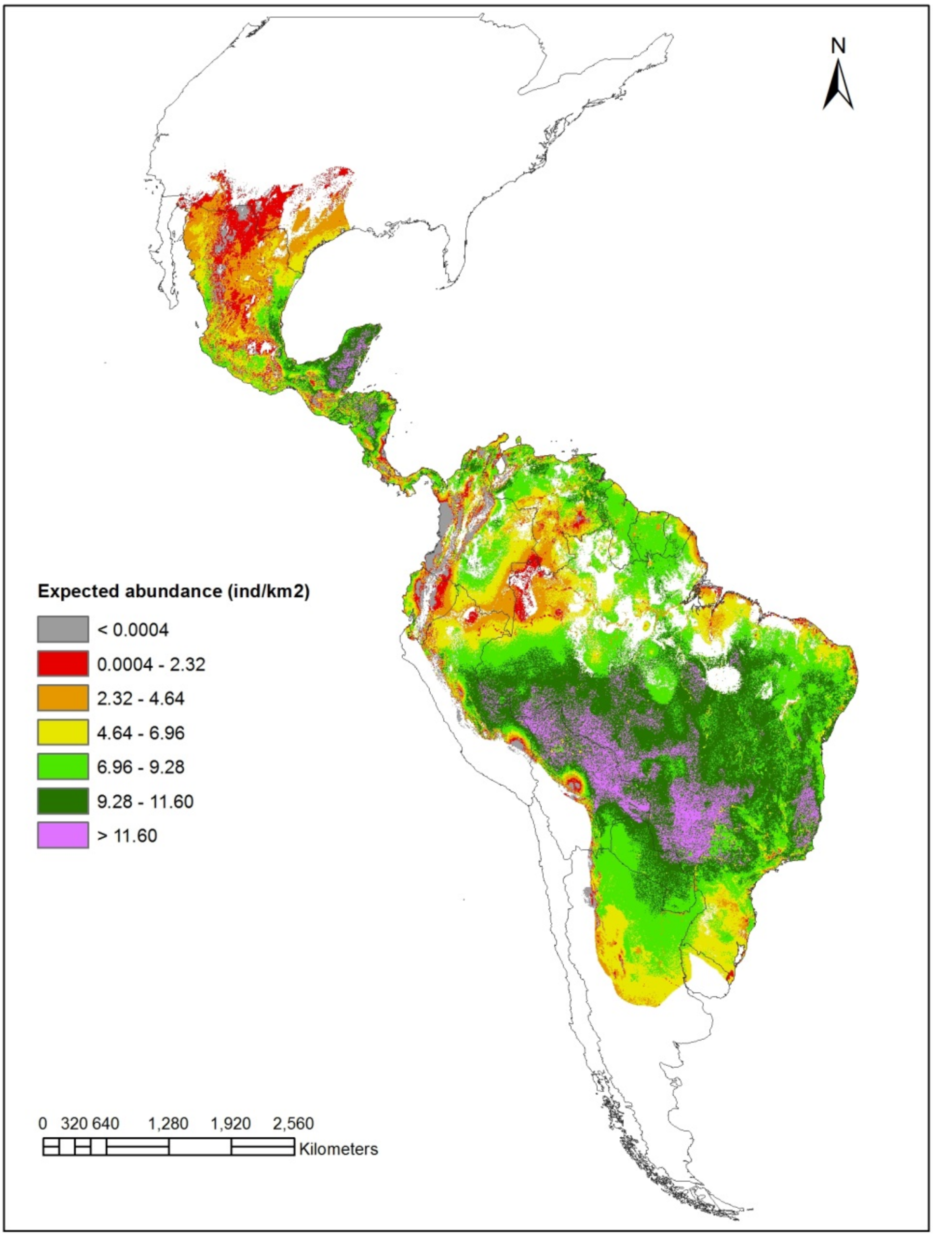


Figure 5. Abundance prediction of *Pecari tajacu* along its potential geographic range based on the effect of distance to the niche centroid on the observed carrying capacity (90th percentile). We only extrapolated spatial predictions for the observed rank of abundances, therefore in gray we represent areas with an abundance prediction below the minimum observed; and in purple areas with an abundance prediction above the maximum observed. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Discussion

We investigated range-wide spatial patterns in population abundance in relation to the niche centrality hypothesis and human influence using a broadly-distributed prey mammal of high conservation and societal importance as case study. Specifically, we assessed whether distance to the niche centroid (DNC) could predict geographic patterns of population abundance of the collared peccary; since very few studies have empirically tested the niche-centrality hypothesis (Yañez-Arenas *et al*. 2012, Martínez-Meyer *et al*. 2013, Jiménez-Cervantes 2015, Ureña-Aranda *et al*. 2015, Ureta *et al*. 2015). Further, we tested the relationship between abundance and distance to the geographic centroid (DGC), and evaluated whether abundance predictions from DNC were improved by including effects of the human influence. The latter test was particularly important since population abundance of many species is affected by it, and yet it has often been overlooked in broad-scale studies of the relationship between abundance and the ecological niche of the species.

We found a significant, negative relationship between local population abundance and DNC. In contrast, the relationship between population abundance and DGC was not significant. These two results support the hypotheses that spatial patterns in local abundances are associated with the environmental structure of the Hutchinsonian niche (Yañez-Arenas *et al*. 2012, Martínez-Meyer *et al*. 2013, Jiménez-Cervantes 2015, Ureña-Aranda *et al*. 2015, Ureta *et al*. 2015), but not to the geographic position in relation to the species distribution (Yañez-Arenas *et al*. 2012, Martínez-Meyer *et al*. 2013). Nonetheless, our analyses point out additional characteristics of this relationship with important implications for the niche modeling of spatial patterns in population abundance.

First, variability in local population abundances increases with the proximity to the niche centroid, indicating that abundance is limited by the set of environmental variables used to determine the ecological niche (climatic, topographic, and primary productivity), but it can be modified and reduced by other factors not considered at the first place.

Second, the influence of human activities decreases realized abundances below values predicted under the niche centrality hypothesis. Negative effects of human impact on abundances of wildlife species are widely documented (e.g. Brashares *et al*. 2001, Peres 2001, Barlow & Peres 2006, Aquino *et al*. 2007, Peres & Palacios 2007, Fahring & Rytwinski 2009, Urquiza-Haas *et al*. 2011, Gutzwiller *et al*. 2015), and therefore should be taken into account to depict spatial patterns of abundance. In the case of the collared peccary, population abundances are affected by hunting (Peres 1996, Altrichter 2005, Peres & Nascimento 2006, De Azevedo & Conforti 2008, Flesher & Laufer 2013, Suarez *et al*. 2013) and habitat degradation (Peres *et al*. 2003, De Azevedo & Conforti 2008, Parry *et al*. 2009, Suarez *et al*. 2013). In this regard, the global human influence index used in this study turned out to be a useful proxy for these threats.

Model selection results showed that although maximum abundance is driven primarily by the environmental dimensions, median abundance is better explained by models also considering the human pressure. Thus, our results point out the need to include other variables that may be limiting abundances to below its potential, to improve accuracy of abundance predictions; otherwise, predictions based on the DNC would be informing us about carrying capacity rather than actual abundance patterns. However, to include such variables as predictors in the niche modeling process itself (rather than in *post hoc* processing steps) might be not feasible because it could reduce sample size, since occurrence records must correspond temporally to predictor data sets (Peterson *et al*. 2011), and data available for these kind of predictors (e.g. the human influence index) usually correspond to a narrow period of time. Further, including such information separately in exploratory models allows explicit assessment of human impacts as a separate factor that may or may not be significant.

Some limitations of the DNC approach are that it assumes centrality and unimodality in the distribution of abundance in relation to environmental variables, and that it doesn't capture the population fluctuations in time (Yañez-Arenas *et al*. 2012). Its performance in predicting patterns of abundance is affected by sampling bias in the occurrence data, and sample size; therefore, the accuracy of the predictions will depend on the quantity and quality of the data used (Yañez-Arenas *et al*. 2014). Additionally, the strength of the relationship between DNC and abundance decreases when dispersal capacity is high (Osorio-Olvera *et al*. 2016). Finally, any representation of the ecological niche may be only partial, since in most instances it is very difficult to consider all the axes of the multidimensional niche (Yañez-Arenas *et al*. 2014). Other approaches (different from the DNC) that have tested the relationship between abundance and environmental suitability values from niche models (e.g. Nielsen *et al*. 2005, VanDerWal *et al*. 2009, Torres *et al*. 2012, Weber & Grelle 2012, Gutiérrez *et al*. 2013, Bean *et al*. 2014, Thuiller *et al*. 2014, Carrascal 2015, Weber *et al*. 2016) have reported a wide range of results, from strong to non-significant relationships.

We conclude that the species abundance is related to the structure of the Hutchinsonian niche (here defined in a reduced set of environmental dimensions), in particular the maximum abundance expected in an area. Therefore, the DNC approach can be useful in obtaining a spatial approximation of the potential abundance patterns at biogeographic scales. To achieve a better spatial approximation of realized abundances it is important to take into account effects of human impact and other factors that could influence abundance like dispersal capacity (Boulangeat *et al*. 2012, Osorio-Olvera *et al*. 2016) or biotic interactions (Boulangeat *et al*. 2012, Lois *et al*. 2014). DNC abundance estimates can be generated from public databases, its calculation is simple, it is effective for large regions, and it is based on ecological foundations; as such, our findings are particularly relevant in planning conservation strategies and setting public policies for species with geographic ranges for which only occurrence data are available.

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Supporting Information

Figure S1 Extent of the study area to model the ecological niche of collared peccaries.

Table S1 Data documenting known occurrences of collared peccary across its range.

Table S2 Summary of reference studies documenting local abundances of collared peccaries (ind/km^2).

Appendix S1 Complete references for abundance studies of collared peccary.

Biosketch

Patricia G. Martínez-Gutiérrez is a PhD candidate at the Universidad Autónoma de Barcelona, and is working on her thesis at Estación Biológica de Doñana-CSIC (Spain). She is interested in macroecology, species distribution modeling, and applications to conservation of mammals.

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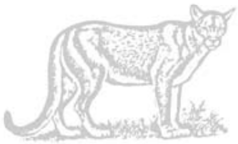
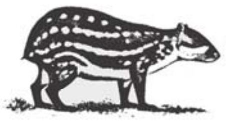


CAPÍTULO 4

Large scale modeling of the distribution and abundance of three Neotropical mammals: the white-lipped peccary (*Tayassu pecari*), the spotted paca (*Cuniculus paca*), and the giant anteater (*Myrmecophaga tridactyla*)

Martínez-Gutiérrez, P.G., Palomares, F., Martínez-Meyer, E. & Fernández, N.



Abstract

Aim

To assess the relative importance of human influence in determining the broad-scale patterns in the distribution and abundance of the white-lipped peccary, the giant anteater, and the spotted paca. In addition, to generate spatial predictive maps of population abundance across each species range using a predictive modeling framework based on the niche centrality hypothesis and including human influence.

Location

The Neotropical region.

Methods

For each species, we assessed the predictive capacity of niche-models based on occurrence data, and on climatic, topographic, and human footprint (HF) data. We evaluated whether the addition of HF to the set of climatic-topographic variables improved the performance of niche-model predictions. We retained the best niche-model for each species and generated a spatial model of distance to the niche centroid (DNC). Finally, we tested the relationships between population abundance and niche centrality, abundance and HF, and abundance and both factors together. We used the abundance models best supported by the data to generate broad-scale predictive maps of population abundance.

Results

Niche-model predictions improved with the inclusion of HF for two of the three studied species. However, its relative importance was high only for the spotted paca. Quantile regression analyses revealed significant niche centrality-abundance patterns and a significant influence of HF for the white-lipped peccary, especially at the upper-quantile limit. HF was the best abundance predictor for the spotted paca, whereas spatial abundance patterns of the giant anteater could be associated only with climatic- topographic variables.

Main Conclusions

Although the inclusion of HF improved niche predictions of most species, climatic factors had a stronger influence. The contrasting importance of HF in the distribution of the species might be related to differences in their characteristics rather than their threats. For most of the species, population abundances were related to the structure of the ecological niche as defined by both climatic-topographic variables and HF. Exceptions might be related to the influence of local-scale factors, and to the degree of tolerance to human influence, respectively.

Keywords

abundance prediction, *Cuniculus paca,* distance to the niche centroid, ecological niche modeling, giant anteater, human footprint, *Myrmecophaga tridactyla,* spotted paca, *Tayassu pecari,* white-lipped peccary.

Introduction

The white-lipped peccary (*Tayassu pecari*), the giant anteater (*Myrmecophaga tridactyla*), and the spotted paca (*Cuniculus paca*), are three widespread Neotropical mammals that are important components of the diet of large-sized predators, such as jaguars and cougars (Martínez-Gutiérrez *et al.* 2015). In addition, they are also important sources of food and trade for humans (Bodmer & Lozano 2001, Fang 2003, Bodmer *et al.* 2004a, Bodmer *et al.* 2004b, Aquino *et al.* 2009, Gallina *et al.* 2012, Ferreira *et al.* 2013, Miranda *et al.* 2014, Patton

2015). Knowing their distribution and abundance would be of interest for effective conservation and management planning not only for these species, but also for the largest Neotropical felids. At this regard, ecological niche modeling based on ecological niche theory can be a useful approach, since it can help us to predict the geographic distribution of the species from occurrence data only (Peterson *et al.* 2011).

Additionally, ecological niche models have been used to predict geographic patterns of abundance (e.g. Torres *et al.* 2012, Martínez-Meyer *et al.* 2013, Weber *et al.* 2016), although this approach is less common. Expanding the use of ecological niche models to predict population abundance over large geographic areas is particularly important for designing management and conservation strategies.

Theory predicts that geographic patterns in species abundance are influenced by the position of populations in relation to the ecological niche centroid. Considering the niche as *n*-dimensional hyper-volume, higher abundances are expected to occur in populations closer to the centroid, and lower abundances towards the edges (Maguire 1973). The relationship between abundance and distance to the niche centroid has been empirically tested by Yañez-Arenas *et al.* 2012; Martínez-Meyer *et al.* 2013; Jiménez-Cervantes 2015; Ureta *et al.* 2015; Ureña-Aranda *et al.* 2015; and Martínez-Gutiérrez *et al.* Chap. 3 in this volume. Most of these studies have addressed the niche-abundance relationship through a definition of the niche based on environmental variables (mainly climatic). However, in a contemporary scenario where humans dominate ecosystems globally (Dirzo *et al.* 2014), the role of human activities should be considered more explicitly in this type of studies. In a previous study, Martínez-Gutiérrez *et al.* (Chap. 3 in this volume) found that broad scale patterns of population abundance of the collared peccary were strongly affected by human influence, contributing to the explanation of spatial heterogeneity patterns in population abundance that were not predicted by the position in the niche hyper-volume (Martínez-Gutiérrez *et al.* Chap. 3 in this volume). Additionally, human influence has also shown to be a good predictor of mammal's range sizes (Di Marco & Santini 2015) and range contractions (Channell & Lomolino 2000, Murray & Dickman 2000, Laliberte & Ripple 2004, Woodroffe *et al.* 2004, Yackulic *et al.* 2011). Human influence is spread worldwide and rapidly increasing, especially in tropical ecoregions (Venter *et al.* 2016), making even more urgent to assess its relative contribution in the determination of neotropical species distribution and abundance patterns as compared to other environmental factors.

Here we assessed the importance of human influence in determining broad-scale patterns in the distribution and abundance of the white-lipped peccary, the giant anteater, and the spotted paca. Specifically, we evaluated whether the addition of the human influence to a set of environmental variables (climatic and topographic) improved the performance of niche-model predictions for these species. Additionally, we analyzed the relationships between human influence and DNC with population abundances of the species across their geographic ranges, and we evaluated whether accounting for human influence as well as DNC explained geographic variation in population abundance better than DNC alone or human influence alone. We finally used the best model obtained to generate spatial predictive maps of population abundance across each species geographic range.

Methods

Species data

We compiled occurrence data for the white-lipped peccary, the giant anteater, and the spotted paca from the following digital public databases: VertNet beta (http://portal.vertnet.org/search), UNIBIO (http://unibio.unam.mx/), REMIB (http://www.conabio.gob.mx/remib/doctos/remib_esp.html), SpeciesLink (http://splink.cria.org.br), ArctosDatabase (http://arctos.database.museum/ Specimen

Search.cfm), Global Biodiversity Information Facility (http://www.gbif.org/), and Mammal Species of the World, Smithsonian Institution (http://collections.nmnh.si.edu/search/mammals/). We reviewed the geographic coordinates of each observation based on the descriptions of localities in the original databases, and only used observations from 1980 onward, so we could relate them to data of human influence (see below). We collected 125 observations for the white lipped peccary, 66 for the giant anteater, and 364 for the spotted paca. Finally, we translated point data into a grid of 0.02-degrees spatial resolution to match the resolution of the layers used in the niche modeling process (see below), resulting in 117 unique grid cells with known presence of white-lipped peccary (see Table S1, and Fig. S1 in Supporting Information, where 'S' indicates Supporting), 56 with known presence of giant anteater (see Table S2, and Fig. S2), and 204 with known presence of spotted paca (see Table S3, and Fig. S3).

We collected independent population abundance data from across each species range by systematically searching publications in research journals and theses, using the bibliographic databases Scopus (https://www.scopus.com/), Google Scholar (https://scholar.google.com/) and Web of Science (http://www.webofknowledge.com). From each publication, we georeferenced the study location in a 0.02° grid (as with the occurrence data) and recorded population density estimates (ind/km^2). Again, we only used data from 1980 onward, so we could relate them with the human influence data (see below). For the spotted paca we only retained estimations based on line transect methods (Buckland *et al.* 2005), and for the giant anteater those based on strip transect (Burnham *et al.* 1980) and line transect methods, because for these two species density estimates clearly differed to other methods employed. We excluded outliers from the analyses, one for the white-lipped peccary (with a density estimate more than 15 times higher than the average from the other data points), and one for the giant anteater (with a density estimate more than 5 times higher than the average from the other data points). Thus, we obtained a total of 58 density data for white-lipped peccaries (see Table S4, and Appendix S1), 9 for giant anteaters (see Table S5, and Appendix S1), and 15 for spotted pacas (see Table S6, and Appendix S1), which resulted in the same number of unique grid cells with density data for each species.

Model variables

We analyzed the species' niches by using two sets of variables: one purely environmental, that included bioclimatic and topographic variables; and one that also included an aggregated indicator of human influence. Nineteen climate variables were drawn from the WorldClim database, version 1.4, which provides monthly average information for the period 1950-2000 at spatial resolution of 30'' (approx. 1 km) (Hijmans *et al.* 2005). Topographic variables included elevation, aspect, and slope, all calculated from the digital elevation model of the shuttle radar topography mission (STRM), also at a spatial resolution of 30'' (Farr *et al.* 2007). For computational tractability, all layers were resampled to a grid size of 0.02-degrees resolution (approx. 2 km in the study region).

We excluded from our analyses variables that were highly correlated (Pearson's $r \geq 0.90$). As a result of this process we selected 15 environmental variables for the white-lipped peccary, 12 for the giant anteater, and 14 for the spotted paca, which are shown in Table 1.

To analyze human influence, we used the Global Terrestrial Human Footprint (HF) Index for years 1993 and 2009 (Venter *et al.* 2016). These datasets integrate information on the extent of built-up environments, cropland, pastureland, human population density, night-time lights, railways, roads, and navigable waterways, at spatial resolution of $1km^2$. As before, these layers were resampled to a grid size of 0.02-degrees resolution.

Table 1. Environmental variables used to model the niche of the species in Maxent.

Variables	*Tayassu pecari*	*Myrmecophaga tridactyla*	*Cuniculus paca*
Annual mean temperature	x	x	
Mean diurnal range	x		x
Temperature seasonality	x	x	x
Max temperature of warmest month	x		x
Min temperature of coldest month	x		
Mean temperature of wettest quarter	x	x	x
Mean temperature of driest quarter			x
Mean temperature of warmest quarter		x	
Annual precipitation	x	x	x
Precipitation of wettest month			x
Precipitation seasonality	x	x	x
Precipitation of wettest quarter	x		
Precipitation of driest quarter	x	x	x
Precipitation of warmest quarter	x	x	x
Precipitation of coldest quarter	x	x	x
Elevation	x	x	x
Aspect	x	x	x
Slope	x	x	x

Ecological niche modeling

We modeled the ecological niches of the species and their potential distributions using the maximum entropy approach (Maxent; Phillips *et al.* 2006). Maxent has performed well in comparisons of modeling techniques that do not require recorded absences and allows fitting of complex responses (Elith *et al.* 2006, 2011).

We specifically used the following modeling protocol for each species. First, we delimited the study area by identifying the ecoregions, including the distributional range of the species and the occurrence data, regardless the year of record and the number of occurrences in a grid cell. For this, we used the IUCN range maps (Reyna & WCS 2013, IUCN 2014, IUCN-SSC-SMSG 2016), and the digital map of Terrestrial ecoregions of the World (Olson *et al.* 2001). We assumed that the resulting areas reflect the geographic ranges that have been accessible to the species over relevant time periods (Peterson *et al.* 2011; see Figs. S1-S3). Then, using the software Maxent, we model the ecological niche of the species with the occurrence dataset and the environmental values (climatic and topographic) correspondent to the extent of the study area. We chose the most appropriate Maxent settings for each species using the R package *ENMeval* (Muscarella *et al.* 2014) in R (R Core Team 2014) as described below. Models were fitted with *ENMeval* using the 'random *k*-fold' method of data partitioning (Muscarella *et al.* 2014), which consisted in using 75% of the presence records as training data and the remaining 25% for evaluation by cross-validation in 4 replicates. We built and compared models that varied in the use of feature classes (six different combinations: L, LQ, H, LQH, LQHP, LQHPT; where L = linear, Q = quadratic, H = hinge, P = product, and T = threshold) and in the regularization multiplier value (from 0.5 to 4 every 0.05). Thus, 192 individual model runs were generated for each species using *ENMeval*. As a result of this process, we built a final "purely environmental" model in Maxent using the settings that resulted in lowest AICc according to these analyses (see Table S7).

