UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
ECOLOGÍA

PATRONES DE SIMPATRÍA Y EFECTOS DEL CAMBIO CLIMÁTICO EN LOS CARNÍVOROS (MAMMALIA: CARNIVORA) DE AMÉRICA

TESIS
QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN CIENCIAS

PRESENTA:

M. en C. ANDRÉS ARIAS ALZATE

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MÉXICO, D. F. SEPTIEMBRE DE 2016.

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Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 13 de junio de 2016, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **ARIAS ALZATE ANDRÉS** con número de cuenta **513451764** con la tesis titulada: **"Patrones de simpatría y efectos del cambio climático en los carnívoros (Mammalia: Carnivora) de América"**, realizada bajo la dirección del **DR. ENRIQUE MARTÍNEZ MEYER:**

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 29 de agosto de 2016.

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
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Andrés Arias-Alzate
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Dedicatoria

A mi familia, al cosmos y a la fuerza cuántica por ser mis aliados,
Darme fuerza y luz en mi alma, en mi cabeza y en mi corazón
Gracias por iluminarme y mostrarme el camino.

"Let us define our present reality by an intention of a great vision of the future instead of the same memories of the past"

Dr. Joe Dispenza

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RESUMEN

A lo Largo de la historia evolutiva del planeta, los mamíferos han sido y siguen siendo uno de los grupos de especies más importantes para el funcionamiento de los ecosistemas, sin embargo, actualmente son uno de los grupos bajo mayor amenaza por el cambio global y las presiones humanas en general. Entre estos podemos encontrar a los carnívoros (Mammalia: Carnivora), especies altamente sensible al desequilibrio ambiental, por lo que la pérdida de sus poblaciones y su consecuente pérdida de su diversidad funcional, potencialmente representaría una amenaza sobre el funcionamiento y la provisión de bienes y servicios de los ecosistemas y más aun con los grandes problemas ambientales que afronta la humanidad actualmente.

El objetivo de la presente tesis fue el evaluar y entender la dinámica de como los ensamblajes de carnívoros (Mammalia: Carnivora) se estructuraron ecológica y espacialmente durante los últimos 130 mil años hasta la actualidad y comprender si estos están respondiendo a reglas de ensamble, o muy posiblemente a reglas de des-ensamble y re-ensamble a lo largo del tiempo, a partir de factores ambientales (escenopoéticos, o nicho Grinneliano) y/o a factores ecológicos funcionales (bionómicos, o Nicho Eltoniano) a diferentes escales geográficas en el continente. Para realizar este objetivo, construimos una base de datos con los registros de presencia y atributos ecológicos funcionales de las especies de carnívoros extintos y actuales documentados durante los últimos 130 mil años hasta la actualidad, separándolos en tres periodos principales, último periodo interglaciar (LIG, ~130-80 Ka), ultimo máximo glaciar (LGM, ~20-10 Kyrs BP [representando ~21 Ka en años astronómicos]) y periodo actual (C). A partir de estos e implementando análisis de nicho ecológico, macroecológicos y análisis estructurales de redes complejas, elucidamos algunos patrones biogeográficos e identificamos que factores ambientales y ecológicos funcionales juegan un papel importante como mecanismos en la distribución y la estructuración de los ensamblajes (en términos de riqueza y composición) de estas especies a nivel espacial y temporal en América.

Nuestros resultados muestran por un lado los factores ambientales a través del tiempo como uno de los principales determinantes que restringen y moldean las distribuciones de las especies de carnívoros y por tanto de su estructuración a nivel de ensamblajes, principalmente a escala continental en América. No obstante esta influencia también fue importante hacia la escala local y de manera diferencial a lo largo del continente. Estas restricciones durante los cambios ambientales en la transición LIG-LGM-C muestran un cambio considerable en la riqueza y la composición de los ensamblajes, lo que sugiere que el clima y sus variaciones principalmente en las tendencias anuales (temperatura media anual, precipitación media anual), estacionales (estacionalidad de la precipitación y temperatura, isotermalidad) y tendencias limitantes (precipitación del cuarto trimestre más caliente, temperatura media del cuarto trimestre más húmedo y frio, mínimo de temperatura del mes más frío, y máximo de temperatura del mes más caliente) funcionaron como un

filtro ambiental durante el último máximo glacial (LGM), explicando entre el 30 y el 75% de estas variaciones a nivel espacial y temporal.