In a second step, we built a model including the HF variable in addition to the environmental variables, using the same species occurrence data, settings, and data partitioning strategy employed in the "purely environmental model" in order to be able to compare results. In these analyses we used the 1993 HF dataset since the majority of the occurrences were closer to 1993 than to 2009. Finally, we projected the resulting model using the 2009 dataset.

We used the area under the curve (AUC) of the receiver operating characteristic (ROC) to compare Maxent predictions with and without HF. Specifically, we used the AUC of the evaluation data (AUC_{Test}) (Lecours *et al.* 2016), and retained the model with the highest AUC_{Test} score for further analyses (i.e. the binary model of potential distribution and the model of DNC). AUC evaluates the discriminatory capacity of the model between locations where observations are present and absent (Fielding & Bell 2002). An AUC = 0.5 indicates that model performance is equal to a random prediction, and values > 0.5 indicate that predictions are better than random, with values closer to 1 indicating a better model performance. We are aware that AUC is not an absolute measure of model fitness and its reliability as a comparative measure of accuracy between model results is under debate, especially when different modeling algorithms are used, or when different species or areas are compared (Peterson *et al.* 2008; Lobo *et al.* 2008; but see McPherson *et al.* 2004, Vaughan & Ormerod 2005). However, AUC is considered a robust measure of relative model performance for comparing models that have been developed using the same algorithm and for the same species and study area, as in our case (Edrén *et al.* 2010, Merow *et al.* 2013, Lecours *et al.* 2016).

We assessed the relative importance of each variable to the niche-models through the permutation importance calculated by Maxent. To calculate it, the values of each variable on training presence and background data are randomly permuted; the model is reevaluated on the permuted data, and the resulting drop in training AUC is normalized to percentages (Phillips *et al.* 2006).
In all cases, Maxent’s cumulative outputs were converted into binary maps of potential distributions using the minimum training presence threshold value.

Geographic variation in local population abundance

We analyzed the effects of the distance to the niche centroid (DNC), and human footprint (HF) on the spatial heterogeneity in local population abundances. To calculate the distance to the niche centroid (DNC), we followed Martínez-Meyer *et al.* (2013). For each species, we used the binary distribution map to calculate the niche centroid and then we calculated the Euclidian distance in "environmental space" from each pixel with predicted presence to the centroid. We extracted the values of the characteristics of each grid cell with predicted presence, and standardized these variables to a common scale with mean = 0 and standard deviation = 1. Finally, we calculated multidimensional Euclidean distance from each grid cell to the niche centroid as follows:

$$DNC = \sqrt{\Sigma(\mu_j - a_{ij})^2}$$

where DNC = distance to the niche centroid, μ_j = mean of variable *j* (standardized value = 0), and a_{ij} = value of the variable *j* in grid cell *i*. We represented DNC in a raster map, and rescaled the values between 0 and 1, with 0 representing the niche centroid and 1 the largest distance to this centroid.

It should be mentioned that when the binary models of potential distribution included the HF variable, we obtained two models of DNC, one associated to the 1993 dataset, and other one to the 2009 dataset, so we could relate the abundance data to the DNC value closest to the year when the abundance study was conducted.

To test for the effect of the human influence on the population abundances of the species, we assigned the HF value closest to the year (i.e. 1993 or 2009) when the abundance study was conducted.

White-lipped peccary

To test for the effect of DNC on the local abundance of the white-lipped peccary, we used a Generalized Least Square regression (GLS) including a power variance-function structure (Pinheiro & Bates 2000) in order to account for heterogeneous variance in the data. We also assessed the shape of the abundance-niche centrality relationship evaluating whether the rate of change in local abundance was steeper near the upper boundary of the conditional distribution, using quantile regression analysis (Martínez-Gutiérrez *et al.* Chap. 3 in this volume). Quantile regression (Koenker & Bassett 1978) is a method for estimating functional relationships between variables at any portion of the probability distribution of the relationship between the response and the predictor, instead of only in the mean response (Cade & Noon 2003). The significance of the regression at each quantile was assessed by constructing confidence intervals through a Huber sandwich estimate of the covariance (Koenker & Machado 1999). We evaluated the 50th and 93th percentiles representing the central response in population abundance, and the upper limit of abundance, respectively. When using quantile regression to estimate changes in the upper edge of distributions, it is tempting to consider the maximum percentile (tau = 1) as the best possible estimate for the limiting relation (Cade *et al.* 1999). However, when calculating the standard errors for values of tau near 1, there's a possibility that the function will lead to a tau greater than 1. Thus, we chose the 93th percentile because with our data it was the maximum value of tau that we could estimate with precision by calculating a confidence interval and for which we could assess the significance. We compared the results using an ANOVA test of equality of slopes (Koenker 2005).

We tested for the effect of human influence on the population-abundance niche-centrality relationship by fitting quantile regression models for the 50th and 93th percentiles including both factors, DNC and HF. To compare the relative contributions of the DNC and the HF, we standardized the variables to convert them to a common scale with mean = 0 and standard deviation = 1. Besides, we also fitted quantile regression models for both percentiles only considering the HF.

We selected the best model of abundance at each quantile analyzed between four competing models: a model with DNC exclusively; a model including DNC and HF; a model with HF exclusively; and a null model of no effect. Model selection was performed calculating the Akaike Information Criterion (AIC) and Akaike weights (w_i) (Burnham & Anderson 2002). All the analyses were conducted in R (R Core Team 2014), using the package *nlme* for estimation of generalized least squares linear models (Pinheiro & Bates 2000), and the *quantreg* package for quantile regressions (Koenker 2015).

It should be mention that since density data of the white-lipped peccary were obtained using different field sampling methods, we preliminarily tested the influence of the method on the density data using a linear model, but we found no significant effect, thus we pooled together all density data. Furthermore, using linear models, we also tested if the residuals obtained in the GLS and in the quantile regressions, described above, were explained by the sampling methods, but again, we didn’t find significant effects (Table S8).

Spotted paca and giant anteater

For the spotted paca and the giant anteater, preliminary analyses did not reveal variance heterogeneity, nor a wedge-shaped relationship between abundance and DNC or between abundance and HF, possibly because of the small sample sizes (15 and 9 population abundance observations, respectively). Thus, we used linear models to analyze the effect of DNC, HF, and both factors together over population abundances. Again, we also included a null model of no effect, and selected the best of these four models by calculating AIC and w_i values (Burnham & Anderson 2002). All analyses were conducted in R (R Core Team 2014).

Spatial predictions of abundance

Finally, we used the coefficients of the best model selected for each species to generate spatial predictions of local abundances at biogeographical extents. In the cases when we considered the human influence to obtain the abundance predictions, we used the most recent human footprint dataset (i.e. 2009). We only extrapolated spatial predictions for the observed rank of abundances.

Results

Ecological niche modeling

The inclusion of the human footprint (HF) improved the predictive accuracy of Maxent models for the spotted paca (mean AUC_{Test} of the 4 replicates including and excluding HF, respectively: AUC_{Test} = 0.888, SD = 0.041 *vs* 0.860, SD = 0.051) and for the white-lipped peccary (mean AUC_{Test} = 0.855, SD = 0.025 *vs* 0.849, SD = 0.016), but not for the giant anteater (mean AUC_{Test} = 0.816, SD = 0.045 vs. 0.840, SD = 0.027). We retained the best niche model for each species in subsequent analyses, i.e. including HF for the spotted paca and the white-lipped peccary, and excluding this variable for the giant anteater.

The most important variables according to niche analyses, i.e. those that together accounted for more than 60% of the permutation importance (mean value of the 4 replicates for each species), were the precipitation of the driest quarter (37.2%), the temperature seasonality (17.5%), and the mean temperature of wettest quarter (12.6%) for the white-lipped peccary; the mean temperature of warmest quarter (35.5%) and the annual mean temperature (28.4%) for the giant anteater; and the precipitation of driest quarter (27.6%), the human footprint (16.1%), the mean temperature of driest quarter (10.2%), and the elevation (9.3%) for the spotted paca. The relative contribution of each variable to the niche models according to the permutation importance is shown in Tables S9 for the white-lipped peccary, S10 for the giant anteater, and S11, for the spotted paca.

The potential distributional areas derived from the niche models, as well as the DNC models are shown in Figs. 1, 2, and 3, for the white-lipped peccary, the giant anteater, and the spotted paca, respectively.

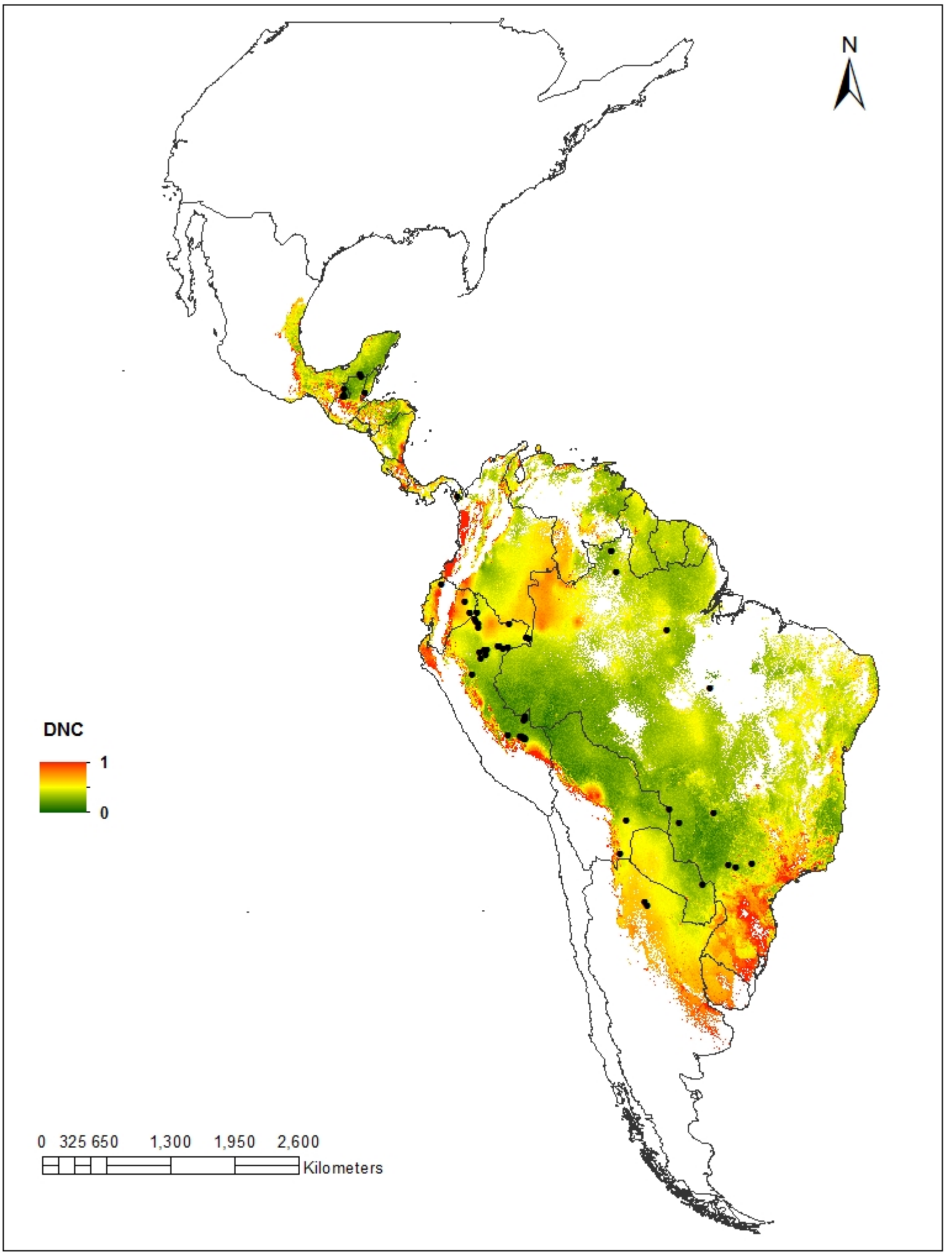


Figure 1 Geographic representation of the distance to niche centroid (DNC) of *Tayassu pecari*), with values from 0 = niche centroid (green) to 1 = farthest from niche centroid (red). Black points represent 58 abundance data of the species (ind/km^2). Here, we present the DNC model built with the human footprint dataset of 1993. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

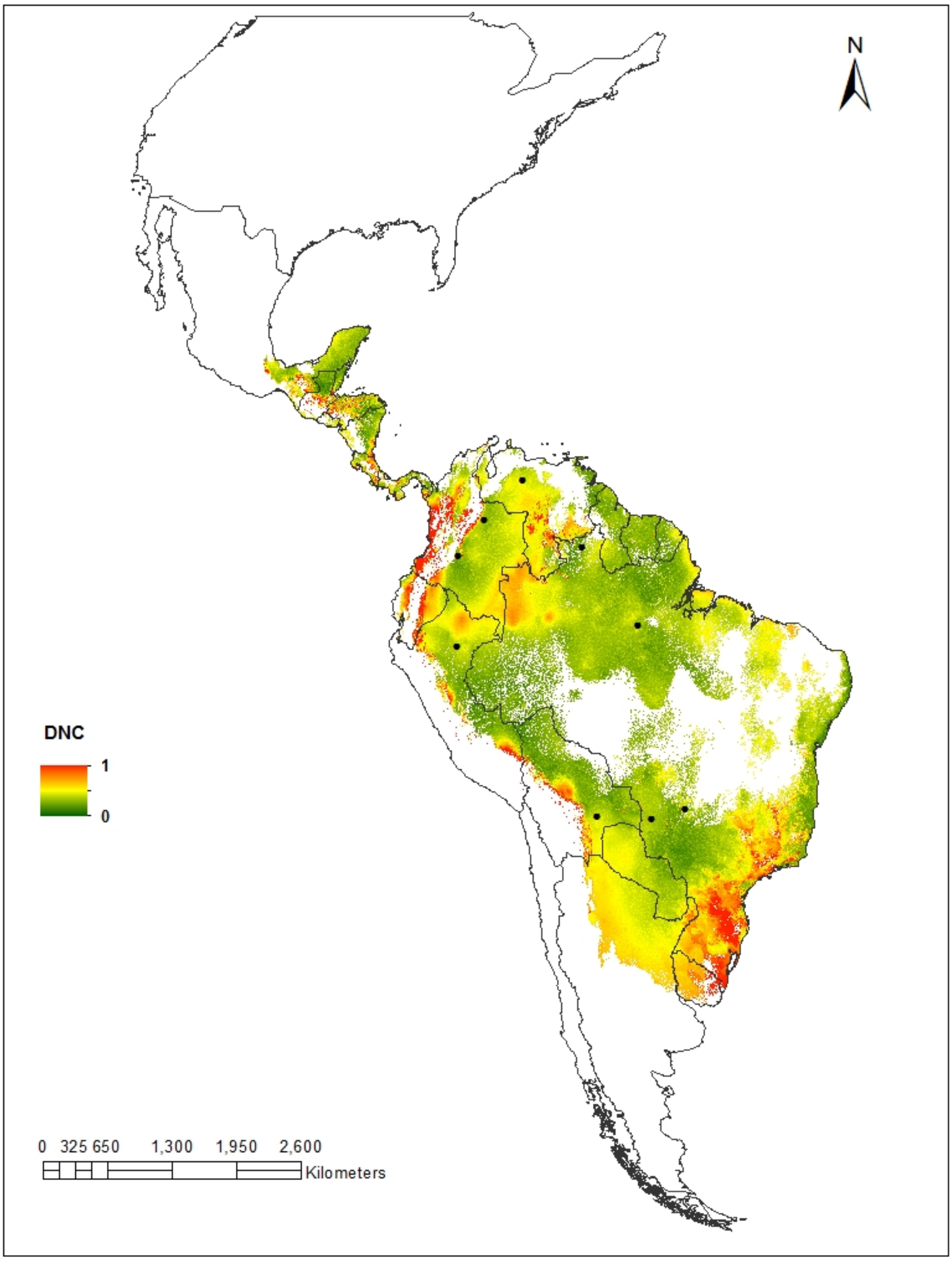


Figure 2. Geographic representation of the distance to niche centroid (DNC) of *Myrmecophaga tridactyla*), with values from 0 = niche centroid (green) to 1 = farthest from niche centroid. Black points represent 9 abundance data of the species (ind/km^2). Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

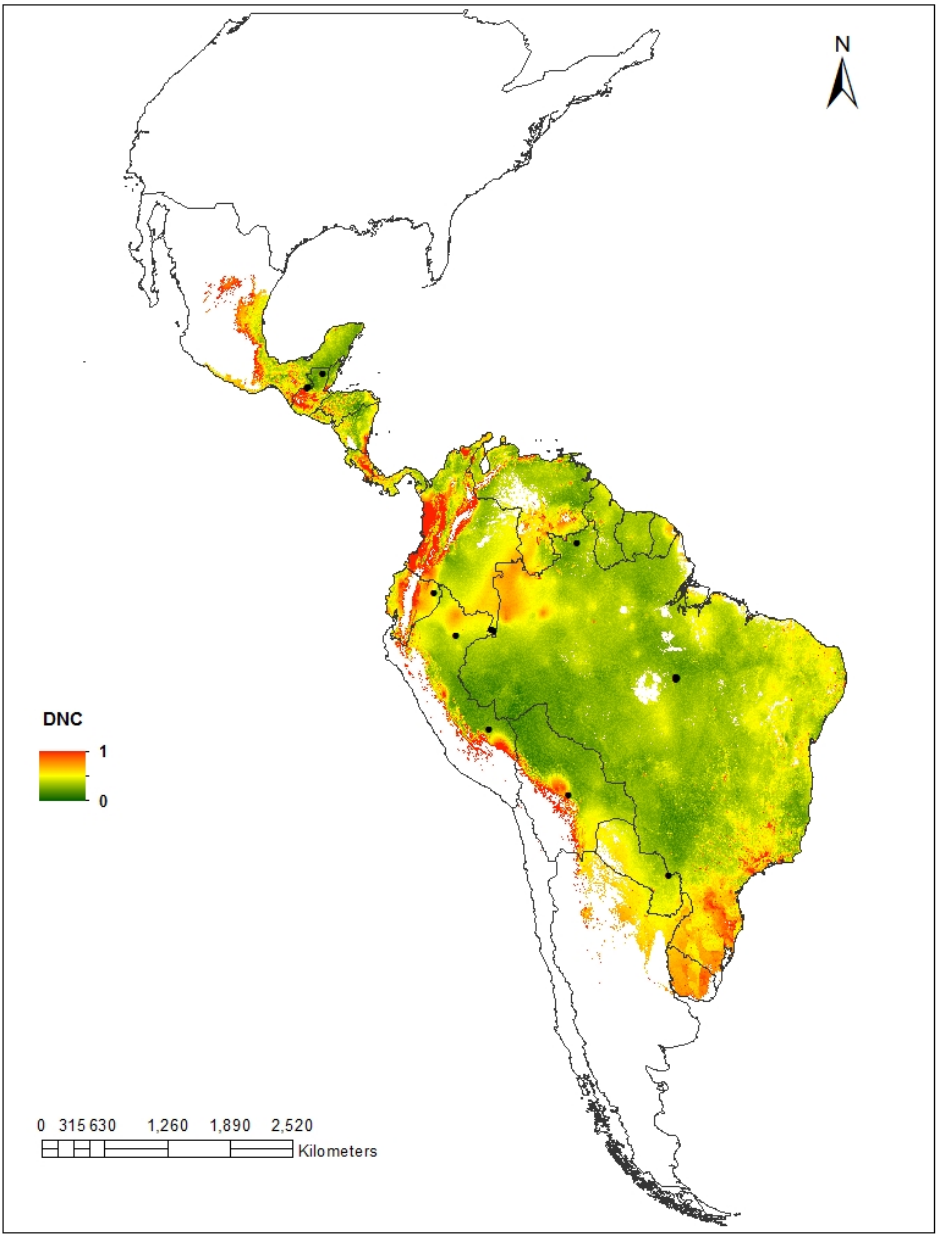


Figure 3. Geographic representation of the distance to niche centroid (DNC) of *Cuniculus paca*, with values from 0 = niche centroid (green) to 1 = farthest from niche centroid. Black points represent 15 abundance data of the species (ind/km^2). Here, we present the DNC model built with the human footprint dataset of 1993. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Geographic variation in local population abundance and abundance predictions

White-lipped peccary

GLS model showed that the relationship between local population abundance and DNC was negative and significant (regression coefficient = -58.25 ± 13.62 SE; *P* = <0.001), (Fig. 4).

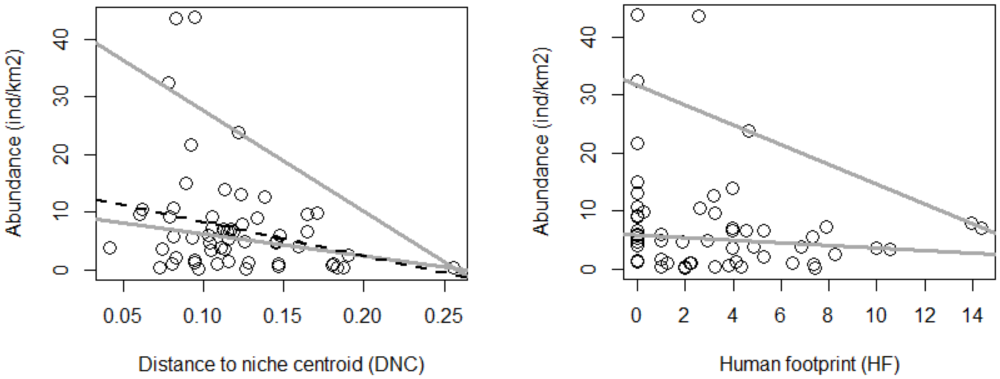


Figure 4. Relationship of local population abundance of *Tayassu pecari* with distance to the niche centroid (from 0 = niche centroid to 1 = farthest from niche centroid) and human footprint. Gray lines represent the quantile regressions for the 93th (upper line) and 50th percentiles. The dashed line represents the linear regression (GLS) with power variance function structure.

Model selection results showed that for the 50th percentile, the best model considered only DNC; while for the 93th percentile the best model included both DNC and HF as predictors (Table 2). Quantile regression analyses indicated a steeper relationship between abundance and DNC for the 93th percentile than for the median (Table 3, Fig. 4), and the difference between these two slopes was significant according to the ANOVA test of equality of slopes ($F_{1,\ 115}$ = 10.40, $P < 0.01$). The effect of both factors for the 93th percentile was also negative and comparatively stronger for the DNC than for the HF (Table 3). Again, the ANOVA test of equality of slopes between 50th and 93th percentiles showed that this difference was significant ($F_{2, 114} = 4.8$, $P = 0.001$). Based on the model selection results, we built spatial models of expected abundances for the 50th and 93th percentile, which ranked 0.03 - 9.90 ind/km^2 for the 50th, and up to 40.63 ind/km^2 for the 93th percentile (Figs. 5a and 5b, respectively).

Table 2**.** Model selection between quantile regression models (Akaike Information Criterion - AIC, and the Akaike weights - w_i) on the median (0.50 quantile) and upper limit (0.93 quantile) of abundance of *Tayassu pecari* (ind/km^2). Y~1 = null model of no effect. Y~DNC = abundance as a function of distance to the niche centroid. Y~HF = abundance as a function of human footprint. Y~DNC+HF = abundance as a function of distance to the niche centroid and human footprint. The best model for each quantile according to the Akaike weights is indicated in bold.

Model	Quantile (τ) 0.50		Quantile (τ) 0.93	
	AIC	w_i	AIC	w_i
Y~1	394	0.05	514	0.00
Y~DNC	390	**0.63**	497	0.11
Y~HF	394	0.04	505	0.00
Y~DNC+HF	392	0.28	492	**0.89**

Table 3. Quantile regression model results for the effects of distance to niche centroid (DNC) and human footprint (HF), on the median (0.50 quantile) and upper limit (0.93 quantile) of abundance of *Tayassu pecari* (ind/km^2). For the model with two predictors we also show the standardized coefficients (between parentheses) so that they can be compared.

Model		Quantile (τ) 0.50		Quantile (τ) 0.93	
		Coefficient	SE	Coefficient	SE
Y~DNC		-37.72	11.96	-169.36	145.54
Y~HF		-0.22	0.28	-1.70	0.64
Y~DNC+HF	DNC	-37.39 (-1.45)	18.53	-150.40 (-5.85)	34.25
	HF	-0.26 (-0.91)	0.21	-1.25 (-4.38)	0.47

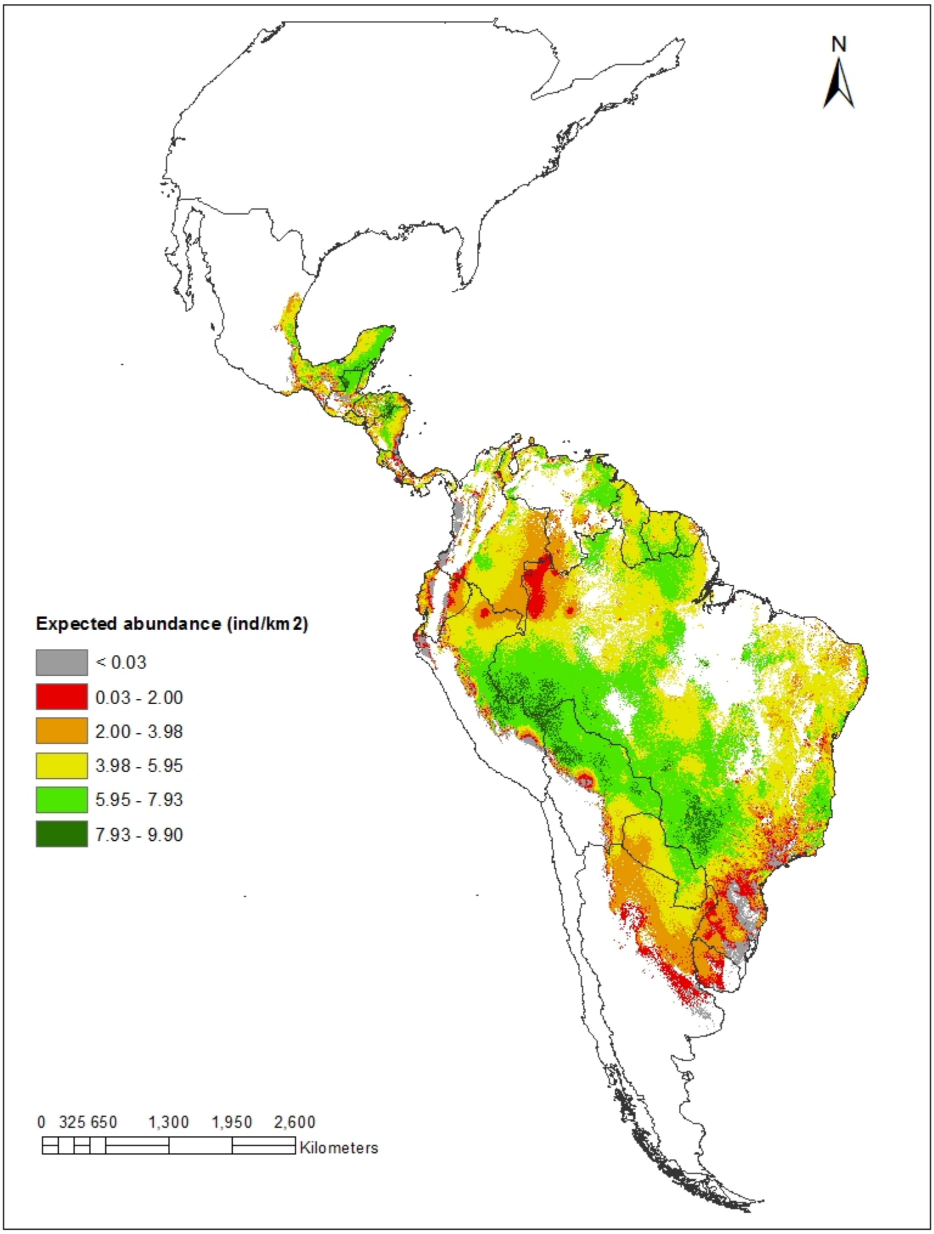


Figure 5a. Abundance prediction of *Tayassu pecari* along its potential geographic range based on the effect of distance to the niche centroid on the observed median density (50th percentile). We only extrapolated spatial predictions for the observed rank of abundances, therefore in gray we represent areas with an abundance prediction below the minimum observed. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

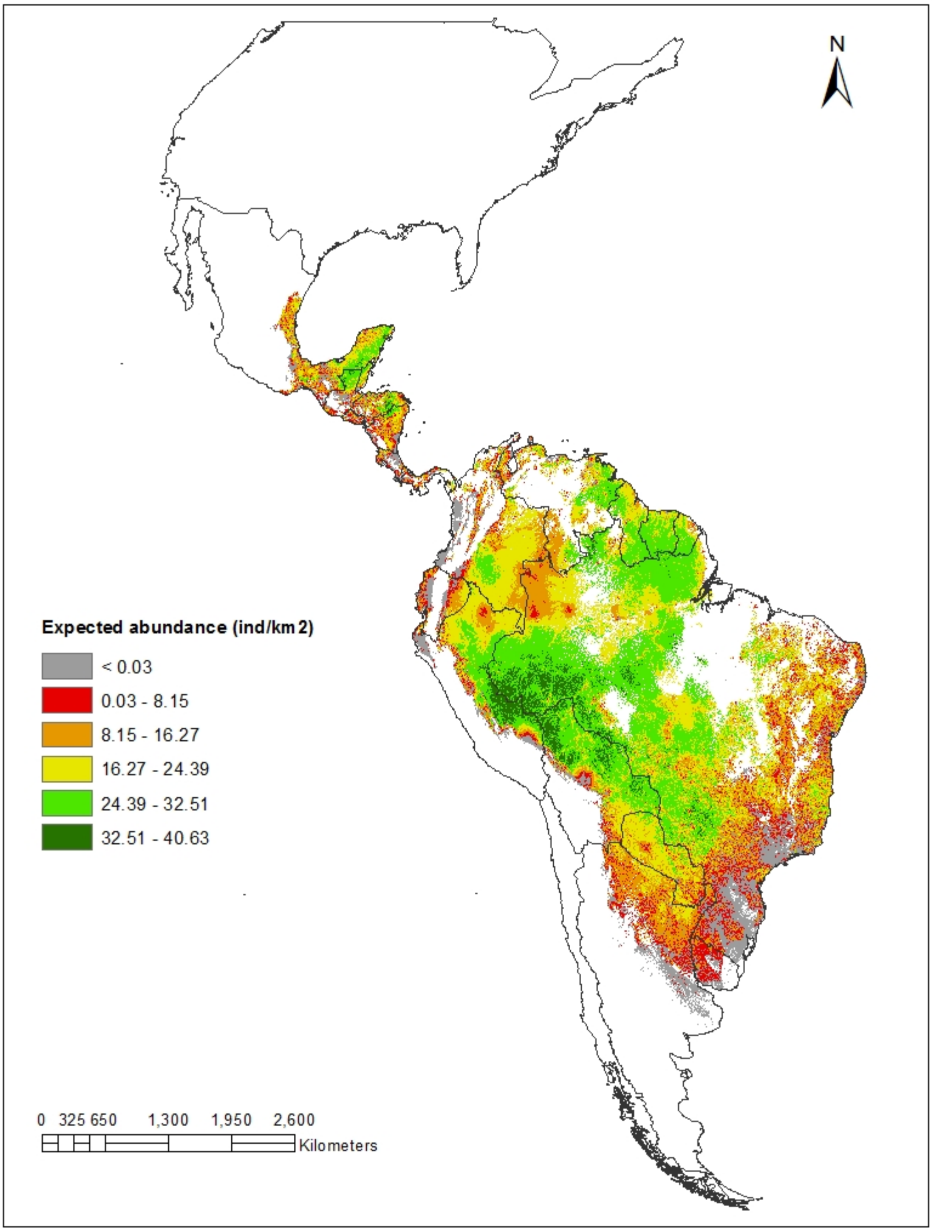


Figure 5b. Abundance prediction of *Tayassu pecari* along its potential geographic range based on the effect of distance to the niche centroid and human footprint on the observed carrying capacity (93th percentile). We only extrapolated spatial predictions for the observed rank of abundances, therefore in gray we represent areas with an abundance prediction below the minimum observed. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Giant anteater

According to the model selection results, the local population abundance of giant anteater was better explained by DNC (Table 4) with a negative relationship (Table 5, Fig. 6). Spatial prediction of abundance derived from this equation shows expected abundances ranking from 0.03 - 0.80 ind/km^2 (Fig. 7).

Table 4. Model selection between linear regression models (Akaike Information Criterion - AIC, and the Akaike weights - w_i) on the abundance of *Myrmecophaga tridactyla* and *Cuniculus paca* (ind/km^2). Y~1 = null model of no effect. Y~DNC = abundance as a function of distance to the niche centroid. Y~HF = abundance as a function of human footprint. Y~DNC+HF = abundances as a function of distance to the niche centroid and human footprint. The best model according to the Akaike weights is indicated in bold.

	Myrmecophaga tridactyla		*Cuniculus paca*	
Model	AIC	w_i	AIC	w_i
Y~1	6.31	0.09	72.2	0.24
Y~DNC	2.54	**0.61**	74.1	0.09
Y~HF	6.93	0.07	71	**0.45**
Y~DNC+HF	4.53	0.23	72.5	0.21

Table 5. Linear regression results for the effects of distance to niche centroid (DNC) and human footprint (HF), on the abundance of *Myrmecophaga tridactyla* (ind/km^2). For the model with two predictors we also show the standardized coefficients (between parentheses) so that they can be compared.

Model		Coefficient	SE	R^2
Y~DNC		-12.06	4.81	0.47
Y~HF		-0.04	0.04	0.14
Y~DNC+HF	DNC	-11.89 (-0.20)	6.12	0.47
	HF	-0.00 (-0.01)	0.04	

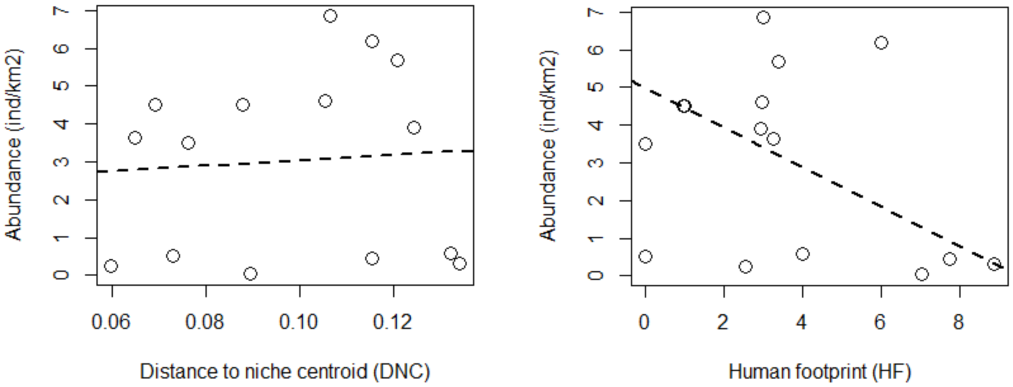


Figure 6. Linear regression representing the relationship of local population abundance of *Myrmecophaga tridactyla* with distance to the niche centroid (from 0 = niche centroid to 1 = farthest from niche centroid) and human footprint. The DNC doesn't include the human footprint variable.

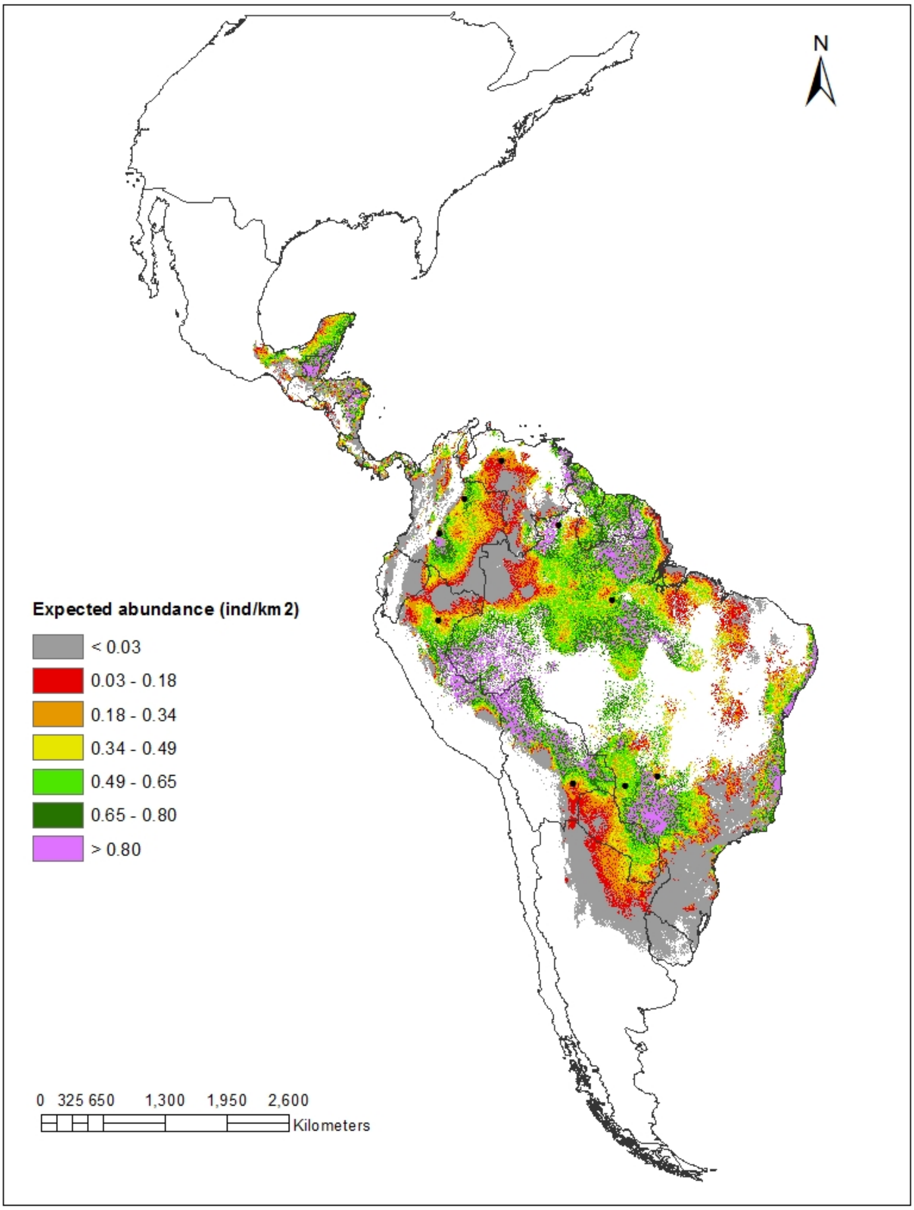


Figure 7. Abundance prediction of *Myrmecophaga tridactyla* along its potential geographic range based on the effect of distance to the niche centroid on the observed mean density. We only extrapolated spatial predictions for the observed rank of abundances, therefore in gray we represent areas with an abundance prediction below the minimum observed; and in purple areas with an abundance prediction above the maximum observed. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Spotted paca

The model selection results showed that including HF only was the best model to describe the geographic abundance patterns of the spotted paca (Table 4). The relationship between abundance and HF was negative, although with a low regression coefficient (Table 6, Fig. 8). We used this model to generate the spatial model of expected abundance, resulting in predictions ranking from 0.03 - 4.08 ind/km^2 (Fig. 9).

Table 6. Linear regression results for the effects of distance to niche centroid (DNC) and human footprint (HF), on the abundance of *Cuniculus paca* (ind/km^2). For the model with two predictors we also show the standardized coefficients (between parentheses) so that they can be compared.

Model		Coefficient	SE	R^2
Y~DNC		7.07	26.44	0.005
Y~HF		-0.29	0.23	0.11
Y~DNC+HF	DNC	39.55 (1.01)	30.30	0.22
	HF	-0.51 (-1.39)	0.28	

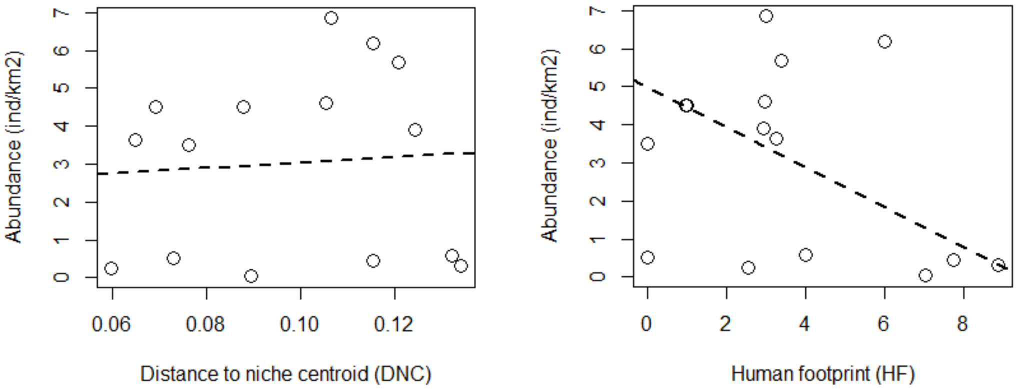


Figure 8. Linear regression representing the relationship of local population abundance of *Cuniculus paca* with distance to the niche centroid (from 0 = niche centroid to 1 = farthest from niche centroid) and human footprint.