Así mimo, el nicho funcional de las especies expresado a nivel geográfico como una diversidad funcional, también juega un papel clave y determinante en cómo pueden coexistir las especies al interior de los ensamblajes. Como patrón general las especies de carnívoros simpátricos muestran una tendencia a diferenciarse en la proporción de tamaño medio (S_R) como uno de los principales mecanismos que limitan el número de especies que pueden coexistir dentro de los ensambles, y este mecanismo tiende a ser conservador, no sólo a través de los ensamblajes sino también a través de diferentes grupos de atributos ecológicos al interior de los mismos, explicando entre el 30 al 90% de estas variaciones a nivel espacial y temporal en América. Esto igualmente sugiere un filtrado funcional desde el nivel local, promovido principalmente por la relación de tamaño de peso promedio (S_R). Esto significa que las especies dentro de los mismos ensamblajes y con el mismo rasgo ecológico presentan una mayor probabilidad de presentar desplazamiento en su tamaño con el fin de coexistir (i.e *Leopardus pardalis* y *Leopardus wiedii*; *Nasua nasua* y *Nasuella olivacea*; *Eira barbara* y *Mustela frenata*; *Smilodon populator* y *Panthera onca; Cerdocyon thous y Atelocynus microtis*). Siendo menos probable encontrar especies del mismo tamaño y con los mismos rasgos ecológicos de lo esperado por azar. Sin embargo, si las especies se aproximan a un mismo tamaño, entonces estas muestran una segregación en al menos uno de los demás atributos ecológicos, permitiendo así la simpatría, lo que refleja una gran diversidad funcional a nivel espacial y temporal en América.

Los cambios ambientales prolongados, principalmente durante el último máximo glaciar, fueron críticos en las adaptaciones funcionales y la distribución de las especies y por tanto de sus poblaciones. En términos del riesgo de extinción por ejemplo, algunas de estas especies al encontrarse con la reducción de áreas climáticamente adecuadas durante la transición LIG-LGM, sufrieron grandes contracciones y fragmentaciones de sus distribuciones y consigo reducciones de las poblaciones, principalmente en Norte América. Esto comparado con las especies con distribuciones en áreas climáticamente más estables como las zonas tropicales. Por ello, al mantenerse esta tendencia durante largos periodos de tiempo (más de 10 mil años), el riesgo de extinción puede incrementarse debido los cuellos de botella demográficos, el cual puedo ser más crítico si otros factores estresantes actuaron sobre las distribuciones remanentes. Este proceso pudo ser más crítico en la reducción de las poblaciones de las especies más grandes (e.g. *Smilodon fatalis*, *Panthera atrox*, *Arctodus simus*, *Tremarctos floridanus*), jugando así un papel importante en su extinción como se ha propuesto para otras especies de mega-mamíferos. En este sentido es posible que muchas de estas especies de carnívoros que pasaron por el "filtro de extinción" durante el último máximo glaciar representan el conjunto de especies con los atributos ecológicos más adecuada para hacer frente a los cambios ambientales naturales. Donde las características y requerimientos biológicos juegan un papel clave en el riesgo de extinción.

De este modo, con este trabajo mostramos nuevas luces sobre la historia, los patrones y mecanismos que juegan un papel importante en la distribución y la estructuración de los ensamblajes de carnívoros a nivel espacial y temporal en América. Las restricciones impuestas por el nicho ecológico y dos de sus principales dimensiones (nicho ambiental y funcional) son en parte los principales mecanismos de coexistencia y estructuración de los ensamblajes, denominamos aquí como "***ecological niche clustering effect***", Donde la coexistencia en parte es el resultado y un efecto combinado a diferentes escalas entre determinantes ambientales y funcionales. En este sentido es importante considerar y aprender las lecciones del pasado, si queremos tomar hoy las decisiones correctas para el futuro. En la medida que se conozcan cada vez más sobre el porqué y cómo podrían cambiar estos ensamblajes, podremos anunciar las posibles consecuencias sobre estas especies y su dinámica ecológica con implicaciones para la conservación de estas especies en América.

ABSTRACT

Throughout the evolutionary history of the planet, mammals have been and remain one of the most important groups for ecosystem functioning, however, now are one of the mayor groups under great threat due to global change and human pressures in general. Among these we can find carnivoran species (Mammalia: Carnivora), highly sensitive to environmental imbalance, so the loss of their populations and the consequent loss of their functional diversity represent a potentially threat to ecosystem services and functioning even more with the major environmental problems that mankind are facing today.

The aim of this thesis was to evaluate and understand the dynamics of how carnivoran species (Mammalia: Carnivora) were ecological and spatially structured over the last 130,000 years to the present, and understand if they are responding to some assembly or de-assembly and re-assembly rules over time base on environmental and / or functional ecological factors at different geographical scales in Americas. To achieve this objective, we construct a database with occurrence records and functional ecological attributes of extinct and current carnivoran species documented over the past ~130,000 years until today, and were classify into three main periods, last interglacial period (LIG, ~130-80 Kyrs BP), last glacial maximum (LGM, ~20-10 Kyrs BP [representing ~21 Kyrs BP in astronomical years]) and current period (C). Afterwards we implemented ecological niche, macroecological and structural complex networks analysis, to elucidate some biogeographic patterns and identify which environmental and functional ecological factors play an important role as mechanisms in the distribution and assemblages structuring (in terms of richness and composition) across the space and time in the continent.

On one hand our results show that the influence of some environmental factors over time are one of the main determinants that restrict and shape carnivoran species distributions and therefore its assemblages structuring patterns mainly at continental scale in America. Nevertheless, this influence was also important toward the local level and was differentially throughout the space in the continent. These climatic restrictions during the environmental changes in the LIG-LGM-C transition show a considerable assemblages richness and composition shift, suggesting that the climate and its variations mainly in annual trends (annual average annual temperature, rainfall), seasonal (seasonality of precipitation and temperature, isotermalidad) and limiting tendencies (precipitation fourth warmest quarter, average temperature of the room more humid and cold, at least quarter of temperature of the coldest month and maximum temperature hottest month) worked as an species environmental filtering meanly during the last glacial maximum (LGM), explaining between 30 and 75% of these variations through space and time. With more accentuated changes in North than South America.

Likewise, the ecological functional niche or ecological trairt-space expressed in the geography as a functional diversity pattern also plays a key role in how species can coexist within assemblage. As a general pattern the sympatric carnivoran species show a tendency

to differentiate in the mean body size ratio (SR) as one of the main potential mechanisms that limited the number of carnivoran species that could coexist, and it tends to be conservative not only through assemblage but also over different ecological trait-space groups, explaining between 30 to 90% of spatial and temporal variations in Americas. This also suggests a species functional filtering from the local level meanly promoted by this SR. In these sense, carnivoran species within the same geographic space and with a tendency to occupy the same ecological traits have a greater likelihood to display body size differences (character displacement) in order to coexist (i.e. *Leopardus pardalis* and *L. tigrinus*; *Nasua nasua* and *Nasuella olivacea*, *Eira barbara* and *Mustela frenata*; *Smilodon Populator†* and *Panthera onca*; *Cerdocyon thous* and *Atelocynus microtis*). Therefore, it is less likely to find sympatric species within the same size and within the same ecological trait-space (Functional diversity redundancy among species) than expected by chance. However, if species approximate to display the same body size, then these show a segregation in at least in one of the other ecological attributes allowing the sympatry and avoid competitive exclusion, which reflects a great functional diversity patterns through space and time in Americas.

In this sense, prolonged environmental changes, especially during the last glacial maximum, were critical in terms of carnivoran species functional adaptations, distribution patterns and therefore in their populations' persistence. In terms of extinction, risk for example, some of these species facing the reduction of appropriate climatic areas during the LIG-LGM transition, suffered large range reduction and fragmentation along with viable populations' reductions, mainly in North America. Therefore, if this trend continues for long periods of time (more than 10,000 years), environmental filtering is likely a leading factor which played a critical portion in the extinction context, increasing the susceptibility of remaining populations (extinction risk increases due to demographic bottlenecks), especially if other stressors were operating synergistically on the remaining fragmented distributions. In contrast, persistence in the face of environmental changes occurred for those species containing relatively stable climates areas across important portions of their geographic ranges, such tropical regions. In this sense, this process could be more critical in reducing larger species populations (e.g. *Smilodon Fatalis*, *Panthera atrox*, *Arctodus simus*, *Tremarctos floridanus*) due to their biological requirements, thus playing an important role in their extinction as proposed for other species of mega-mammals. It is possible that many of these carnivoran species that passed through the climate change "extinction filter" represent the current set of species within the ecological trait-space best suited to face natural environmental changes. Thus, the carnivoran ecological traits and biological requirements play a key role in the extinction risk context as seen today.

With this work, we show new insights about the biogeographic history and mechanisms that play important roles in shaping the carnivoran distribution and structuring assemblage patterns at spatial and temporal scales in America. The restrictions imposed by the ecological niche and two of its main dimensions (environmental and ecological trait-space) are partly the main mechanisms of coexistence and assemblages structuring, that we call here as "***ecological niche clustering effect”***, where coexistence is partly the result and a differential and combined effect of environmental and functional determinants at different scales. In this sense, it is important to consider and learn these lessons of the past, if we want to make today the right decisions for the future of carnivoran species persistence. The more we know and understand about why and how these assemblage might change in space and time, the more we can take actions and announce the possible consequences of losing these species and their ecological dynamics with implications for carnivorans conservation in Americas.

1. ESTRUCTURA DE LA TESIS

La presente tesis doctoral está estructurada en cuatro capítulos principales. Así mismo, incluye una introducción general que aborda el marco teórico de todo el trabajo así como sus correspondientes objetivos e hipótesis. Dada la escala y resolución de los análisis, la tesis se estructura con una conexión de análisis macroecológicos, de nicho ecológico y ecológico de redes complejas, se explora la influencia de determinantes ambientales y de atributos ecológicos en la estructuración de los ensamblajes de carnívoros a lo largo del tiempo y el espacio en América.

El primer capítulo compuesto por un artículo aborda de manera integral el marco conceptual y metodológico en el que se enmarca el estudio de la distribución de especies y su conexión con los cambios en el clima desde el nivel individual de los organismos y sus rangos geográficos, hasta las intrincadas interacciones de las especies en los ensamblajes o comunidades bióticas a diferentes escalas espacio-temporales en áreas como la macroecología, biogeografía y ecología geográfica.