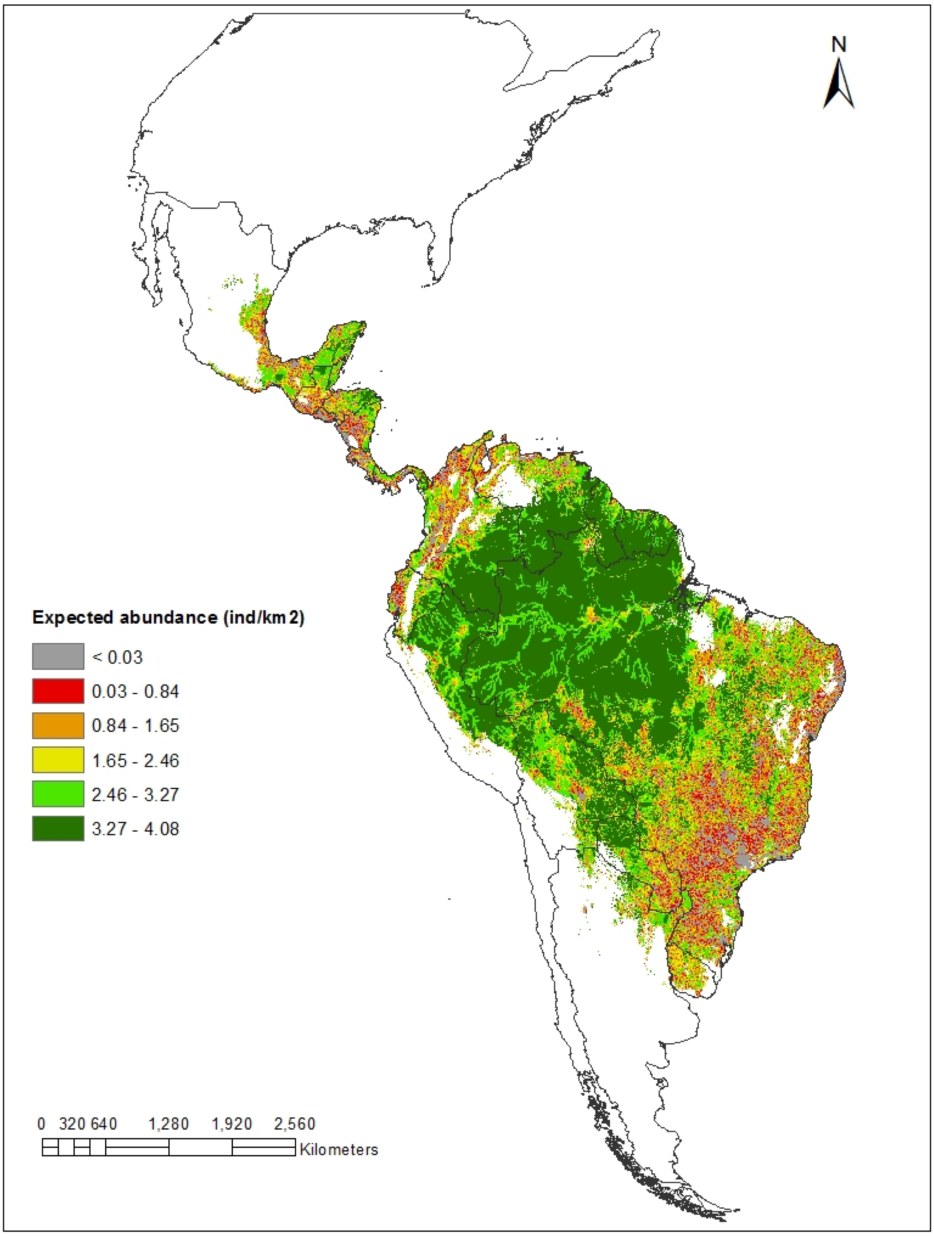


Figure 9. Abundance prediction of *Cuniculus paca* along its potential geographic range based on the effect of human footprint on the observed mean density. We only extrapolated spatial predictions for the observed rank of abundances, therefore in gray we represent areas with an abundance prediction below the minimum observed. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Discussion

We found that the addition of the human footprint to the climatic and topographic set of variables in ecological niche models improved accuracy for the white-lipped peccary and for the spotted paca. However, the relative contribution of the human footprint was high only for the latter, since it was the second most important variable to model its ecological niche (16.1%), while for the white-lipped peccary contributed less than 5%. Therefore, we concluded that, except for the spotted paca, the climatic factors had a stronger influence in driving the potential distribution of the species analyzed here.

In the case of the spotted paca, ecological niche models for this species based only on climate and topography could have led to an over-prediction of the amount of suitable habitat by overlooking the human footprint. The spotted paca is heavily hunted by humans for consumption (Pérez 1992, Gallina *et al.* 2012, Patton 2015) and as it is considered a pest (Pérez 1992, Lobão & Nogueira-Filho 2011), and local extinctions have occurred due to habitat destruction in the southeast of its range (Emmons 2016).

Hunting and habitat loss are threats have been described for the other two species as well (Keuroghlian *et al.* 2013, Miranda *et al.* 2014). Giant anteaters are affected by road kills and wildfires (Miranda *et al.* 2014), whereas competition with livestock (Keuroghlian *et al.* 2013), zoonotic diseases, (Fragoso 2004, De Freitas *et al.* 2010) and introduced species (Herrera *et al.* 2008) have been described as threats to the white-lipped peccary. The fact that the human footprint significantly affected the occurrence of only one of the three species studied might be related to differences in their traits, since the spotted paca is smaller, has smaller home ranges (Pérez 1992, Beck-King & Von Helversen 1999), and presumably less dispersal ability compared to the white-lipped peccary (Mayer & Wetzel 1987) and the giant anteater (Shaw *et al.* 1987, Eisenberg & Redford 1999). All these traits would make the spotted paca more sensitive to the human influence.

The best models to describe abundances included the negative effect of the human footprint except for the giant anteater (although a negative relationship can be appreciated in Fig. 5). Previous local studies have found that intermediate or low levels of human disturbance may favor anteaters by providing greater habitat heterogeneity and lower jaguar abundance (Quiroga *et al.* 2016). Humanized environments, like timber plantations of *Acacia mangium*, can also provide to the giant anteater food and cover from extreme temperatures and potential predators (Kreutz *et al.* 2012).

Results showed that higher local population abundances in all species occurred at shorter distances to the niche centroid, except for the spotted paca, for which we did not find any effect of DNC. This might be indicating that the spotted paca is to a great extent influenced by local-scale factors such as microclimate conditions, or densities of natural predators.

Furthermore, the association between local population abundance and DNC varied with the species. For the giant anteater, population abundances were better described only by DNC, while for the white-lipped peccary, the relationship was different depending on the quantile analyzed, so that median abundance was better predicted solely by DNC, but the carrying capacity by considering both DNC and HF. That is, the relationship between abundance of white-lipped peccary and the predictors was wedge-shaped, as was found previously for the collared peccary (Martínez-Gutiérrez *et al.* Chap. 3 in this volume); with both low and high abundances closer to the niche centroid and at lower levels of HF, but with consistently low abundances farther from the niche centroid and at higher levels of HF. Moreover, as found for the collared peccary, model selection results showed that the best model to describe the median abundance differed from the model fitted at the upper-quantile limit (Martínez-Gutiérrez *et al.* Chap. 3 in this volume). However, for the white-lipped peccary results were contrary to what we found for the collared peccary, for which the upper limit of abundance was better explained solely by DNC as defined by environmental variables (Martínez-

Gutiérrez *et al.* Chap. 3 in this volume). This might be due to a more vulnerability of the white lipped peccary to human influence, since it requires large and ecologically intact areas to maintain viable populations (Mayer & Wetzel 1987, Altrichter & Boaglio 2004, Keuroghlian & Eaton 2008)

We should also mention that we didn’t find wedge-shaped relationships for the giant anteater and the spotted paca, possibly as a consequence of the low sample sizes, which compromises the capacity of quantile regressions for detecting this type of pattern (and which made unnecessary the use of quantile regressions). In fact, this low number of observations might be also influencing the results obtained in the abundance models.

Our findings point out the importance of including the human footprint in both species distribution and abundance models, especially in the case of species hunted by humans like the ones studied here. If the human footprint has an important effect on the presence/absence of a species, it is expected that it also affects its abundance. However, we have shown that in some cases population abundance responds to the human influence even if it does not critically determines the species distribution. In summary, the human footprint can be a factor of vulnerability or local extinction risk, with the aggravating circumstance that its magnitude can change abruptly.

Predicting spatial patterns of abundance at biogeographic extents is critical to identify areas of special interest for conservation, since extinction risk is enhanced at low population densities (Purvis *et al.* 2000) due to their greater vulnerability to local catastrophes, demographic stochasticity, inbreeding, and mutational meltdown (Brown 1995, Lande 1999). This is particularly meaningful for vulnerable species such as the white-lipped peccary (Keuroghlian *et al.* 2013) and the giant anteater (Miranda *et al.* 2014). Furthermore, given the importance of biotic interactions in ecological processes, the spatial models of abundance for these prey species can be, in turn, used to predict the indirect effects that the human influence can have on large predators such as the jaguar and the cougar. Finally, spatial predictions of prey abundance are critically needed to forecast the dynamics and population trends of threatened predators (Fernández *et al.* 2007).

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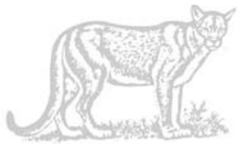

CAPÍTULO 5

Discusión General y Conclusiones

Discusión General

Los jaguares y los pumas se ven amenazados tanto por la pérdida y fragmentación de sus hábitats naturales, como por la disminución de sus presas (Sanderson *et al.* 2002, Negri y Quigley 2010). Bajo este contexto, es muy importante que los programas de conservación y manejo de estos felinos se basen en un conocimiento preciso de su ecología trófica. Sin embargo, nosotros encontramos que si bien existe un número relativamente de alto de estudios de dieta, son muy pocos los estudios en los que se usan métodos altamente fiables para identificar al depredador (5 de 27 para jaguares y 11 de 50 para pumas). Además, estos solamente cubren una pequeña fracción de la distribución total de estas especies, ya que corresponden a 4 países en el caso de los jaguares (Brasil, Guatemala, Belice y Paraguay), y a 6 en el caso de los pumas (Estados Unidos, Canadá, Guatemala, Belice, Brasil y Paraguay).

En consecuencia, es muy poco lo que a ciencia cierta conocemos sobre la variabilidad geográfica en la alimentación de jaguares y pumas. Este problema puede generar errores más allá de la mera descripción de la dieta, ya que estos resultados frecuentemente son usados para calcular amplitud y traslape de nicho trófico, peso medio de las presas y biomasa consumida (e.g. Levins 1968, Colwell y Futuyma 1971, Hurlbert 1978, Ackerman *et al.* 1984, Iriarte *et al.* 1990); así como también pueden ser usados para entender procesos ecológicos como competencia, coexistencia entre especies, o conflictos con intereses humanos (e.g. Núñez *et al.* 2000, De Azevedo 2008, Rosas-Rosas *et al.* 2008). Sin embargo, esta es la primera vez que se evalúa el impacto que tiene el método usado para identificar al depredador sobre los resultados reportados en estudios de dieta, tanto publicados, como de literatura gris.

Basándonos únicamente en la información fiable, las presas que pudieron ser identificadas hasta especie y que fueron importantes en la dieta de ambos felinos fueron: el pecarí de collar (*Pecari tajacu*), la paca común (*Cuniculus paca*), el perezoso de dos dedos (*Choloepus didactylus*), el oso melero (*Tamandua tetradactyla*) y la corzuela (*Mazama gouazoubira*). Aunque cabe mencionar que la primer especie fue importante en la dieta del puma en el Neártico.

Por otro lado, el oso hormiguero gigante (*Myrmecophaga tridactyla*), el coatí de cola anillada sudamericano (*Nasua nasua*) y el coatí de nariz blanca (*Nasua narica*) fueron especies importantes en la dieta del jaguar. Mientras que el pecarí de labios blancos (*Tayassu pecari*), el agutí centroamericano (*Dasyprocta punctata*), el cuis moro (*Galea musteloides*) y la comadreja (*Didelphis albiventris*) lo fueron en la dieta del puma.

No encontramos estudios de dieta de jaguar altamente fiables en el Neártico pero sí de puma, siendo sus presas más importantes en dicha región: el puercoespín norteamericano (*Erethizon dorsatum*), el venado bura (*Odocoileus hemionus*), el venado cola blanca (*Odocoileus virginianus*), el ciervo común (*Cervus elaphus*), el alce (*Alces alces*) y la oveja (*Ovis aries*).

Es necesario conocer los patrones geográficos de abundancia de estas especies presa para entender mejor la distribución, abundancia y amenazas potenciales de jaguares y pumas; sin embargo, en esta tesis nos centramos en 4 especies: el pecarí de collar, el pecarí de labios blancos, el oso hormiguero gigante y la paca común, debido principalmente al número de estudios de densidad disponibles y al tamaño y solapamiento de sus áreas de distribución.

Con respecto a los patrones geográficos de abundancia de las especies presa seleccionadas, nuestros análisis mostraron que en la mayoría de los casos (i.e. excepto para la paca común) se cumplió la hipótesis de la centralidad del nicho ecológico. Es decir, la abundancia poblacional de la mayoría de las especies estuvo influenciada por su posición con respecto al centroide de su nicho ecológico, observándose abundancias más bajas hacia la periferia de la nube multivariada del nicho, donde las condiciones ambientales son menos favorables. Por el contrario, la relación entre la abundancia poblacional y su ubicación con respecto al centroide geométrico de su distribución geográfica no fue significativa (aunque esta relación solamente se probó con una especie). Lo cual implica que la abundancia se relaciona más fuertemente con el espacio ambiental que con el espacio geográfico, y que el centroide ambiental no siempre coincide con el geográfico. Nuestros resultados concuerdan con lo reportado en estudios previos, por lo que contribuyen a soportar la hipótesis de la centralidad del nicho ecológico sobre la hipótesis de la centralidad geográfica (Yañez-Arenas *et al*. 2012, Martínez-Meyer *et al*. 2013); así como también aportan evidencia sobre la adecuabilidad del método empleado para generar los modelos de distancia al centroide del nicho.

Por otro lado, en la mayoría de los casos (i.e. excepto para la el oso hormiguero gigante) se cumplió la hipótesis de que la influencia humana afecta negativamente las abundancias poblacionales. Para ambas especies de pecaríes, su inclusión contribuye a mejorar las predicciones de abundancia basadas en la hipótesis de la centralidad del nicho ecológico; mientras que para la paca común, es el único factor que predice su abundancia.

Para las dos especies de pecaríes también se cumplió la hipótesis de que la relación entre la abundancia y la distancia al centroide del nicho ecológico puede tener una forma de cuña, debido a que el grado de influencia humana puede limitar la abundancia en sitios cercanos al centroide del nicho.

Por otra parte, nuestros análisis muestran que al adicionar la influencia humana al conjunto de variables climáticas y topográficas mejoran los modelos de nicho de la mayoría de las especies en las que se puso a prueba esta hipótesis (i.e. excepto el oso hormiguero gigante), y en consecuencia también los modelos de distribución y de distancia al centroide del nicho. No obstante, su importancia relativa en la construcción del modelo de nicho depende de la especie.

Esta es la primera vez que se evalúa el efecto de la influencia humana en los estudios que usan la aproximación de distancia al centroide del nicho ecológico propuesta por Martínez-Meyer *et al.* 2013. Tanto *a posteriori*, en lo referente a los modelos de abundancia, como desde el modelado de nicho *per se*. En este sentido, nuestros resultados, por un lado, evidencian la importancia de considerar explícitamente el papel de las actividades humanas en la ecología de las especies, y por otro, demuestran que los índices globales, que agregan varios factores de influencia humana, pueden ser una herramienta adecuada en este tipo de análisis.

En cuanto a los modelos espaciales de predicción de abundancia generados, se pretende que en un futuro puedan servir en la obtención de predicciones espaciales de riqueza y diversidad de especies presa. Las cuales a su vez podrían evaluarse como predictores de la distribución y abundancia de jaguares y pumas.

Por último, como síntesis de los resultados obtenidos en esta tesis, hemos elaborado un mapa de *localización de puntos calientes de disponibilidad de presas* que presentamos a continuación (Fig. 1). Pretendemos que en un futuro pueda contribuir en la determinación de la calidad del hábitat de jaguares y/o pumas. En él mostramos las zonas que coinciden en tener predicciones altas de abundancia para 4 o 3 especies presa. Para generarlo, consideramos las dos categorías más altas de abundancia predicha para cada especie resultantes de los capítulos 3 y 4. En el caso de los pecaríes incluimos tanto la predicción de abundancia del cuantil superior como de la mediana.

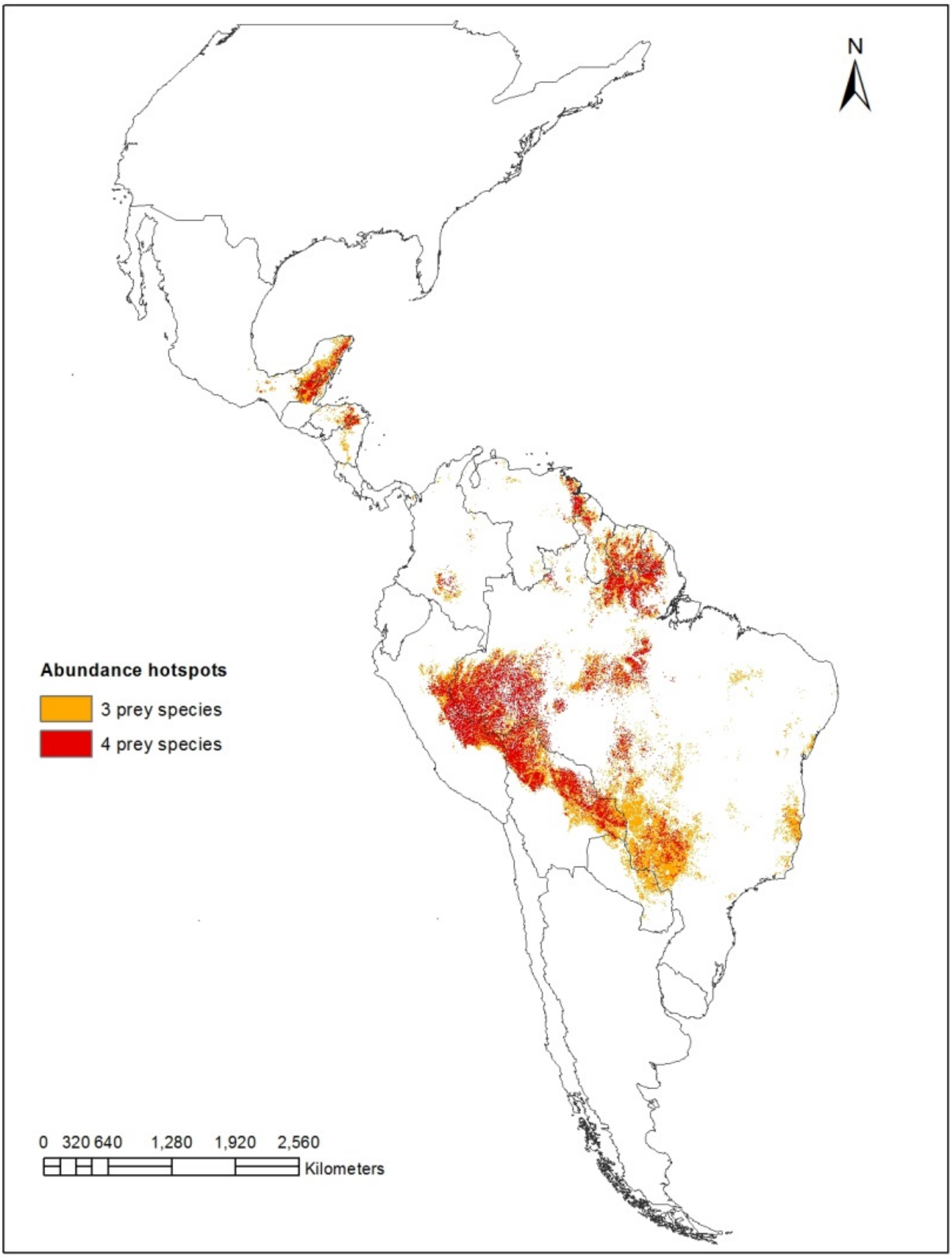

Figura 1. Aréas en las que se espera una alta abundancia de presas potenciales de jaguares y pumas.

Como resultado, encontramos que las áreas en las que se espera una mayor abundancia de presas se concentran principalmente en la subrregión Amazónica de la región Neotropical (Morrone 2002). De acuerdo a la clasificación de ecorregiones terrestres del mundo de la WWF (Olson *et al*. 2001), estos puntos calientes de abundancia esperada de presas en su mayoría corresponden a los bosques húmedos del suroeste Amazónico (20.31% del área total), seguidos por el cerrado (13.6% del área total), los bosques húmedos de Guayana (8.69% del área total), los bosques secos chiquitanos (5.51% del área total), los bosques húmedos de Madeira-Tapajós (5.10% del área total) y el pantanal (5.06% del área total); ya que juntos suman el 57.83% del área total de los puntos calientes, mientras que el resto de ecorregiones (84) tienen una importancia relativa individual menor al 5% (Fig. 2).