El segundo capítulo está compuesto por dos artículos. El primer artículo aborda el papel y la influencia de determinantes ambientales y como estos influyen en la estructuración y distribución de los ensamblajes de carnívoros (en términos de riqueza y composición) a escala continental en América. El segundo artículo aborda y valida metodológicamente la reconstrucción y caracterización de estos patrones espaciales a partir de las predicciones de nichos ecológicos junto con una aproximación macroecológica.

El Tercer capítulo compuesto por un artículo, aborda el efecto de las variaciones climáticas sobre los rangos de distribución de las especies y como estos al limitar y contraer las distribuciones durante largos periodos de tiempo, son el reflejo y un proxy de una dinámica poblacional que a través de eventos demográficos de cuellos de botella juegan un papel importante como una fuente en el riesgo de extinción relacionado directamente con las características y requerimientos biológicas de las especies. Para esto se tomó como ejemplo a las especies de felinos de América.

El cuarto capítulo compuesto por un artículo, aborda el papel y la influencia de los atributos ecológicos de las especies de carnívoros (proxy del nicho funcional) como determinantes funcionales en la estructuración de los ensamblajes de carnívoros a escalas más finas, y como la diversidad funcional subyacente en estos ensamblajes y su expresión a nivel geográfico varío a través del tiempo y el espacio en el continente.

Por último, la tesis incluye una sección de discusión y conclusiones generales que conectan el contenido de todo el trabajo, resaltando los principales hallazgos y futuras líneas de investigación relacionadas con el tema.

2. INTRODUCCIÓN GENERAL

A lo Largo de la historia evolutiva del planeta, los mamíferos siguen siendo uno de los grupos de especies más importantes para el funcionamiento de los ecosistemas (Asquith et al. 1997; Bakker et al. 2006; Ceballos & Ehrlich 2002). Representan uno de los últimos clados de vertebrados donde se observa el desarrollo de innovaciones anatómicas que los distinguen de otros grupos, permitiendo así agruparlos en una clase única y monofilética. Sin embargo, actualmente la mayoría de las especies de mamíferos y sus poblaciones se encuentran amenazadas de extinción (Schipper et al. 2008; Ceballos et al. 2010; Barnosky et al. 2011). Entre las principales causas de amenaza (principalmente de origen antrópico actualmente) se encuentran la ampliación de la frontera agrícola-ganadera, la fragmentación, la contaminación, la introducción de especies exóticas, y el actual cambio climático global.

Dentro de los mamíferos podemos encontrar uno de los grupos más diversos, el orden Carnívora, el cual aparece en el Paleoceno Temprano, pero no es hasta el final del Eoceno que las familias de carnívoros modernos comenzaron a divergir. Organizándose en dos grupos principales por diferencias en sus características morfológicas. Feliformia los cuales comprenden carnívoros con forma de felino, como el jaguar o los smilodones, y el grupo Caniformia que comprenden animales con forma de cánido, como los zorros o los osos (Carroll 1988, Wilson y Reeder 2005; Wilson y Mittermeier 2009). Además de ser notablemente diversos en su fisiología, estructura social y hábitos alimenticios, con relación a su morfología, los carnívoros presentan rangos corporales que sobrepasan los cuatro órdenes en magnitud (Farlow y Pianka 2003; Goswami y Friscia 2010), lo que ha demostrado ser un predictor importante de la capacidad competitiva entre las especies (Loveridge y Macdonald 2002; Donadio y Buskirk 2006).

En este sentido, en los carnívoros se pueden observar características claves que reflejan sus nichos ecológicos, como sus hábitos alimenticios y la masa corporal. Esta última es una de las características fundamentales de un organismo en cuanto a la adaptación a su entorno (Peters 1983; Farlow y Pianka 2003; Raia et al. 2012). No obstante, existen otros factores importantes o dimensiones del nicho ecológico (condiciones climáticas, tipo de forrajeo, patrón alimenticio, patrón de actividad) que son esenciales a la hora de explicar la manera en cómo los ensamblajes se estructuran y organizan espacialmente. Por ello, los patrones de distribución y la estructura de los ensamblajes de especies potencialmente competidoras como los carnívoros, pueden ser evaluados en varias escalas espaciales y temporales.

De esta manera, el nicho ecológico ha servido como base conceptual durante casi 100 años y ha sido fundamental para la biogeografía, la ecología y la paleontología, desempeñado un papel importante para explicar la coexistencia y entender los procesos macroecológicos y de diversificación en diferentes grupos (Brown et al. 1995; Ferraz et al. 2012;; Agosta and Bernardo 2013Lieberman & Saupe 2016), donde los carnívoros no serían la excepción. Por ejemplo, la teoría neutral sostiene que la coexistencia y los patrones de distribución, en este caso los mamíferos carnívoros, son el resultado del azar junto con un tamaño poblacional histórico inicial (Hubbell 2001). En contraste el "principio de exclusión competitiva", plantea que sólo las especies con nichos diferenciados podrían coexistir dentro de los mismos ensamblajes o comunidades ecológicas (Hutchinson y MacArthur 1959; Hutchinson 1959; Chesson 1990; Leibold 1995; Mikkelson 2005). De esta forma la presencia o ausencia de factores del nicho ecológico (expresados como trade-offs) parecen desempeñar un papel fundamental para determinar cómo se estructuran los ensamblajes a diferentes escalas espaciales y temporales (Mikkelson 2005).

En este sentido, es de esperarse que las especies de carnívoros simpátricos deberían evolucionar nichos ecológicos (nicho ambiental o nicho funcional) diferenciados que les permita distinguirse de otras especies al interior del mismo ensamblaje. Presentando una capacidad similar de adaptación a las mismas condiciones del ambiente, e igualmente podrían presentar diferencias en sus atributos ecológicos lo que reduciría las interacciones inter-especificas, permitiendo así la simpatría (Brown y Wilson 1956; Hutchinson 1959). Por ello, es importante considerar estas dimensiones en la estructura y los patrones de distribución de los ensamblajes en el pasado, no solo porque son una tema clave para la paleobiología, y ahora más recientemente para la neobiología, sino porque estos patrones y sus cambios a través del tiempo son fundamentales para entender la evolución de la biodiversidad junto con sus patrones ecológicos y geográficos actuales (Lomolino *et al.* 2010).

El potencial para la reconstrucción de los patrones de distribución histórica y las estructuras de los ensamblajes de las especies o linajes, más aun con los eventos de cambio climático a finales del Pleistoceno, proporcionan un marco geográfico importante para hacer frente a muchas preguntas biogeográficas actuales y futuras (Peterson *et al.* 2004). De este modo, la aproximación histórica por medio de los modelos de nicho ecológico han mostrado el potencial de reconstruir patrones y cambios importantes en las distribuciones pasadas de las especies, en regiones como Europa y Norte América (Martínez-Meyer *et al.* 2004; Peterson *et al.* 2004; Morris *et al.* 2010; Ceballos *et al.* 2010b), por lo que cambios en las estructuras ecológicas y los patrones de distribución e interacciones en los ensamblajes actuales de las especies de carnívoros, los cuales podrían ser un reflejo de cambios en ensamblajes en el pasado, podrían traer efectos en cascada con posibles modificaciones en los procesos ecológicos a lo largo del continente. Siendo esto fundamental incluso para la definición de prioridades de conservación actuales a diferentes escalas.

Considerando estos patrones en el pasado y el actual alto riesgo de extinción que enfrentan muchas de estas especies a diferentes escalas (Schipper et al. 2008), unido con la creciente pérdida de poblaciones y extinciones locales (Ceballos et al. 2010a), el comprender los patrones y mecanismos asociados a la estructuración de los ensamblajes podría resultar en un mejor entendimiento de los procesos ecológicos y biogeográficos subyacentes, y consecuentemente informar con mejor resolución la toma de decisiones y en general los esquemas de conservación futuras.

Con base en lo anterior, el propósito de este trabajo fue examinar y entender la dinámica de cómo las especies de carnívoros (Tabla 1) se estructuraron ecológica y espacialmente durante los últimos 130 mil años hasta la actualidad a partir de factores ambientales y factores ecológicos funcionales a diferentes escales geográficas en América. Es de gran importancia comprender estos procesos y en la medida que se conozcan más a cerca del porqué y cómo podrían cambiar estos grupos debido a diferentes factores y a diferentes escalas espaciales y temporales, podremos anunciar las posibles consecuencias e implicaciones sobre estos ensamblajes y su conservación a lo largo del continente.

Tabla 1. Especies de carnívoros extintos y vivientes durante los últimos 130 mil años en el continente Americano. † Especies extintas; †* especies extintas localmente.

Familia	Especie
Canidae	*Vulpes lagopus*
	Atelocynus microtis
	Canis dirus †
	Canis latrans
	Canis lupus
	Cerdocyon thous
	*Cuon alpinus †**
	Chrysocyon brachyurus
	Dusicyon avus †
	Protocyon troglodytes †
	Lycalopex culpaeus
	Lycalopex fulvipes
	Lycalopex griseus
	Lycalopex gymnocercus
	Lycalopex sechurae
	Lycalopex vetulus
	Speothos venaticus
	Speothos pacivorus †
	Theriodictis tarijensis †
	Urocyon littoralis
	Urocyon cinereoargenteus
	Vulpes velox
	Vulpes vulpes
	Vulpes macrotis
Felidae	*Leopardus colocolo*
	Leopardus geoffroyi
	Leopardus guigna
	Leopardus pardalis
	Leopardus tigrinus
	Leopardus jacobitus
	Leopardus wiedii
	Lynx rufus
	Lynx canadensis
	Panthera atrox †
	Panthera onca
	Puma concolor
	Puma yaguaroundi