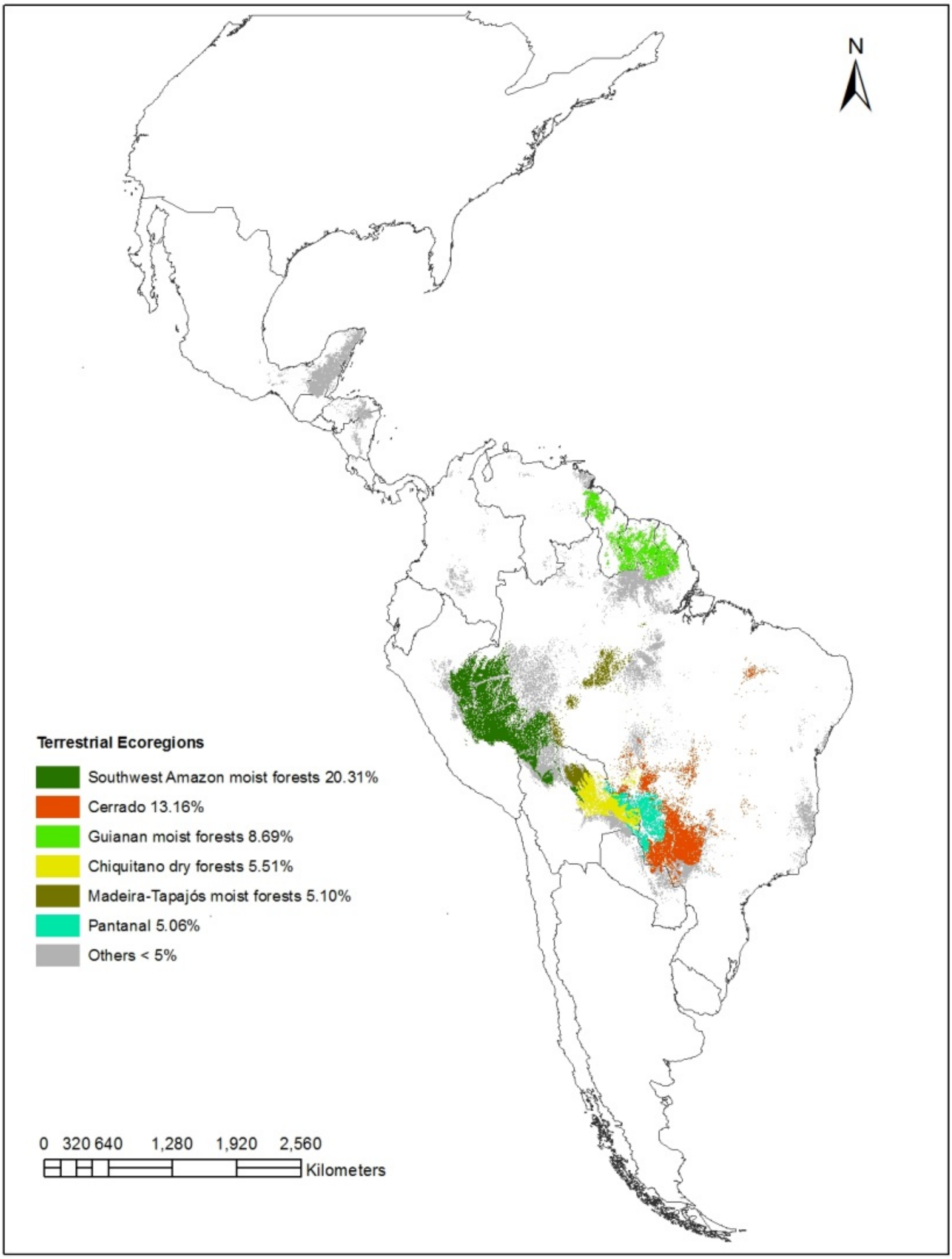

Figura 2. Ecorregiones terrestres más representativas de las aréas en las que se espera una alta abundancia de presas potenciales de jaguares y pumas.

Los puntos calientes de abundancia esperada de presas coinciden con zonas de alta densidad (selva maya de Belice, Silver *et al.* 2004; pantanal de Brasil, Soisalo y Cavalcanti 2006; y Gran Chaco boliviano, Maffei *et al.* 2004) y de alta probabilidad de persistencia de jaguares a largo plazo, que están en los bosques húmedos de la cuenca del Amazonas y en las áreas contiguas correspondientes al pantanal y al Gran Chaco; así como en la selva maya de Guatemala, México y Belice (Sanderson *et al*. 2002). En cuanto al puma, no es de nuestro conocimiento que se cuente con información sobre probabilidad de persistencia en la región Neotropical, de hecho, el puma ha sido mucho menos estudiado en el Neotrópico que en el Neártico y son también muy pocos los estudios de densidad con los que se cuenta para la región Neotropical (Kelly *et al*. 2008). Sin embargo, se han reportado comparativamente densidades más altas en el Parque Nacional del Gran Chaco de Bolivia y en el Parque Nacional Chiquibul de Belice, que en la Reserva de la Biosfera Yabotí en Argentina (Rich *et al*. 2014), lo cual coincide con las áreas de puntos calientes de abundancia esperada de presas.

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Conclusiones

Las principales conclusiones a las que llegamos como producto de las investigaciones realizadas en esta tesis son las siguientes:

1. Los resultados encontrados en los estudios de dieta de jaguares y pumas se ven significativamente influenciados por el tipo de método empleado para identificar al depredador. La dieta resultante de estudios en los que identifican al depredador mediante la apariencia de sus excretas, es significativamente diferente a la de los estudios basados en la identificación química o genética de las excretas, o en el contenido estomacal o intestinal. Ello indica que la fiabilidad de los estudios de dieta tradicionales no es comparable a la de los estudios que usan métodos de laboratorio para identificar al depredador a través de sus excretas, o bien que se basan en el contenido estomacal o intestinal.

2. La mayoría de los estudios de dieta de jaguares y pumas se basan en el análisis de sus excretas, sin embargo son escasos los estudios que usan un método altamente fiable para identificar al depredador a través de éstas (i.e. mediante análisis de ácidos biliares o análisis genéticos) en comparación con los que usan métodos de baja fiabilidad (i.e. identificación en el campo examinando su morfología y los indicios asociados).

3. En la región Neotropical, el pecarí de collar, el pecarí de labios blancos, el oso hormiguero gigante y la paca común son especies importantes en la dieta de jaguares y/o pumas.

4. La relación entre las abundancias poblacionales de pecarí de collar y su ubicación con respecto al centroide geográfico de su distribución no es

significativa. Por el contrario, éstas decrecen significativamente a medida que se alejan del centroide de su nicho ecológico, donde las condiciones ambientales (clima, topografía y productividad primaria) son las más favorables. No obstante, la capacidad predictiva mejora al incluir la influencia humana, la cual tiene un efecto negativo sobre la abundancia.

5. Los modelos de nicho del pecarí de labios blancos y de la paca común basados en un conjunto de variables climáticas y topográficas, mejoran al incluir también un índice de influencia humana. Sin embargo, la importancia relativa de esta variable en la construcción del modelo es alta solamente para la paca común. En contraparte, el modelo de nicho del oso hormiguero gigante no mejora significativamente al incluir la influencia humana. Esto indica que los factores ambientales (principalmente climáticos) son los más importantes para predecir la distribución de la mayoría de estas especies presa.

6. No se observa relación alguna entre las abundancias poblacionales de la paca común y su posición con respecto al centroide de su nicho ecológico (estimado en función de clima, topografía e influencia humana). Ello puede deberse a que esta especie se ve muy influenciada por factores locales no incluidos a escala gruesa. Por otro lado, sus abundancias poblacionales decrecen a medida que aumenta el nivel de influencia humana.

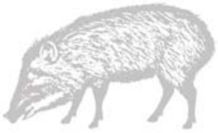
7. Las abundancias poblacionales del oso hormiguero gigante decrecen a medida que se alejan del centroide de su nicho ecológico, donde las condiciones ambientales (clima y topografía) son las más favorables. El nivel de influencia humana no contribuye a mejorar la predicción de abundancia de esta especie, posiblemente debido a que puede verse favorecida por un bajo nivel de influencia humana.

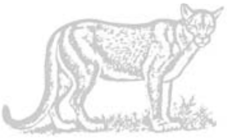
8. En las dos especies de pecaríes, la relación entre abundancia y distancia al centroide del nicho ecológico, así como la relación entre abundancia e influencia humana, tienen forma de cuña, es decir, presentan tanto altas como bajas abundancias cerca de las condiciones óptimas y sólo bajas lejos de éstas. En consecuencia, el mejor modelo para predecir las abundancias poblacionales de dichas especies depende del cuantil analizado y de la tolerancia de la especie a la presión humana. Así, en la predicción del límite alto de abundancia el efecto de la influencia humana es más importante para el pecarí de labios blancos que para el pecarí de collar. Para la paca común y el oso hormiguero gigante no encontramos este tipo de relación.

9. El número de datos de abundancia disponibles para la paca común y el oso hormiguero gigante fue bajo, lo cual posiblemente influyó en que algunas de las relaciones evaluadas en esta tesis no fueran significativas. Esto evidencia la poca información que existe sobre las densidades poblacionales de los mamíferos neotropicales, aun tratándose de especies relativamente comunes y con distribuciones amplias como las aquí estudiadas.

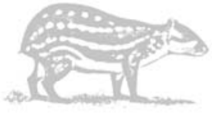
10. En términos generales, el método usado para calcular la distancia al centroide del nicho ecológico, así como los índices globales de influencia humana usados en esta tesis, pueden funcionar como indicadores de la abundancia relativa esperada cuando sólo se cuenta con datos de presencia de la especie. Sin embargo, el modelo que mejor prediga la abundancia dependerá de la tolerancia de la especie a la presión humana y de su susceptibilidad a la influencia de factores que no son percibidos a escalas espaciales gruesas. Así como también dependerá del número de datos disponibles.

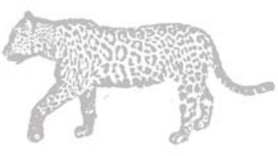
11. Las áreas en las que se predice una mayor abundancia de presas coinciden con zonas de alta densidad de jaguares y pumas, así como de alta probabilidad de persistencia de jaguares a largo plazo. Se localizan principalmente en la subregión Amazónica de la región Neotropical, y en su mayoría corresponden a la ecorregión de los bosques húmedos del suroeste Amazónico.





MATERIAL SUPLEMENTARIO





Material Suplementario

Capítulo 2

Material Suplementario: Capítulo 2

Appendix 1

Table A1. Studies used to evaluate the influence of predator identification method on jaguar and cougar diet analyses. Method, refers to the type of predator identification method used; N, indicates the number of samples used to analyze the diet in each study; HCI, refers to high confidence identification of the predator (identification of faeces through DNA or bile acids, or stomach and colon content); LCI, indicates low confidence identification of the predator (field identification of faeces through general appearance).

Reference	Predator	Country	Method	N	Notes
Robinette et al. 1959	Cougar	USA	HCI	65	
Spalding & Lesowski 1971	Cougar	Canada	HCI	(62,37)[a]	2 data obtained
Toweill & Meslow 1977	Cougar	USA	HCI	25	
Maser & Rohweder 1983	Cougar	USA	HCI	60	
Ackerman et al. 1984	Cougar	USA	LCI	239	
Toweill & Maser 1985	Cougar	USA	HCI	61	
Leopold & Krausman 1986	Cougar	USA	LCI	433	
Rabinowitz & Nottingham 1986	Jaguar	Belize	LCI	228	

Yáñez et al. 1986	Cougar	Chile	LCI	291	Same site & method than Iriarte et al. 1991 (we averaged both data)
Maehr et al. 1990	Cougar	USA	LCI	284	
Iriarte et al. 1991	Cougar	Chile	LCI	405	Same site & method than Yáñez et al. 1986 (we averaged both data)
Rau et al. 1991	Cougar	Chile	LCI	65	
Cashman et al. 1992	Cougar	USA	LCI	159	
Olmos 1993	Jaguar & Cougar	Brazil	LCI	7[b],3[c]	Same site & method than Wolf 2001 (we averaged both data for cougar)
Aranda 1994	Jaguar	Mexico	LCI	37	
Branch et al. 1996	Cougar	Argentina	LCI	280	Same site & method than Pessino et al. 2001 (we averaged both data)
Facure & Giaretta 1996	Jaguar & Cougar	Brazil	LCI	13[b],3[c]	Same site & method than Garla et al. 2001 (we averaged both data for jaguar)
Chinchilla 1997	Jaguar & Cougar	Costa Rica	LCI	22[b],11[c]	

Cunningham et al. 1997	Cougar	USA	LCI	370	
Heinen & Canon 1997	Cougar	USA	HCI	23	
Taber et al. 1997	Jaguar & Cougar	Paraguay	HCI	(40,58)[ab] (29,59)[ac]	2 data obtained for each predator
Harveson et al. 2000	Cougar	USA	LCI	25	
Novaro et al. 2000	Cougar	Argentina	LCI	70	
Nuñez et al. 2000	Jaguar & Cougar	Mexico	LCI	50[b],65[c]	
Garla et al. 2001	Jaguar	Brazil	LCI	101	Same site & method than Facure & Giaretta 1996 (we averaged both data)
Pessino et al. 2001	Cougar	Argentina	LCI	198	Same site & method than Branch et al. 1996 (we averaged both data)
Wolff 2001	Cougar	Brazil	LCI	65	Same site & method than Olmos 1993 (we averaged both data)
Dalponte 2002	Jaguar	Brazil	LCI	(13,7,15)[a]	3 data obtained
Kuroiwa & Ascorra 2002	Jaguar	Peru	LCI	13	

Leite & Galvao 2002	Jaguar & Cougar	Brazil	LCI	32[b],131[c]	
Rosas-Rosas et al. 2003	Cougar	Mexico	LCI	60	
Scognamillo et al. 2003	Jaguar & Cougar	Venezuela	LCI	42[b],42[c]	
Pacheco et al. 2004	Cougar	Bolivia	LCI	53	
Silveira 2004	Jaguar & Cougar	Brazil	LCI	18[b],11[c]	Same site than Sollmann et al. 2003 for jaguar but different method
Luna-Soria & López-González 2005	Cougar	Mexico	LCI	20	
Novack et al. 2005	Jaguar & Cougar	Guatemala	HCI	(23,53)[ab] (82,63)[ac]	2 data obtained for each predator
Zuñiga et al. 2005	Cougar	Chile	LCI	31	
Moreno 2006	Jaguar & Cougar	Panama	LCI	8[b],13[c]	
Moreno et al. 2006	Cougar	Panama	LCI	88	
Ramalho 2006	Jaguar	Brazil	LCI	29	
Cruz et al. 2007	Jaguar	Mexico	LCI	45	

De Azevedo & Murray 2007	Jaguar	Brazil	LCI	149	
Bustamante-Ho 2008	Jaguar & Cougar	Costa Rica	LCI	15[b],42[c]	
Ciocheti 2008	Cougar	Brazil	LCI	68	
De Azevedo 2008	Jaguar & Cougar	Brazil	LCI	51[b],54[c]	
Martins et al. 2008	Cougar	Brazil	LCI	12	
McCain 2008	Cougar	USA	HCI	117	
Rocha 2008	Cougar	Brazil	LCI	23	
Rosas-Rosas et al. 2008	Jaguar & Cougar	Mexico	LCI	27[b],88[c]	
De la Torre & De la Riva 2009	Cougar	Mexico	LCI	38	
De Oliveira 2009	Jaguar	Brazil	LCI	134	
Donadio et al. 2010	Cougar	Argentina	LCI	(366,10,8,7,31,18,20)[a]	7 data obtained
Foster et al. 2010	Jaguar & Cougar	Belize	HCI	322[b], 127[c]	Same site than Rabinowitz & Nottingham 1986 for jaguar but different method
Gómez-Ortíz	Jaguar &	Mexico	LCI	13[b],209[c]	

2010	Cougar				
McBride et al. 2010	Jaguar	Paraguay	LCI	41	
Oliveira et al. 2010	Jaguar & Cougar	Brazil	HCI	(18,4,5)[ab] (49,16,6)[ac]	3 data obtained for each predator
Rocha-Mendes et al. 2010	Cougar	Brazil	LCI	10	
Bacon et al. 2011	Cougar	Canada	LCI	211	
Hernández-Guzmán et al. 2011	Cougar	Colombia	LCI	60	
Zanon-Martínez et al. 2012	Cougar	Argentina	LCI	(186,15,55,18)[a]	4 data obtained
Sollmann et al. 2013	Jaguar	Brazil	HCI	35	Same site than Silveira 2004 but different method
50 for cougar & 27 for jaguar		14 for cougar & 9 for jaguar			61 data for cougar (16-HCI, 45-LCI) & 32 data for jaguar (9-HCI, 23-LCI)

[a] sample size for different areas reported in the same study; [b] sample size for jaguar [c] sample size for cougar reported in the same study.

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Appendix 2

Effect of the number of diet studies on the similarity index

We performed a randomization procedure to ensure that differences found in the diet similarity index were not affected by the different number of HCI and LCI studies. For each species, we iteratively sampled without replacement LCI studies using a sample size equal to the number of HCI studies. We performed 1000 iterations and then calculated the expected distribution of the mean similarity index between LCI studies after reducing sample size. Finally, the observed mean similarity index between HCI studies was compared with this expected distribution using the Z-statistic (Sokal and Rohlf 1981). A (one-tailed, α = 0.05) significant difference would confirm that the greater similarity between HCI studies remained after matching the number of studies. The same procedure was repeated to estimate the similarity distribution of HCI-LCI studies after reducing the number of LCI studies. The results are shown in Table A2, and they confirmed for both cougar and jaguar a significant departure of HCI-HCI mean similarity from the above-mentioned sampling distributions (although from LCI-LCI distribution for jaguars it was marginally significant), therefore differences between types of studies remained after matching sample sizes.

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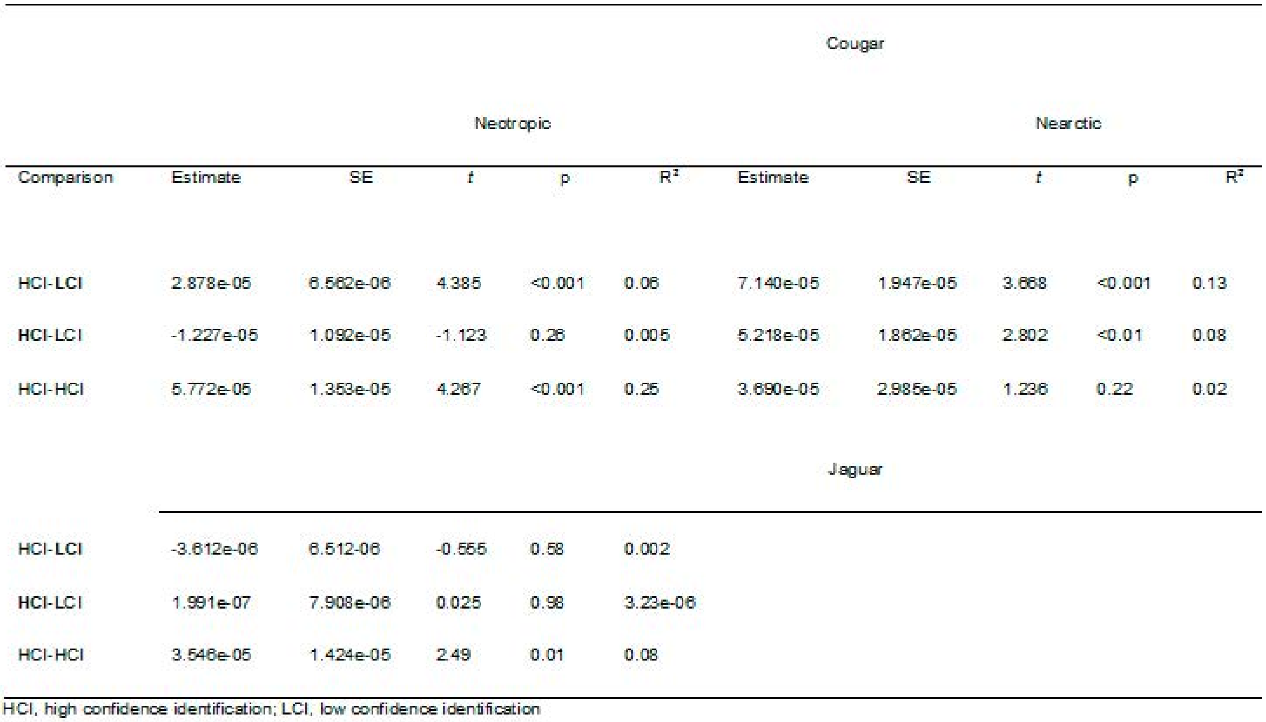
Table A2. Results obtained from the randomization procedure (1000 iterations) to test the effect of the number of diet studies (HCI, high confidence identification; LCI, low confidence identification) on the trophic similarity index obtained for jaguars and cougars. Mean, refers to the mean value obtained for the 1000 similarity means; SD, refers to the mean value obtained for the 1000 standard deviations.

	Jaguar				Cougar			
	Mean	SD	*z*	p	Mean	SD	*z*	p
LCI-LCI	0.298	0.055	1.504	0.06	0.223	0.029	5.562	<0.001
HCI-LCI	0.261	0.034	3.521	<0.001	0.23	0.034	4.538	<0.001

Appendix 3

Table A3. Linear Models results for the effect of distance (km) between study sites in the percentages of exclusive prey obtained in HCI-LCI comparisons and HCI-HCI comparisons for cougars and jaguars by ecoregion. For HCI-LCI pairs we indicated in bold which study is used as the reference for the comparison. When HCI studies are used as the reference, the percentage of exclusive prey represents potential erroneous omission of prey in LCI studies, and vice-versa.



	Cougar									
	Neotropic					Nearctic				
Comparison	Estimate	SE	*t*	p	R²	Estimate	SE	*t*	p	R²
HCI-**LCI**	2.878e-05	6.562e-06	4.385	<0.001	0.06	7.140e-05	1.947e-05	3.668	<0.001	0.13
HCI-LCI	-1.227e-05	1.092e-05	-1.123	0.26	0.005	5.218e-05	1.862e-05	2.802	<0.01	0.08
HCI-HCI	5.772e-05	1.353e-05	4.267	<0.001	0.25	3.690e-05	2.985e-05	1.236	0.22	0.02
	Jaguar									
HCI-**LCI**	-3.612e-06	6.512-06	-0.555	0.58	0.002					
HCI-LCI	1.991e-07	7.908e-06	0.025	0.98	3.23e-06					
HCI-HCI	3.546e-05	1.424e-05	2.49	0.01	0.08					

HCI, high confidence identification; LCI, low confidence identification

Appendix 4

Table A4. Number of cougar and jaguar diet studies where percentage of occurrence of the listed prey items was ≥10% according to the predator identification method used (HCI, high confidence identification; LCI, low confidence identification) within the potential distribution area of each prey. In brackets is the total number of available studies within the potential distribution area of each prey.

Prey	Jaguar		Cougar	
	HCI	LCI	HCI	LCI
Alces			1 (3)	0 (1)
Aves	1 (9)	4 (23)	1 (16)	5 (45)
Bradypus	0 (3)	2 (8)	1 (2)	1 (10)
Caiman	0 (ND)[1]	3 (ND)[1]	0 (ND)[1]	1 (ND)[1]
Caviinae			1 (2)	2 (23)
Cerdocyon	0 (3)	1 (13)		
Cervus			1 (5)	1 (3)
Choloepus	2 (3)	2 (5)	3 (3)	1 (4)
Cricetidae			0 (16)	4 (45)
Ctenomys			0 (1)	1 (6)
Ctenosaura			0 (ND)[1]	1 (ND)[1]
Cuniculus	1 (7)	1 (17)	5 (6)	3 (15)
Dasypodidae	7 (9)	6 (22)	1 (9)	9 (32)
Dasyprocta	2 (8)	2 (16)	4 (7)	2 (11)
Didelphis			1 (9)	1 (25)
Dolichotis			0 (2)	3 (6)
Erethizon			3 (8)	0 (8)
Hydrochoerus	0 (6)	5 (15)	0 (5)	2 (12)
Iguana	0 (ND)[1]	1 (ND)[1]	0 (ND)[1]	1 (ND)[1]
Lagomorpha	2 (4)	1 (18)	3 (11)	18 (41)
Lagostomus			0 (1)	1 (4)
Mazama	2 (9)	3 (18)	5 (8)	1 (13)
Mephitidae			1 (13)	0 (31)
Myrmecophaga	1 (6)	2 (14)	0 (5)	1 (9)
Nasua	3 (10)	7 (20)	2 (9)	5 (19)
Odocoileus	0 (5)	1 (10)	8 (13)	12 (19)
Ovis			0 (1)	1 (3)

Primates	0 (9)	1 (20)	2 (8)	2 (15)
Procyon			0 (11)	2 (25)
Proechimys	0 (5)	1(12)	0 (4)	1 (5)
Serpentes			0 (16)	1 (45)
Tamandua	1 (9)	1 (21)	1 (8)	1 (15)
Tayassuidae	4 (9)	12 (22)	4 (10)	14 (24)

[1] prey distribution range was not available in a GIS format in order to formally count the number of studies within the range, but at least one HCI and one LCI study were included in distributions in Uetz (2013).

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Appendix 5

Main prey consumed by jaguars and cougars in HCI (high confidence identification) studies

According to the total number of studies that used HCI methods, armadillos were the prey most widely consumed by jaguars (7 of 9 studies; representing up to 46% of occurrence in some studies), while pacas (6 of 8 studies; up to 58% of occurrence) and deer (5 of 8 studies; up to 21% of occurrence) were the most important prey for cougars in the Neotropic. In the Nearctic, deer were present in all eight studies of cougars with an occurrence in the diet up to 69% (Table A4).

Taking into account only items identified to species level, 9 were representative prey species in the diet of Neotropical jaguars, with *Myrmecophaga tridactyla* (although only in one study) and *Dasypus novemcinctus* reaching the highest percentages of occurrence (Table A4). In cougars, *Choloepus didactylus* and *Cuniculus paca* were the most important of the 8 prey species with PO ≥ 10% in the Neotropic; while in the Nearctic, *Odocoileus hemionus* and *Pecari tajacu* (although they appeared in a single study) presented the highest values of the 9 representative prey species (Table A4).

Table A5. Prey items (taxonomic resolution as originally reported in the bibliography sources) with percentage of occurrence (PO) ≥ 10% in diet studies of jaguars and cougars that used high confidence identification methods, and the number of studies (n) where these prey items were recorded (the ranges of PO reported in the studies are given in brackets).

Main prey	Jaguar		Cougar			
	Neotropic		Neotropic		Nearctic	
	(N=9)		(N=8)		(N=8)	
	n	(range)	n	(range)	n	(range)
MAMMALIA	9	(10.1-74)	8	(10.2-62.7)	8	(10.2-68.5)
Pilosa	3	(14.8-74)	3	(10.2-62.7)		
Megalonychidae	2	(20-26)	3	(11.1-62.7)		
Choloepus didactylus	2	(20-26)	3	(11.1-62.7)		
Myrmecophagidae	2	(14.8-74)	1	(11.1)		
Tamandua tetradactyla	1	(14.8)	1	(11.1)		
Myrmecophaga tridactyla	1	(74)				
Bradypodidae			1	(10.2)		
Bradypus			1	(10.2)		
Rodentia	3	(10.1-20)	8	(10.2-57.9)	3	(10.2-13.5)
n.i.	1	(10.1)	2	(12.1-20)		
Cuniculidae	1	(20)	6	(10.2-57.9)		
Cuniculus paca	1	(20)	6	(10.2-57.9)		
Dasyproctidae	2	(20)	4	(11.1-22.4)		
Dasyprocta			4	(11.1-22.4)		
D. punctata			2	(17.7-22.4)		
D. sp.	2	(20)	2	(11.1-11.8)		
Caviidae			1	(14.3)		
Galea musteloides			1	(14.3)		
Erethizontidae					3	(10.2-13.5)
Erethizon dorsatum					3	(10.2-13.5)
Artiodactyla	4	(20-24.1)	5	(11.1-21.2)	8	(11-68.5)
Cervidae	2	(21.7-24.1)	5	(11.1-21.2)	8	(11-68.5)
Mazama	2	(21.7-24.1)	5	(11.1-21.2)		
M. gouazoubira	2	(21.7-24.2)	1	(21.2)		
M. sp.			4	(11.1-20.3)		

Odocoileus			1	(15.2)	8	(27-68.5)
O. hemionus					6	(28-68.5)
O. virginianus			1	(15.2)	1	(31.5)
O. sp.					1	(39.1)
Cervus elaphus					1	(18.6)
Alces alces					1	(11)
Tayassuidae	2	(20-20.6)	2	(11.1-12.1)	1	(39.1)
n.i.			1	(12.1)		
Tayassu pecari			1	(11.1)		
Pecari tajacu	2	(20-20.6)			1	(39.1)
Bovidae					1	(18.2)
Ovis aries					1	(18.2)
Cingulata	7	(11.1-46.4)	1	(21.2)		
Dasypodidae	7	(11.1-46.4)	1	(21.2)		
n.i.	4	(11.1-40)	1	(21.2)		
Dasypus novemcinctus	3	(26.5-46.4)				
Lagomorpha	2	(22.2-24.6)	1	(15.2)	2	(15.4-27)
n.i.	2	(22.2-24.6)	1	(15.2)		
Leporidae					2	(15.4-27)
Lepus americanus					1	(27)
Sylvilagus floridanus					1	(15.4)
Didelphimorphia			1	(12.9)		
Didelphidae			1	(12.9)		
Didelphis albiventris			1	(12.9)		
Primates			1	(11)		
n.i.			1	(11)		
Carnivora	3	(10.8-23.5)			1	(11.2)
Mephitidae					1	(11.2)
n.i.					1	(11.2)
Procyonidae	3	(10.8-23.5)				
Nasua	3	(10.8-23.5)				
N. nasua	2	(22.4-23.5)				
N. narica	1	(10.8)				
Carrion					1	(13)
Cattle					1	(11.9)
AVES	1	(20)	1	(12.1)		
PLANTAE					1	(17.1)

Material Suplementario

Capítulo 3

Material Suplementario: Capítulo 3

Table S1. Data documenting known occurrences of *Pecari tajacu* across its range, used to model its ecological niche using GARP.

No.	Longitude	Latitude	Source	Country
1	-61.76873	-29.23101	GBIF	Argentina
2	-60.664737	-28.78566	GBIF	Argentina
3	-50.720389	-28.285167	SpeciesLink	Brazil
4	-54.20722	-27.29199	GBIF	Argentina
5	-54.853078	-26.822228	GBIF	Argentina
6	-58.810454	-26.812118	GBIF	Argentina
7	-59.60699	-26.81131	GBIF	Argentina
8	-59.62662	-26.79596	GBIF	Argentina
9	-53.896057	-26.468384	GBIF	Argentina
10	-63.783333	-26.216667	GBIF	Argentina
11	-65.933174	-26.154338	GBIF	Argentina
12	-60.62291	-25.94883	GBIF	Argentina
13	-54.256221	-25.937071	GBIF	Argentina
14	-58.8854	-25.86364	GBIF	Argentina
15	-54.4406	-25.71516	GBIF	Argentina
16	-54.36029	-25.70615	GBIF	Argentina
17	-54.48111	-25.69141	GBIF	Argentina
18	-54.45944	-25.68624	GBIF	Argentina
19	-54.16444	-25.68085	GBIF	Argentina
20	-54.31929	-25.68029	GBIF	Argentina
21	-54.27138	-25.67342	GBIF	Argentina
22	-54.25618	-25.67215	GBIF	Argentina
23	-54.50696	-25.66255	GBIF	Argentina
24	-54.46916	-25.64699	GBIF	Argentina

25	-58.12925	-25.17366	GBIF	Argentina
26	-58.12558	-25.15391	GBIF	Argentina
27	-58.15239	-25.15092	GBIF	Argentina
28	-58.07641	-25.14876	GBIF	Argentina
29	-58.1753	-25.12303	GBIF	Argentina
30	-57.9672	-25.12231	GBIF	Argentina
31	-58.12102	-25.12209	GBIF	Argentina
32	-58.17995	-25.12195	GBIF	Argentina
33	-58.13772	-25.12024	GBIF	Argentina
34	-58.0455	-25.11585	GBIF	Argentina
35	-58.17225	-25.11401	GBIF	Argentina
36	-47.9622	-25.1084	SpeciesLink	Brazil
37	-58.18246	-25.0987	GBIF	Argentina
38	-58.20625	-25.08551	GBIF	Argentina
39	-58.13245	-25.06494	GBIF	Argentina
40	-58.08139	-25.02649	GBIF	Argentina
41	-58.12965	-25.02126	GBIF	Argentina
42	-59.962252	-24.807644	GBIF	Argentina
43	-47.5381	-24.4753	SpeciesLink	Brazil
44	-61.81596	-24.30288	GBIF	Argentina
45	-61.80257	-24.29577	GBIF	Argentina
46	-47.2428	-23.9574	SpeciesLink	Brazil
47	-59	-23.36667	ArctosData	Paraguay
48	-61	-22.66667	ArctosData	Paraguay
49	-49.0833	-22.3167	SpeciesLink	Brazil
50	-47.8	-21.5833	SpeciesLink	Brazil
51	-48.9106	-20.7542	SpeciesLink	Brazil
52	-59.86667	-20.63333	GBIF	Paraguay

53	-60.1	-20.35	GBIF	Paraguay
54	-40.477777	-20.2725	SpeciesLink	Brazil
55	-59.7667	-20.0167	VertNet	Paraguay
56	-40.53722	-19.98333	SpeciesLink	Brazil
57	-40.05	-19.10333	SpeciesLink	Brazil
58	-40.17666	-19.01333	SpeciesLink	Brazil
59	-39.81333	-18.28666	SpeciesLink	Brazil
60	-63.55	-17	GBIF	Bolivia
61	-51.867222	-14.748056	SpeciesLink	Brazil
62	-66.21	-14.51	GBIF	Bolivia
63	-69.683	-13.503	GBIF	Peru
64	-69.607	-13.142	GBIF	Peru
65	-69.083	-13	GBIF	Peru
66	-69.295	-12.838	GBIF	Peru
67	-55.931433	-12.778863	GBIF	Brazil
68	-71.269	-12.66833	GBIF	Peru
69	-68.7	-12.517	GBIF	Peru
70	-71.3667	-11.9	GBIF	Peru
71	-41.2851	-11.28517	GBIF	Brazil
72	-66.83333	-11.28333	GBIF	Bolivia
73	-75.316667	-11.05	GBIF	Peru
74	-66.733	-10.767	GBIF	Bolivia
75	-68.2825	-10.567222	SpeciesLink	Brazil
76	-40.8608	-10.16	GBIF	Brazil
77	-71.217	-10.133	GBIF	Peru
78	-68	-10.092778	SpeciesLink	Brazil
79	-67.616667	-10.066667	SpeciesLink	Brazil
80	-66.811111	-10.045278	SpeciesLink	Brazil

81	-66.818056	-10.005	SpeciesLink	Brazil
82	-66.774444	-9.991111	SpeciesLink	Brazil
83	-66.802222	-9.976667	SpeciesLink	Brazil
84	-67.8	-9.966667	SpeciesLink	Brazil
85	-66.755556	-9.953333	SpeciesLink	Brazil
86	-65.7	-9.867	GBIF	Bolivia
87	-71.663889	-9.523056	SpeciesLink	Brazil
88	-71.016667	-9.356667	SpeciesLink	Brazil
89	-68.25	-9.333333	SpeciesLink	Brazil
90	-71.9	-9.316667	SpeciesLink	Brazil
91	-68.725	-9.25	SpeciesLink	Brazil
92	-42.7	-9.02	GBIF	Brazil
93	-72.5	-9	SpeciesLink	Brazil
94	-42.6144	-8.9308	GBIF	Brazil
95	-72.775	-8.829167	SpeciesLink	Brazil
96	-72.783333	-8.666667	SpeciesLink	Brazil
97	-73.266667	-7.383333	SpeciesLink	Brazil
98	-78.26667	-4.55	ArctosData	Peru
99	-78.15333	-4.45667	ArctosData	Peru
100	-71.783333	-4.45	VertNet	Peru
101	-78.135	-4.4367	ArctosData	Peru
102	-78.31667	-4.41667	ArctosData	Peru
103	-70.316667	-3.8	SpeciesLink	Colombia
104	-79.817	-3.783	GBIF	Ecuador
105	-80.033	-2.167	GBIF	Ecuador
106	-80.717	-1.567	GBIF	Ecuador
107	-79.45248	-1.5475	GBIF	Ecuador
108	-72.854444	-1.423333	SpeciesLink	Colombia

109	-79.383	-1.35	GBIF	Ecuador
110	-79.583	-1.333	GBIF	Ecuador
111	-69.5	-1.093333	SpeciesLink	Colombia
112	-79.617	-1.05	GBIF	Ecuador
113	-79.45	-1.033	GBIF	Ecuador
114	-80.733	-0.95	GBIF	Ecuador
115	-80.1	-0.683	GBIF	Ecuador
116	-78.367	-0.433	GBIF	Ecuador
117	-74.995	0.158333	SpeciesLink	Colombia
118	-79.5	0.2	GBIF	Ecuador
119	-79.467	0.333	GBIF	Ecuador
120	-79.47747	0.39638	GBIF	Ecuador
121	-79.4	0.4	GBIF	Ecuador
122	-75.333333	0.466667	GBIF	Colombia
123	-79.8667	0.8167	GBIF	Ecuador
124	-79.617	0.95	GBIF	Ecuador
125	-58.2	1.783333	GBIF	Guyana
126	-68.241667	2.085	SpeciesLink	Colombia
127	-73.916667	2.75	GBIF	Colombia
128	-77.346278	2.770167	GBIF	Colombia
129	-59.51666	2.83333	GBIF	Guyana
130	-59.31607	2.83333	GBIF	Guyana
131	-58.64819	2.83333	GBIF	Guyana
132	-58.21395	2.83333	GBIF	Guyana
133	-59.04862	3.02826	GBIF	Guyana
134	-56.45	3.116667	GBIF	Suriname
135	-65.55	3.18	GBIF	Venezuela
136	-58.812	3.192	GBIF	Guyana

137	-59.25	3.25	GBIF	Guyana
138	-58.779	3.268	GBIF	Guyana
139	-73.883333	3.283333	GBIF	Colombia
140	-55.45	3.35	GBIF	Suriname
141	-59.43794	3.38333	GBIF	Guyana
142	-73.833333	3.433333	GBIF	Colombia
143	-76.95	3.733333	GBIF	Colombia
144	-56.5	3.75	GBIF	Suriname
145	-72.955278	4.085	SpeciesLink	Colombia
146	-54.589	4.82	GBIF	Suriname
147	-76.95	5.05	GBIF	Colombia
148	-67.833889	5.195	SpeciesLink	Colombia
149	-74.883333	5.556083	GBIF	Colombia
150	-75.82	5.6	GBIF	Colombia
151	-75.98	5.97	GBIF	Colombia
152	-74.58	6.18	GBIF	Colombia
153	-61.32	6.32	GBIF	Venezuela
154	-74.79	6.56	GBIF	Colombia
155	-75.02	6.6	GBIF	Colombia
156	-63.48	6.82	GBIF	Venezuela
157	-75.07	6.91	GBIF	Colombia
158	-75.15	7.07	GBIF	Colombia
159	-71.95	7.32	GBIF	Venezuela
160	-74.87	7.5	GBIF	Colombia
161	-75.35	7.58	GBIF	Colombia
162	-75.2	7.99	GBIF	Colombia
163	-77.23333	8.08333	GBIF	Panama
164	-78.05	8.363	VertNet	Panama

165	-67.5833	8.5667	GBIF	Venezuela
166	-70.5	8.83	GBIF	Venezuela
167	-79.62577	8.95	GBIF	Panama
168	-82.95596	9.01666	GBIF	Costa Rica
169	-79.859	9.121	GBIF	Panama
170	-79.857201	9.145945	GBIF	Panama
171	-79.836	9.153	GBIF	Panama
172	-79.836	9.164	GBIF	Panama
173	-79.798566	9.176073	GBIF	Panama
174	-68.63	11.23	GBIF	Venezuela
175	-68.63	11.27	GBIF	Venezuela
176	-84.96	12.05	GBIF	Nicaragua
177	-86.4	13.27	GBIF	Nicaragua
178	-90.35	13.85	VertNet	Guatemala
179	-89.9425	15.0817	GBIF	Guatemala
180	-92.229	15.158	GBIF	Mexico
181	-92.457	15.382	GBIF	Mexico
182	-92.895	15.41	GBIF	Mexico
183	-92.918	15.42	GBIF	Mexico
184	-92.913	15.422	GBIF	Mexico
185	-92.433	15.548	GBIF	Mexico
186	-92.52	15.557	GBIF	Mexico
187	-92.808	15.657	GBIF	Mexico
188	-93.753	16.092	GBIF	Mexico
189	-90.970833	16.097222	GBIF	Mexico
190	-93.655	16.125	GBIF	Mexico
191	-90.852778	16.125	REMIB	Mexico
192	-90.849	16.144	GBIF	Mexico

193	-90.883333	16.15	REMIB	Mexico
194	-90.869	16.157	GBIF	Mexico
195	-93.591	16.21	GBIF	Mexico
196	-93.904	16.325	GBIF	Mexico
197	-93.928889	16.335	REMIB	Mexico
198	-89.125	16.358	GBIF	Belize
199	-93.898333	16.413611	REMIB	Mexico
200	-93.323	16.477	GBIF	Mexico
201	-91.52	16.62	GBIF	Mexico
202	-91.083333	16.716667	REMIB	Mexico
203	-91.064	16.719	GBIF	Mexico
204	-93.1	16.727	GBIF	Mexico
205	-91.13	16.76	GBIF	Mexico
206	-91.367	16.8	GBIF	Mexico
207	-91.25	16.825	REMIB	Mexico
208	-93.123	16.898	GBIF	Mexico
209	-92.07	16.91	GBIF	Mexico
210	-93.175	16.937	GBIF	Mexico
211	-93.732	16.982	GBIF	Mexico
212	-93.773	16.984	GBIF	Mexico
213	-93.767	17.056	GBIF	Mexico
214	-89.4	17.0694	GBIF	Guatemala
215	-95.04	17.16	GBIF	Mexico
216	-94.9	17.17	GBIF	Mexico
217	-90.547	17.246	GBIF	Guatemala
218	-94.84	17.27	GBIF	Mexico
219	-94.88	17.3	GBIF	Mexico
220	-94.72	17.32	GBIF	Mexico

221	-94.81	17.35	GBIF	Mexico
222	-93.007	17.355	GBIF	Mexico
223	-88.93333	17.36667	GBIF	Belize
224	-91.918	17.432	GBIF	Mexico
225	-90.0564	17.4611	GBIF	Guatemala
226	-92.046	17.483	GBIF	Mexico
227	-91.982222	17.509167	ArctosData	Mexico
228	-88.38	17.54	GBIF	Belize
229	-92.938	17.548	GBIF	Mexico
230	-90.897	17.6	GBIF	Guatemala
231	-89.689	17.868	GBIF	Mexico
232	-89.688611	17.913056	GBIF	Mexico
233	-89.99	17.94	GBIF	Mexico
234	-91.536	17.989	GBIF	Mexico
235	-89.962	18.017	GBIF	Mexico
236	-89.480833	18.049167	GBIF	Mexico
237	-89.8	18.1	GBIF	Mexico
238	-90.017	18.15	GBIF	Mexico
239	-99.614	18.169	GBIF	Mexico
240	-97.089	18.303	GBIF	Mexico
241	-88.702	18.429	GBIF	Mexico
242	-88.752	18.435	GBIF	Mexico
243	-89.917	18.5	GBIF	Mexico
244	-90.31	18.6	GBIF	Mexico
245	-90.358	18.631	GBIF	Mexico
246	-88.392	18.677	GBIF	Mexico
247	-89.223	18.687	GBIF	Mexico
248	-89.35	18.867	GBIF	Mexico