	Smilodon fatalis †
	Smilodon populator †
	Miracinonyx trumani †
	Homotherium serum †
Mephitidae	*Brachyprotoma obtusata†*
	Conepatus chinga
	Conepatus humboldtii
	Conepatus leuconotus
	Conepatus semistriatus
	Mephitis macroura
	Mephitis mephitis
	Spilogale gracilis
	Spilogale angustifrons
	Spilogale putorius
	Spilogale pygmaea
Mustelidae	*Eira barbara*
	Enhydra lutris
	Enhydra macrodonta †
	Galictis cuja
	Galictis vittata
	Gulo gulo
	Lontra canadensis
	Lontra felina
	Lontra longicaudis
	Lontra provocax
	Lyncodon patagonicus
	Martes americana
	Martes pennanti
	Mustela africana
	Mustela erminea
	Mustela felipei
	Mustela frenata
	Mustela nigripes
	Mustela nivalis
	Neovison vison
	Pteronura brasiliensis
	Taxidea taxus
Procyonidae	*Bassaricyon alleni*
	Bassaricyon gabbii
	Bassaricyon medius
	Bassaricyon neblina
	Bassariscus astutus
	Bassariscus sumichrasti

	Nasua narica
	Nasua nasua
	Nasuella olivacea
	Potos flavus
	Procyon cancrivorus
	Procyon insularis
	Procyon lotor
	Procyon pygmaeus
Ursidae	*Arctodus simus †*
	Arctotherium tarijense †
	Arctotherium wingei †
	Arctotherium bonariense †
	Tremarctos floridanus †
	Tremarctos ornatus
	Ursus americanus
	Ursus arctos
	Ursus maritimus

3. OBJETIVOS

3.1. OBJETIVO GENERAL

Examinar cómo la estructura ecológica y los patrones de distribución de los ensamblajes de carnívoros americanos respondieron a los efectos del cambio climático pasado.

3.2. OBJETIVOS ESPECÍFICOS

- Determinar la estructura ecológica y los patrones de distribución de los ensamblajes de carnívoros al final del Pleistoceno y en la actualidad
- Determinar los factores de riesgo de extinción de los carnívoros en función de las características de sus nichos ecológicos.
- Inferir qué otros factores han permitido que estas estructuras de los ensamblajes de carnívoros se mantengan o cambien en el tiempo.

4. HIPÓTESIS

Hipótesis principal: La estructura y los patrones de distribución de los ensamblajes de carnívoros del Pleistoceno y del presente en América son el resultado de reglas de ensamble determinadas por limitantes climáticos y atributos ecológicos de las especies.

Hipótesis derivadas:

1. Los nichos grinnellianos de las especies determinan la estructuración y distribución de los ensamblajes de carnívoros a escalas amplias.

2. . La reducción de las áreas climáticamente adecuadas en la transición de UIG, UGM al presente, jugó un papel importante en la persistencia y la probabilidad de extinción de algunas especies principalmente de las especies grades.

3. Los nichos eltonianos de las especies (principalmente en el tamaño) determinan la coexistencia y estructuración de los ensamblajes de carnívoros a escalas geográficas locales, por tanto este patrón debe reflejar una alta diversidad funcional a nivel espacial y temporal en el continente.

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5. CAPÍTULO 1. Distribución geográfica de especies y su conexión con el clima en el espacio-tiempo: conceptos y herramientas metodológicas

Distribución geográfica de especies y su conexión con el clima en el espacio-tiempo: conceptos y herramientas metodológicas.

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Resumen

A lo largo de la historia de la tierra, el clima ha tenido grandes fluctuaciones debido a diferentes causas (ej., actividad solar, impacto de asteroides, vulcanismo), conforme la temperatura, la precipitación y otras variables ambientales cambian, éstas pueden tener consecuencias importantes (favorables o desfavorables) en los patrones y procesos de las especies, como su sobrevivencia, reproducción y dinámica poblacional. Estos efectos pueden observarse y rastrarse a distintos niveles, desde el nivel individual de los organismos y sus rangos geográficos, hasta las intrincadas interacciones de las especies en los ensamblajes o comunidades bióticas a diferentes escalas espacio-temporales. Este ensayo tiene como objetivo presentar el marco conceptual y metodológico en el que se enmarca el estudio de la distribución de especies y su conexión con los cambios en el clima en áreas como la macroecología, biogeografía y ecología geográfica. Diferentes estudios muestran que las especies pueden ampliar, mantener o reducir su distribución en función de sus características y diferentes procesos de adaptación, migración y/o extinción. Es de gran importancia comprender estos procesos y patrones espacio-temporales de la distribución de las especies y en la medida que se conozcan cada vez más sobre el porqué y cómo podrían cambiar o han cambiado, podremos anticipar las posibles consecuencias sobre las especies actuales y su dinámica ecológica con implicaciones para su conservación.

Palabras clave: Conservación, cambio climático, distribución, inteligencia artificial, modelos estadísticos, nicho ecológico.