249	-89.481	18.869	GBIF	Mexico
250	-99.176	18.882	GBIF	Mexico
251	-103.45	18.96	GBIF	Mexico
252	-88.207	19.123	GBIF	Mexico
253	-90.729	19.211	GBIF	Mexico
254	-88.038	19.226	GBIF	Mexico
255	-90.72	19.23	GBIF	Mexico
256	-88.1325	19.26	REMIB	Mexico
257	-87.959722	19.2825	REMIB	Mexico
258	-103.93417	19.31528	GBIF	Mexico
259	-104.979	19.362	GBIF	Mexico
260	-104.967	19.367	GBIF	Mexico
261	-104.942	19.367	GBIF	Mexico
262	-88.074167	19.389722	REMIB	Mexico
263	-104.986	19.397	GBIF	Mexico
264	-104.972	19.442	GBIF	Mexico
265	-105.006	19.45	GBIF	Mexico
266	-89.73	19.45	GBIF	Mexico
267	-105.011323	19.464933	GBIF	Mexico
268	-104.9722	19.470986	GBIF	Mexico
269	-104.958	19.483	GBIF	Mexico
270	-105.006217	19.498983	GBIF	Mexico
271	-105.05	19.5	GBIF	Mexico
272	-105.004175	19.502961	GBIF	Mexico
273	-105.029	19.528	GBIF	Mexico
274	-105.002381	19.532608	GBIF	Mexico
275	-96.9275	19.54	GBIF	Mexico
276	-104.48	19.65	GBIF	Mexico

277	-87.465	20.197	GBIF	Mexico
278	-89.384	20.27	GBIF	Mexico
279	-89.533	20.397	GBIF	Mexico
280	-89.622	20.407	GBIF	Mexico
281	-89.911	20.551	GBIF	Mexico
282	-101.645	20.594	GBIF	Mexico
283	-88.266	20.602	GBIF	Mexico
284	-88.569	20.678	GBIF	Mexico
285	-90.205	20.765	GBIF	Mexico
286	-104.19	20.77	GBIF	Mexico
287	-86.958056	20.856111	REMIB	Mexico
288	-97.73	21.07	GBIF	Mexico
289	-87.183	21.217	GBIF	Mexico
290	-88.703	21.343	GBIF	Mexico
291	-88.27	21.381	GBIF	Mexico
292	-105.065	21.436944	REMIB	Mexico
293	-88.454	21.476	GBIF	Mexico
294	-88.251	21.513	GBIF	Mexico
295	-98.375	22.214	GBIF	Mexico
296	-105.88	22.75	GBIF	Mexico
297	-106.411	24.927	GBIF	Mexico
298	-107.91	27.21	GBIF	Mexico
299	-105.034286	19.481263	UNIBIO	Mexico
300	-91.098087	16.595399	UNIBIO	Mexico
301	-99.010169	22.028089	UNIBIO	Mexico
302	-95.30193	16.325699	UNIBIO	Mexico
303	-99.397947	25.806281	UNIBIO	Mexico
304	-104.760442	19.268242	UNIBIO	Mexico

305	-96.825486	17.528971	UNIBIO	Mexico
306	-96.594128	17.601535	UNIBIO	Mexico
307	-108.980362	29.693471	UNIBIO	Mexico
308	-104.274782	19.585955	UNIBIO	Mexico
309	-104.384527	19.753681	UNIBIO	Mexico
310	-104.64813	19.482473	UNIBIO	Mexico
311	-97.023161	17.960687	UNIBIO	Mexico
312	-100.094878	17.005746	UNIBIO	Mexico
313	-96.917408	17.507005	UNIBIO	Mexico
314	-45.0833	-23.2833	SpeciesLink	Brazil
315	-59.58333	-18.28333	GBIF	Bolivia
316	-69	-14	GBIF	Peru
317	-66.96667	-11.33333	GBIF	Bolivia
318	-72.781944	-8.875278	SpeciesLink	Brazil
319	-72.816667	-8.366667	SpeciesLink	Brazil
320	-74.216667	-4.833333	GBIF	Peru
321	-76.95	-1.1167	GBIF	Colombia
322	-79.167	-0.567	GBIF	Ecuador
323	-79.15	-0.25	GBIF	Ecuador
324	-79.56108	0.04977	GBIF	Ecuador
325	-74.333333	3.85	SpeciesLink	Colombia
326	-73.635	4.153333	SpeciesLink	Colombia
327	-79.827678	9.193358	GBIF	Panama
328	-90.683098	15.916557	GBIF	Guatemala
329	-97.719658	15.980883	GBIF	Mexico
330	-94.032	16.414	GBIF	Mexico
331	-91.129	16.651	GBIF	Mexico
332	-91.09	16.733	GBIF	Mexico

333	-91.133	16.767	GBIF	Mexico
334	-91.162137	16.813208	GBIF	Mexico
335	-91.308	16.813	GBIF	Mexico
336	-88.95	16.874	GBIF	Belize
337	-88.46667	17.98333	GBIF	Belize
338	-104.35	19.183333	GBIF	Mexico
339	-87.174	21.115	GBIF	Mexico
340	-100.241	22.898	GBIF	Mexico
341	-110.6158	33.5368	GBIF	USA
342	-104.82	32.06	GBIF	USA
343	-108.555833	33.015	GBIF	USA
344	-97.782	26.407	GBIF	USA
345	-108.805091	31.868639	GBIF	USA
346	-104.733286	32.720988	GBIF	USA
347	-100.105	25.42	GBIF	Mexico
348	-113.220556	34.271944	GBIF	USA
349	-110.96669	31.7226	GBIF	USA
350	-101.116	21.841	GBIF	Mexico
351	-108.519516	34.325008	GBIF	USA
352	-97.096	27.821	GBIF	USA
353	-98.536667	24.755833	GBIF	Mexico
354	-108.997941	32.123481	GBIF	USA
355	-101.82	28.21	GBIF	Mexico
356	-103.83611	24.73722	GBIF	Mexico
357	-111.044807	28.426602	GBIF	Mexico
358	-107.581	33.017	GBIF	USA
359	-111.0969	32.23	GBIF	USA
360	-112.1	33	GBIF	USA

361	-109.8564	34.0736	GBIF	USA
362	-110.7858	33.3942	GBIF	USA
363	-111.5375	32.43056	GBIF	USA
364	-111.46	33.96	GBIF	USA
365	-108.872837	33.272287	GBIF	USA
366	-109.142625	31.914416	GBIF	USA
367	-108.73255	31.364	GBIF	USA
368	-112.38	30.06	GBIF	Mexico
369	-100.277	28.077	GBIF	Mexico
370	-108.416746	30.014644	GBIF	Mexico
371	-108.809585	33.711005	GBIF	USA
372	-110.35303	31.3968	VERTNET	USA

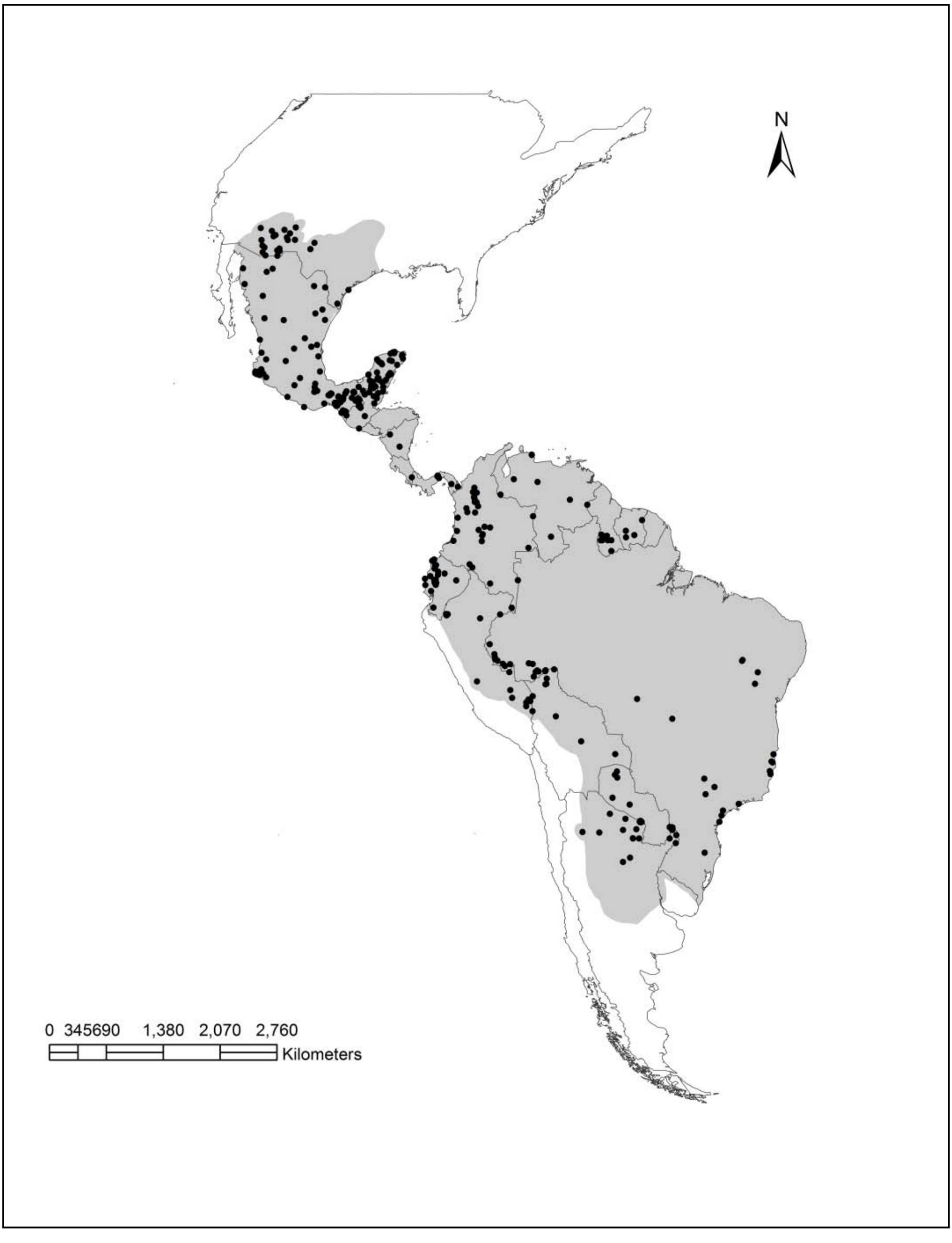

Figure S1 Extent of the study area from which the ecological niche was modeled. Black dots represent 372 occurrence data of *Pecari tajacu*. Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Table S2 Summary of reference studies documenting local abundances of *Pecari tajacu* (ind/km^2), used to evaluate the effects of distance to geographic centroid, distance to the niche centroid, and the human influence index (complete references in Appendix S1).

Reference	Country	Number of sites
Altamirano 2004	Mexico	1
Altrichter 2005	Argentina	2
Aquino *et al*. 1999	Peru	3
Aquino *et al*. 2007	Peru	1
Aquino *et al*. 2007b	Peru	1
Aquino *et al*. 2014	Peru	1
Bodmer 1989	Peru	1
Bodmer & Puertas 2007	Peru	1 (2 years average)
Bolaños & Naranjo 2001	Mexico	1
Cullen *et al*. 2001	Brazil	5
De Araújo *et al*. 2008	Brazil	2
Durango 2011	Ecuador	2
Endo *et al*. 2010	Peru	7
Hill *et al*. 2003	Paraguay	1
Lira & Naranjo 2003	Mexico	1
Mandujano 2007	Mexico	1
Martínez 2014	Colombia	3
Martínez *et al*. 2008	Bolivia	1
Mayor *et al*. 2015	Peru	2
Naranjo & Bodmer 2007	Mexico	2
Novack *et al*. 2005	Guatemala	2
Parry *et al*. 2009	Brazil	2
Peres 1996	Brazil	13
Peres & Nascimento 2006	Brazil	2
Peres *et al*. 2003	Brazil	1

Polisar *et al*. 2008	Venezuela	1
Suárez *et al*. 2013	Ecuador	3
Wright *et al*. 1999	Panama	1
Wright *et al*. 2000	Panama	7
Zimmerman *et al*. 2001	Brazil	1
30 studies	11 countries	72 data

Appendix S1

Complete references for studies used to evaluate the effects of distance to the geographic centroid, distance to the niche centroid, and the human influence index on the local abundances of *Pecari tajacu*.

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Material Suplementario

Capítulo 4

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Table S1. Data documenting known occurrences of *Tayassu pecari* across its range, used to model its ecological niche using Maxent.

No.	Longitude	Latitude	Source	Country
1	-94.017	16.967	GBIF	Mexico
2	-93.124	16.901	GBIF	Mexico
3	-93.1	16.727	GBIF	Mexico
4	-91.16168	16.814599	GBIF	Mexico
5	-91.133	16.767	GBIF	Mexico
6	-91.132	16.693	GBIF	Mexico
7	-91.101	16.08	GBIF	Mexico
8	-91.09	16.733	GBIF	Mexico
9	-91.083	16.717	GBIF	Mexico
10	91.065	16.709	GBIF	Mexico
11	-91.064	16.719	GBIF	Mexico
12	-91.056	16.556	GBIF	Mexico
13	91.05	16.55	GBIF	Mexico
14	-90.95	16.55	REMIB	Mexico
15	-90.917	16.433	GBIF	Mexico
16	90.883	1616.15	GBIF	Mexico
17	-90.867	16.317	GBIF	Mexico
18	-90.866667	16.766667	REMIB	Mexico
19	-90.733	16.533	GBIF	Mexico
20	-90.733	16.536	GBIF	Mexico
21	-90.017	18.15	GBIF	Mexico
22	-89.917	18.5	GBIF	Mexico
23	-89.8	18.1	GBIF	Mexico
24	-89.689	17.913	GBIF	Mexico

25	-89.4	18.683	GBIF	Mexico
26	-89.397	18.6	GBIF	Mexico
27	-89.349	18.61	GBIF	Mexico
28	-89.125	16.358	GBIF	Belize
29	-88.148	21.065	GBIF	Mexico
30	-87.925833	19.389722	REMIB	Mexico
31	-80.033	-2.167	GBIF	Ecuador
32	-79.967	-0.033	GBIF	Ecuador
33	-79.583	-1.333	GBIF	Ecuador
34	-77.2833	-0.5	GBIF	Ecuador
35	-76.95	-1.1167	GBIF	Ecuador
36	-76.38086	7.52066	GBIF	Colombia
37	-76.00728	8.02733	GBIF	Colombia
38	-74.31667	-4.28333	GBIF	Peru
39	-74.2981	5.83924	GBIF	Colombia
40	-73.701389	-7.506111	SPECIESLINK	Brazil
41	-73.266667	-7.383333	SPECIESLINK	Brazil
42	-72.854444	-1.423333	SPECIESLINK	Colombia
43	-72.816667	-8.366667	SPECIESLINK	Brazil
44	-72.783333	-8.666667	SPECIESLINK	Brazil
45	-72.40278	-0.60485	GBIF	Colombia
46	-72.166667	-2.115833	SPECIESLINK	Colombia
47	-71.9	-9.316667	SPECIESLINK	Brazil
48	-71.663889	-9.523056	SPECIESLINK	Brazil
49	-71.38542	-12.77165	GBIF	Peru
50	-71.016667	-9.356667	SPECIESLINK	Brazil
51	-70.1	-12.56667	GBIF	Peru
52	-69.607	-13.142	GBIF	Peru

53	-69.58	-13.13	GBIF	Peru
54	-69.295	-12.838	GBIF	Peru
55	-68.8	-12.7	GBIF	Peru
56	-68.4	-12.21667	GBIF	Bolivia
57	-68.25	-9.333333	SPECIESLINK	Brazil
58	-68.19	2.166667	SPECIESLINK	Colombia
59	-68.18333	-12	GBIF	Bolivia
60	-67.72	-14.55	GBIF	Bolivia
61	-66.96667	-11.33333	GBIF	Bolivia
62	-66.733	-10.767	GBIF	Bolivia
63	-66.3	-14.63333	GBIF	Bolivia
64	-66.21667	-14.46667	GBIF	Bolivia
65	-64.57689	-23.65902	GBIF	Argentina
66	-62.217	-18.75	GBIF	Bolivia
67	-60.0333	-21.4469	GBIF	Paraguay
68	-59.62628	-26.79596	GBIF	Argentina
69	-59.58333	-18.28333	GBIF	Bolivia
70	-59.47209	-20.08525	GBIF	Paraguay
71	-59.36667	-18.18333	GBIF	Bolivia
72	-59.25	3.25	GBIF	Guyana
73	-59.233333	7.65	VERTNET	Guyana
74	-58.812	3.192	GBIF	Guyana
75	-58.779	3.268	GBIF	Guyana
76	-58.2	-20.2	GBIF	Paraguay
77	-58.1702	-25.03998	GBIF	Argentina
78	-58.13245	-25.06494	GBIF	Argentina
79	-58.12827	-25.02703	GBIF	Argentina
80	-58.08139	-25.02649	GBIF	Argentina

81	-58.08012	-25.11613	GBIF	Argentina
82	-58.04924	-25.06625	GBIF	Argentina
83	-58.01453	-25.11748	GBIF	Argentina
84	-58.00127	-25.12058	GBIF	Argentina
85	-57.03909	-19.54588	GBIF	Brazil
86	-54.55304	-25.62943	GBIF	Argentina
87	-54.54579	-25.60398	GBIF	Argentina
88	-54.50596	-25.62967	GBIF	Argentina
89	-54.50073	-25.66061	GBIF	Argentina
90	-54.49128	-25.67501	GBIF	Argentina
91	-54.48111	-25.69141	GBIF	Argentina
92	-54.45676	-25.69113	GBIF	Argentina
93	-54.45628	-25.67946	GBIF	Argentina
94	-54.44145	-25.71336	GBIF	Argentina
95	-54.16259	-25.59643	GBIF	Argentina
96	-54.13884	-25.56084	GBIF	Argentina
97	-52.4833	-22.4	SPECIESLINK	Brazil
98	-52.45	-22.45	SPECIESLINK	Brazil
99	-52.2	-22.1833	SPECIESLINK	Brazil
100	-51.5	-22.6667	SPECIESLINK	Brazil
101	-48.9106	-48.9106	SPECIESLINK	Brazil
102	-47.9622	-25.1084	SPECIESLINK	Brazil
103	-47.8	-21.5833	SPECIESLINK	Brazil
104	-47.5381	-24.4753	SPECIESLINK	Brazil
105	-47.2428	-23.9574	SPECIESLINK	Brazil
106	-47.078412	-24.380166	SPECIESLINK	Brazil
107	-45.0833	-23.2833	SPECIESLINK	Brazil
108	-40.17666	-19.01333	SPECIESLINK	Brazil

109	-40.14556	-18.33333	SPECIESLINK	Brazil
110	-40.05	-19.10333	SPECIESLINK	Brazil
111	-40.03	-19.1866	SPECIESLINK	Brazil
112	-88.460057	17.164368	VERTNET	Belize
113	-67.252804	0.06164	VERTNET	Brazil
114	-52.911486	-18.130047	SPECIESLINK	Brazil
115	-50.75623	-12.804141	VERTNET	Brazil
116	-55.064484	-4.075797	SMITHSONIAN	Brazil
117	-77.482808	-1.733191	VERTNET	Ecuador

Figure S1. Extent of the study area from which the ecological niche of the *Tayassu pecari* was modeled. Dots represent 117 occurrence data (1980-2013). Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Table S2. Data documenting known occurrences of *Myrmecophaga tridactyla* across its range, used to model its ecological niche using Maxent.

No.	Longitude	Latitude	Source	Country
1	-80.033	-2.167	GBIF	Ecuador
2	-74.8166667	-0.15	SPECIESLINK	Colombia
3	-73.5	3.88611111	SPECIESLINK	Colombia
4	-73.2666667	-7.38333333	SPECIESLINK	Brazil
5	-73.2536111	-8.28083333	SPECIESLINK	Brazil
6	-72.8544444	-1.42333333	SPECIESLINK	Colombia
7	-72.7466667	2.92611111	SPECIESLINK	Colombia
8	-72.4033333	5.35166667	SPECIESLINK	Colombia
9	-72.39121	4.89358	GBIF	Colombia
10	-71.7369444	-2.13333333	SPECIESLINK	Colombia
11	-69.605479	-13.142294	GBIF	Peru
12	-69.295	-12.838	GBIF	Peru
13	-69.28	-12.88	VERTNET	Peru
14	-69.27979	7.48775	GBIF	Venezuela
15	-69.083	-13	GBIF	Peru
16	-68.725	-9.25	SPECIESLINK	Brazil
17	-67.1666667	6.55	SPECIESLINK	Venezuela
18	-66.6166667	3.38333333	SPECIESLINK	Venezuela
19	-66.1	5.35	SPECIESLINK	Venezuela
20	-65.6666667	3.41666667	SPECIESLINK	Venezuela
21	-65.55	3.16666667	SPECIESLINK	Venezuela
22	-65.4166667	7.58333333	SPECIESLINK	Venezuela

23	-62.217	-18.75	GBIF	Bolivia
24	-61.81408	-24.30705	GBIF	Argentina
25	-61.80324	-24.31642	GBIF	Argentina
26	-59.25	3.25	GBIF	Guyana
27	-58.811	3.268	GBIF	Guyana
28	-58.21044	-25.0948	GBIF	Argentina
29	-58.18653	-25.0052	GBIF	Argentina
30	-58.17324	-25.12037	GBIF	Argentina
31	-58.16427	-25.09254	GBIF	Argentina
32	-58.16275	-25.10203	GBIF	Argentina
33	-58.15219	-25.11016	GBIF	Argentina
34	-58.14924	-25.02949	GBIF	Argentina
35	-58.14048	-25.04403	GBIF	Argentina
36	-58.13772	-25.07115	GBIF	Argentina
37	-58.13254	-25.01143	GBIF	Argentina
38	-58.13065	-25.09123	GBIF	Argentina
39	-58.12558	-25.15391	GBIF	Argentina
40	-58.11759	-25.11969	GBIF	Argentina
41	-58.1019	-25.04173	GBIF	Argentina
42	-58.06471	-25.0579	GBIF	Argentina
43	-58.05715	-25.06507	GBIF	Argentina
44	-58.00455	-25.08919	GBIF	Argentina
45	-58.00127	-25.12058	GBIF	Argentina
46	-56.71314	-20.76029	GBIF	Brazil
47	-55.96573	-20.09592	GBIF	Brazil

48	-54.738	4.27	GBIF	Suriname
49	-54.5619	-25.8875	GBIF	Argentina
50	-54.51094	-25.66549	GBIF	Argentina
51	-54.50561	-25.66335	GBIF	Argentina
52	-54.4988	-25.66906	GBIF	Argentina
53	-54.44097	-25.70538	GBIF	Argentina
54	-54.38405	-25.62478	GBIF	Argentina
55	-47.8	-21.5833	SPECIESLINK	Brazil
56	-55.782111	-15.473777	SPECIESLINK	Brazil

Figure S2. Extent of the study area from which the ecological niche of the *Myrmecophaga tridactyla* was modeled. Dots represent 56 occurrence data (1983-2013). Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Table S3. Data documenting known occurrences of *Cuniculus paca* across its range, used to model its ecological niche using Maxent.

No.	Longitude	Latitude	Source	Country
1	-74.62296	-3.30578	GBIF	Peru
2	-90.821	18.614	GBIF	Mexico
3	-94.133	16.867	GBIF	Mexico
4	-88.25	21.235	GBIF	Mexico
5	-87.859	19.79	GBIF	Mexico
6	-87.431032	20.221628	GBIF	Mexico
7	-76.874166	0.088889	VERNET	Ecuador
8	-76.783333	0.191667	VERNET	Ecuador
9	-92.8211	15.6564	UNIBIO	Mexic
10	-88.857	18.771	GBIF	Mexico
11	-76.416666	-0.233333	VERNET	Ecuador
12	-91.195	16.74	GBIF	Mexico
13	-91.065	16.709	GBIF	Mexico
14	-77.2833	-0.5	GBIF	Ecuador
15	-72.706	-3.199	GBIF	Peru
16	-88.101	19.224	GBIF	Mexico
17	-93.1	16.727	GBIF	Mexico
18	-91.162	16.812	GBIF	Mexico
19	-90.969	16.901	GBIF	Mexico
20	-90.243	20.507	GBIF	Mexico
21	-86.94	20.849	GBIF	Mexico
22	-90.968	16.096	GBIF	Mexico
23	-88.1325	19.26	REMIB	Mexico
24	-93.409	16.508	GBIF	Mexico
25	-93.265	15.552	GBIF	Mexico
26	-93.257	15.531	GBIF	Mexico

27	-92.07	16.91	GBIF	Mexico
28	-90.25	20.5	GBIF	Mexico
29	-66.73333	-11.31667	GBIF	Bolivia
30	-52.37	-3.63	GBIF	Brazil
31	-93.904	16.325	GBIF	Mexico
32	-93.872	16.308	GBIF	Mexico
33	-89.917	18.5	GBIF	Mexico
34	-89.8	18.1	GBIF	Mexico
35	-91.133	16.767	GBIF	Mexico
36	-91.13	16.761	GBIF	Mexico
37	-88.074167	19.389722	REMIB	Mexico
38	-93.606	16.921	GBIF	Mexico
39	-92.833	15.567	GBIF	Mexico
40	-89.677	17.891	GBIF	Mexico
41	-89.30944	20.1825	GBIF	Mexico
42	-69.05	-12.6	GBIF	Peru
43	-68.725	-9.25	SPECIESLINK	Brazil
44	-68.25	-10.033333	SPECIESLINK	Brazil
45	-72.116667	-2.088611	SPECIESLINK	Colombia
46	-93.653	16.917	GBIF	Mexico
47	-93.124	16.86	GBIF	Mexico
48	-80.717	-1.567	GBIF	Ecuador
49	-80.033	-2.167	GBIF	Ecuador
50	-79.967	-0.033	GBIF	Ecuador
51	-79.583	-1.333	GBIF	Ecuador
52	-93.768066	16.981101	GBIF	Mexico
53	-93.026	17.342	GBIF	Mexico
54	-91.056	16.556	GBIF	Mexico

55	-89.125	16.358	GBIF	Belize
56	-69.683	-13.503	GBIF	Peru
57	-69.607	-13.142	GBIF	Peru
58	-69.295	-12.838	GBIF	Peru
59	-66.833	-10.954	GBIF	Bolivia
60	-66.733	-10.767	GBIF	Bolivia
61	-65.7	-9.867	GBIF	Bolivia
62	-93.671111	16.958889	REMIB	Mexico
63	-68.19	2.166667	SPECIESLINK	Colombia
64	-93.017	17.347	GBIF	Mexico
65	-76.109508	-2.578189	GBIF	Peru
66	-73.949452	-4.668078	GBIF	Peru
67	-59.25	3.25	GBIF	Guyana
68	-89.481	18.049	GBIF	Mexico
69	-78.433	-3.917	GBIF	Peru
70	-78.383	-4.1	GBIF	Peru
71	-54.45177	-25.6878	GBIF	Argentina
72	-68.25	-9.333333	SPECIESLINK	Brazil
73	-68.7	-12.517	GBIF	Peru
74	-99.166667	23.033333	Moreno-Valdez *et al.* 1997	Mexico
75	-89.6392	17.4614	GBIF	Guatemala
76	-89.5994	17.5164	GBIF	Guatemala
77	-89.5808	17.3836	GBIF	Guatemala
78	-74.2981	5.83924	GBIF	Colombia
79	-56.916667	-24.166667	ARCTOS	Paraguay
80	-56.023834	-22.631666	VERNET	Paraguay
81	-54.43975	-25.704	GBIF	Argentina
82	-54.41686	-25.7272	GBIF	Argentina

83	-87.959722	19.2825	REMIB	Mexico
84	-88.026389	19.585278	REMIB	Mexico
85	-71.663889	-9.523056	SPECIESLINK	Brazil
86	-71.016667	-9.356667	SPECIESLINK	Brazil
87	-40.477777	-20.2725	SPECIESLINK	Brazil
88	-40.41589	-20.59178	SPECIESLINK	Brazil
89	-93.082333	17.18614	GBIF	Mexico
90	-89.6486	17.5197	GBIF	Guatemala
91	-89.5661	17.5981	GBIF	Guatemala
92	-59.01	4.75	GBIF	Guayana
93	-58.85	4.73	GBIF	Guayana
94	-54.47802	-25.69073	GBIF	Argentina
95	-40.13	-19.05	SPECIESLINK	Brazil
96	-93.655	-93.655	GBIF	Mexico
97	-96.209	17.593	GBIF	Mexico
98	-54.49878	-25.66891	GBIF	Argentina
99	-54.334772	-25.597704	GBIF	Argentina
100	-68.2825	-10.567222	SPECIESLINK	Brazil
101	-66.878611	-9.916944	SPECIESLINK	Brazil
102	-66.839167	-10.029444	SPECIESLINK	Brazil
103	-66.818056	-10.005	SPECIESLINK	Brazil
104	-66.811111	-10.045278	SPECIESLINK	Brazil
105	-66.802222	-9.976667	SPECIESLINK	Brazil
106	-66.774444	-9.991111	SPECIESLINK	Brazil
107	-66.720278	-9.9575	SPECIESLINK	Brazil
108	-95.060343	18.560449	GBIF	Mexico
109	-93.591	16.21	GBIF	Mexico
110	-91.25	16.825	GBIF	Mexico

111	-91.083	16.717	GBIF	Mexico
112	-90.547	17.246	GBIF	Guatemala
113	-71.269	-12.66833	GBIF	Peru
114	-73.774444	-7.458889	SPECIESLINK	Brazil
115	-73.701389	-7.506111	SPECIESLINK	Brazil
116	-73.678056	-7.446667	SPECIESLINK	Brazil
117	-73.661111	-7.431667	SPECIESLINK	Brazil
118	-73.276667	-7.556667	SPECIESLINK	Brazil
119	-73.266667	-7.383333	SPECIESLINK	Brazil
120	-73.253611	-8.280833	SPECIESLINK	Brazil
121	-72.883333	-8.558333	SPECIESLINK	Brazil
122	-72.857778	-8.405278	SPECIESLINK	Brazil
123	-72.781944	-8.875278	SPECIESLINK	Brazil
124	-67.616667	-10.066667	SPECIESLINK	Brazil
125	-66.755556	-9.953333	SPECIESLINK	Brazil
126	-40.14556	-18.33333	SPECIESLINK	Brazil
127	-40.05	-19.10333	SPECIESLINK	Brazil
128	-39.81333	-18.28666	SPECIESLINK	Brazil
129	-91.95	16.775	GBIF	Mexico
130	-91.95	16.825	GBIF	Mexico
131	-91.25	16.775	GBIF	Mexico
132	-90.853	16.125	GBIF	Mexico
133	-90.849	16.144	GBIF	Mexico
134	-54.43714	-25.70373	GBIF	Argentina
135	-54.42409	-25.72416	GBIF	Argentina
136	-92.116667	16.775	REMIB	Mexico
137	-97.544476	20.064771	Ramírez-Bravo & Hernández-Santín 2012	Mexico
138	-40.53722	-19.97333	SPECIESLINK	Brazil

139	-71.49185	-13.023617	VERNET	Peru
140	-58.779	3.268	GBIF	Guyana
141	-54.48111	-25.69141	GBIF	Argentina
142	-91.31	16.193	GBIF	Mexico
143	-91.31	16.202	GBIF	Mexico
144	-88.148	21.065	GBIF	Mexico
145	-88.067	21.567	GBIF	Mexico
146	-91.056	16.079	GBIF	Mexico
147	-54.2969	-25.67276	GBIF	Argentina
148	-54.17288	-25.6822	GBIF	Argentina
149	-93.069853	16.792188	GBIF	Mexico
150	-93.041873	16.759293	GBIF	Mexico
151	-54.27079	-25.67337	GBIF	Argentina
152	-75.00811	6.35203	GBIF	Colombia
153	-74.86711	6.21986	GBIF	Colombia
154	-74.84778	6.22478	GBIF	Colombia
155	-74.83797	6.21839	GBIF	Colombia
156	-74.01214	6.35236	GBIF	Colombia
157	-54.56323	-25.6805	GBIF	Argentina
158	-97.680083	19.99682	Ramírez-Bravo & Hernández-Santín 2012	Mexico
159	-98.668611	21.095833	Rodríguez-Ruiz *et al.* 2012	Mexico
160	-75.12094	6.41033	GBIF	Colombia
161	-75.04369	6.36778	GBIF	Colombia
162	-74.92081	5.50564	GBIF	Colombia
163	-74.89586	5.57061	GBIF	Colombia
164	-74.88333	5.55608	GBIF	Colombia
165	-54.21113	-25.68426	GBIF	Argentina
166	-74.85342	6.20597	GBIF	Colombia

167	-54.459	-25.66139	GBIF	Argentina
168	-54.38617	-25.635	GBIF	Argentina
169	-54.37577	-25.73724	GBIF	Argentina
170	-96.34747	18.150164	Pérez-Irineo & Santos-Moeno 2012	Mexico
171	-75.013506	6.401487	GBIF	Colombia
172	-74.86667	6.22756	GBIF	Colombia
173	-74.81342	6.20858	GBIF	Colombia
174	-74.02167	6.37133	GBIF	Colombia
175	-72.40235	4.89593	GBIF	Colombia
176	-54.38664	-25.65822	GBIF	Argentina
177	-54.38021	-25.66028	GBIF	Argentina
178	-54.3616	-25.70563	GBIF	Argentina
179	-54.34957	-25.69576	GBIF	Argentina
180	-54.34578	-25.70033	GBIF	Argentina
181	-54.32491	-25.69018	GBIF	Argentina
182	-54.31826	-25.68631	GBIF	Argentina
183	-54.26713	-25.68764	GBIF	Argentina
184	-54.18014	-25.69124	GBIF	Argentina
185	-54.17448	-25.67191	GBIF	Argentina
186	-97.906668	20.208763	Ramírez-Bravo & Hernández-Santín 2012	Mexico
187	-54.24302	-25.69958	GBIF	Argentina
188	-54.23841	-25.70519	GBIF	Argentina
189	-97.855274	20.721681	Ramírez-Bravo & Hernández-Santín 2012	Mexico
190	-97.627301	20.104301	Ramírez-Bravo & Hernández-Santín 2012	Mexico
191	-97.949632	20.276359	Ramírez-Bravo & Hernández-Santín 2012	Mexico
192	-97.660614	19.996864	Ramírez-Bravo & Hernández-Santín 2012	Mexico
193	-97.934605	20.215317	Ramírez-Bravo & Hernández-Santín 2012	Mexico
194	-97.56493	20.029736	Ramírez-Bravo & Hernández-Santín 2012	Mexico

195	-73.76833	7.4325	GBIF	Colombia
196	-55.93115	-9.5976	GBIF	Brazil
197	-51.595833	0.924722	Michalski *et al.* 2015	Brazil
198	-92.788199	15.103138	CONABIO-Naturalista	Mexico
199	-96.15785	17.230753	CONABIO-Naturalista	Mexico
200	-93.602207	15.887459	CONABIO-Naturalista	Mexico
201	-84.798095	10.283263	CONABIO-Naturalista	Costa Rica
202	-92.471065	18.459093	CONABIO-Naturalista	Mexico
203	-80.719417	-1.610361	CONABIO-Naturalista	Ecuador
204	-88.458749	16.78026	CONABIO-Naturalista	Belize

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Figure S3. Extent of the study area from which the ecological niche of the *Cuniculus paca* was modeled. Dots represent 204 occurrence data (1980-2016). Coordinate system: World Mollweide, Projection: Mollweide, Datum: WGS1984.

Table S4. Summary of reference studies documenting local abundances of *Tayassu pecari* (ind/km^2), used to evaluate the effects of distance to the niche centroid and human footprint (complete references in Appendix S1).

Reference	Country	Number of sites
Altrichter 2005	Argentina	2
Aquino & Calle 2003	Peru	1
Aquino *et al.* 1999	Peru	3
Aquino *et al.* 2007	Peru	1
Aquino *et al.* 2014	Peru	1
Aquino *et al.* 2014b	Peru	1
Ayala & Noss 2000	Bolivia	1
Bodmer 1989	Peru	1
Bodmer *et al.* 1997	Peru	4
Bodmer *et al.* 2006	Peru	1
Bodmer & Puertas 2007	Peru	1 (2 years average)
Bolaños & Naranjo 2001	Mexico	1
Cullen *et al.* 2001	Brazil	3
Desbiez *et al.* 2010	Brazil	1
Durango 2011	Ecuador	2
Endo *et al.* 2010	Peru	7
Falconi 2011	Mexico	2
Fragoso 1998	Brazil	1
Hill *et al.* 2003	Paraguay	1
Hofman *et al.* 2016	Belize	1
Keuroghlian *et al.* 2004	Brazil	1 (averaged with Cullen *et al.* 2001)
Lleellish *et al.* 2003	Peru	3
Maldonado 2010	Colombia	2
Martínez *et al.* 2008	Bolivia	1
Mayor *et al.* 2015	Peru	1 (2 periods average)

Mendes-Pontes *et al.* 2010	Brazil	2
Moreno 2006	Panama	1
Naranjo & Bodmer 2007	Mexico	2
Naranjo & Bolaños 2003	Mexico	1
Novack *et al.* 2005	Guatemala	1
Peres *et al.* 2003	Brazil	1
Peres & Nascimento 2006	Brazil	1
Pérez-Peña *et al.* 2012	Peru	1
Reyna-Hurtado *et al.* 2010	Mexico	1
Sánchez & Vásquez 2007	Peru	1
Schaller 1983	Brazil	1
Silveira 2004	Brazil	1 (2 years average)
Zapata-Ríos & Araguillin 2013	Ecuador	1
38 studies	11 countries	58 data

Table S5. Summary of reference studies documenting local abundances of *Myrmecophaga tridactyla* (ind/km^2), used to evaluate the effects of distance to the niche centroid and human footprint (complete references in Appendix S1).

Reference	Country	Number of sites
Ayala & Noss 2000	Bolivia	1
Bodmer *et al.* 2006	Peru	1
De Miranda *et al.* 2006	Brazil	1
Desbiez & Medri 2010	Brazil	1
Mendes-Pontes *et al.* 2010	Brazil	1
Peres *et al.* 2003	Brazil	1
Polisar *et al.* 2008	Venezuela	1
Rojano *et al.* 2015	Colombia	1
Stevenson 1996	Colombia	1
9 studies	5 countries	9 data

Table S6. Summary of reference studies documenting local abundances of *Cuniculus paca* (ind/km^2), used to evaluate the effects of distance to the niche centroid and human footprint (complete references in Appendix S1).

Reference	Country	Number of sites
Aquino *et al.* 2009	Peru	1
Emmons 1987	Peru	1
Falconi 2011	Mexico	2
Hill *et al.* 2003	Paraguay	1
Huanca-Huarachi *et al.* 2011	Bolivia	1
Maldonado 2010	Colombia	2
Mendes-Pontes *et al.* 2010	Brazil	1
Naranjo & Bolaños 2003	Mexico	1
Novack *et al.* 2005	Guatemala	1
Peres & Nascimento 2006	Brazil	2
Suárez *et al.* 2013	Ecuador	1
Zimmerman *et al.* 2001	Brazil	1
11 studies	7 countries	15 data

Table S7. Best settings to model the niches of the species in Maxent resulting from *ENMeval* analyses.

Species	Feature classes	Regularization multiplier
Tayassu pecari	LQH	2.5 (3.5)
Myrmecophaga tridactyla	LQ	0.5 (1)
Cuniculus paca	LQHPT	2.5 (igual)
Maxent's default settings	LQHPT	1

Table S8. Significance of the effect of including abundance data of *Tayassu pecari* from different field sampling methods.

Linear Models	*P* (of the total model)
Abundance ~ Method	0.79
Resid. of abundance-DNC (GLS) ~ Method	0.79
Resid. of abundance-DNC (QR 0.50) ~ Method	0.79
Resid. of abundance-DNC (QR 0.93) ~ Method	0.77
Resid. of abundance-HF (QR 0.50) ~ Method	0.72
Resid. of abundance-HF (QR 0.93) ~ Method	0.27
Resid. of abundance-DNC+HF (QR 0.50) ~ Method	0.71
Resid. of abundance-DNC+HF (QR 0.93) ~ Method	0.44

DNC = Distance to the niche centroid, GLS = Generalized least squares, HF = Human footprint, QR = Quantile regression, Resid. = Residuals.

Table S9. Permutation importance of each variable to generate the final ecological niche model of *Tayassu pecari*.

Variables	Permutation importance (%)
Precipitation of driest quarter	37.2
Temperature seasonality	17.5
Mean temperature of wettest quarter	12.6
Max temperature of warmest month	7.4
Precipitation of warmest quarter	7
Precipitation seasonality	4.5
Human footprint	2.8
Slope	2.4
Precipitation of coldest quarter	2.3
Aspect	2
Precipitation of wettest quarter	1.8
Annual mean temperature	0.9
Elevation	0.9

Min temperature of coldest month	0.4
Mean diurnal range	0.4
Annual precipitation	0

Table S10. Permutation importance of each variable to generate the final ecological niche model of *Myrmecophaga tridactyla*.

Variables	Permutation importance (%)
Mean temperature of warmest quarter	35.5
Annual mean temperature	28.4
Temperature seasonality	13.6
Precipitation of coldest quarter	9.8
Precipitation of warmest quarter	7
Elevation	1.6
Mean temperature of wettest quarter	1.5
Precipitation seasonality	0.9
Annual precipitation	0.5
Aspect	0.4
Slope	0.4
Precipitation of driest quarter	0.3

Table S11. Permutation importance of each variable to generate the final ecological niche model of *Cuniculus paca*.

Variables	Permutation importance (%)
Precipitation of driest quarter	27.6
Human footprint	16.1
Mean temperature of driest quarter	10.2
Elevation	9.3
Mean temperature of wettest quarter	8

Precipitation seasonality	7.8
Temperature seasonality	5.3
Max temperature of warmest month	3.9
Precipitation of warmest quarter	3
Precipitation of coldest quarter	3
Slope	2.7
Precipitation of wettest month	1.6
Aspect	0.6
Annual precipitation	0.5
Mean diurnal range	0.4

Appendix S1

Complete references for studies used to evaluate the effects of distance to the niche centroid and human footprint on the local abundances of *Tayassu pecari*, *Myrmecophaga tridactyla*, and *Cuniculus paca*.

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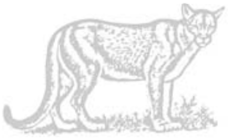

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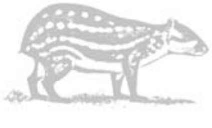

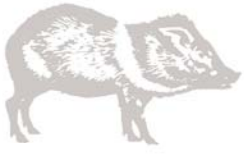

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Jefe Indio Seattle

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