Introducción

Explicar e identificar los patrones espaciales y temporales de cómo las especies se distribuyen y sus procesos asociados, ha sido un aspecto importante a considerar, particularmente en el campo de la biogeografía y, más recientemente, en la macroecología [13, 35]. Este marco geográfico desde sus inicios ha sido una de las bases conceptuales en el desarrollo teórico en el conocimiento biogeográfico [35]. Desde la geobotánica en sus inicios en el siglo XX (50), hasta las expediciones realizadas por los naturalistas tales como Allen [1], Von Humboldt [50], Bates [9] y Roosevelt [55], donde ya se vislumbraba una gran curiosidad e interés por explicar la conexión y relación entre las rangos geográficos tanto de las especies de fauna y flora, y como éstas podrían estar respondiendo a su ambiente y otros factores. Estos cambios a través del tiempo son fundamentales para entender la evolución de la biodiversidad junto con sus patrones ecológicos y geográficos. Según Pliscoff y Fuentes-Castillo [50], las aproximaciones de éstos y otros estudios, principalmente en el campo de la botánica, permitieron formular y plantear en primera instancia, una relación causal entre la distribución geográfica de especies vegetales y los patrones del clima.

En este sentido, pareciera indiscutible que los organismos se ven afectados por el ambiente que los rodea, sin embargo, lo que es menos obvio es el grado y extensión en que el ambiente abiótico esculpe los diferentes niveles jerárquicos, y su influencia sobre las interacciones entre los procesos en los diferentes niveles [10]. Esto sin tener en cuenta la actual influencia antrópica (ej. fragmentación, sobrexplotación y cacería) y los diferentes eventos históricos e interacciones bióticas, los cuales igualmente influyen en la distribución de las especies [10, 11, 57, 49].

Bajo este contexto, este ensayo tiene como objetivo presentar el marco conceptual y metodológico en el que se enmarca el estudio de la distribución geográfica de las especies, sus cambios y su conexión con en el clima. Este manuscrito está dividido en tres secciones. La primera sección abarca el clima y su influencia en las especies y sus distribuciones desde un contexto espacio-temporal, mostrando algunos ejemplos a través de diferentes escalas de tiempo evolutivo (ej., Cenozoico, Cuaternario, Pleistoceno), hasta los patrones de distribución actuales. La segunda sección está enfocada en examinar las técnicas que subyacen al estudio de distribución de especies y discutir cómo estos enfoques pueden o no ser de utilidad. Finalmente la tercera sección se enfoca principalmente a las transferencias en el tiempo y sus problemas asociados. Todo en conjunto nos proporciona un marco importante para abordar preguntas en el avance en áreas como la macroecología, paleoecología y ecología geográfica, y así progresar en nuestra comprensión de estos patrones espaciales y temporales de la distribución geográfica de las especies y su conservación.

Relación especies-distribución-ambiente

La Tierra, a nivel climático, ha tenido grandes fluctuaciones a lo largo de la historia debido a diferentes causas (ej. actividad solar, impacto de asteroides, vulcanismo, ciclos glaciales), por ejemplo, durante la Era Cenozoica se evidencian una serie de eventos climáticos críticos [66] (figura 1), los cuales han permitido examinar las respuestas paleobiológicas de las comunidades a través del registro fósil, esto, teniendo en cuenta que tanto los datos paleoclimáticos marinos y terrestres a menudo ofrecen mejor resolución temporal [10]. Conforme la temperatura, la precipitación y otras variables ambientales cambian con el tiempo, éstas pueden tener consecuencias importantes (favorables o desfavorables) en los patrones y procesos de las especies, así como en la composición y funcionamiento de las comunidades y los ecosistemas a diferentes escalas espacio-temporales [30, 10]. En este sentido, es importante mencionar primero varios conceptos clave en la contextualización de la distribución de las especies desde la ecología, antes de apreciar las respuestas en sí de las especies frente a los cambios en el clima.

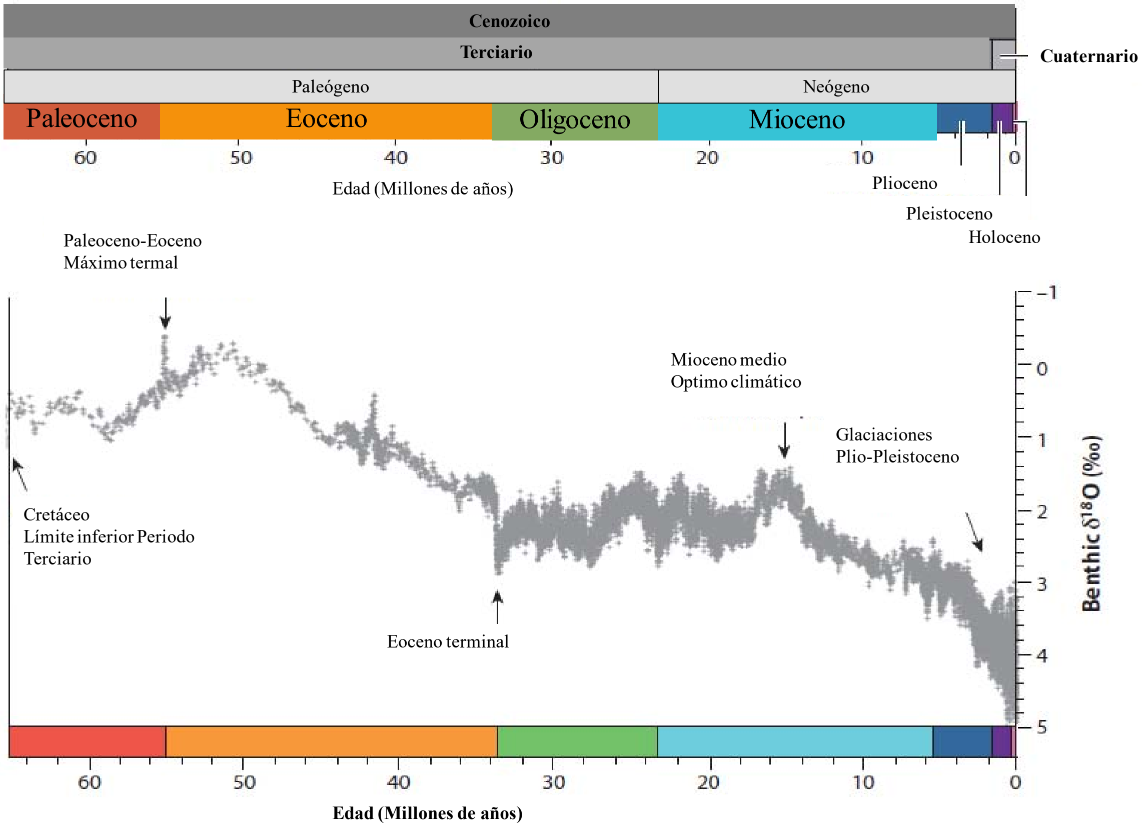

Figura 1. Eventos climáticos a través del Cenozoico. Benthic δ18O (‰) como proxy de los cambios en la temperatura del océano a nivel global, menores valores indican temperaturas más cálidas. (Tomado y modificado de Blois y Hadly, (2009)).

Si pensamos en la diversidad biótica, ésta comúnmente no muestra una distribución uniforme a nivel global, ésta responde, se estructura y se restringe a determinados rangos geográficos, donde una serie de condiciones bióticas y abióticas (conceptos que posteriormente llamaremos escenopoéticos o nicho grinnelliano, y bionómicos o nicho eltoniano) les permite a las especies establecerse o colonizar, y mantener poblaciones a través del crecimiento y la reproducción [65]. Uno de estos ejemplos iniciales para explicar estas asociaciones, son las zonas de vida de Holdridge [72, 73], las cuales desde el punto de vista ecológico representan áreas o hábitats distintivos constituidos según el patrón climático y la fisionomía de la vegetación, teniendo en cuenta además las condiciones edáficas, las etapas de sucesión y las condiciones hídricas [72,73]. Posteriormente surgen los conceptos de nicho ecológico en un intento enfocado también en explicar la relación y conexión de los seres vivos con el ambiente. Las primeras aproximaciones, vienen de los estudios de Grinnell [21] y Elton [18], los cuales independientemente pretendían identificar el hábitat ocupado por las especies como un subconjunto de condiciones del ambiente, y el rol de las especies al interior de las comunidades respectivamente.

Posteriormente en la década de 1950, Hutchinson [28] plantea el concepto de nicho ecológico como un híper-volumen en el espacio ecológico multidimensional dentro del cual una especie puede mantener poblaciones viables (una unificación implícita de los conceptos de Grinnell y Elton, a mi consideración). Este concepto engloba dos compontes importantes, el componente escenopoético, el cual hace referencia a los factores dinámicos y denso-independientes que interactúan con las especies, y el componente bionómico, que comprende los factores denso-dependientes que interactúan y pueden ser modificados por las especies [49]. No obstante este concepto puede presentar una inconsistencia ya que pareciera que los individuos migrantes y/o las poblaciones sumidero de las especies estarían por fuera del nicho según esta definición, resultando así en una contradicción si se considera que el nicho ecológico es una propiedad de la especie y no del ambiente. Posteriormente, el concepto de nicho en el período de 1970 comenzó a ser más abordado en la ecología desde su noción matemática por MacArthur [42], luego en los primeros modelos teóricos sobre su distribución espacial [33], y posteriormente experimental y con carácter predictivo a diferentes escalas y tiempos (décadas de los 80s y 90s) [25, 6, 7]. Estas contextualizaciones constituyen la base teórica de las diferentes aproximaciones metodológicas de los modelos de distribución de especies que presentaré en la siguiente sección.

Retornando a las respuestas de las especies y los cambios en las distribuciones frente a los cambios en el clima, generalmente se han abordado y planteado a diferentes escalas espacio-temporal y/o a diferentes niveles jerárquicos [ej.8, 11, 18, 37, 40, 47, 51, 52, 53, 61]. Por ejemplo, estos cambios pueden generar a un nivel de comunidades, pérdida de hábitats, modificación en las interacciones inter-específicas, variación en la estructura, composición y funcionamiento de los ecosistemas. A nivel individual por ejemplo, los mamíferos y aves, utilizan una combinación de mecanismos para regular la temperatura de su cuerpo; en el transcurso del día un animal puede moverse del sol a la sombra como una respuesta conductual debido a cambios fisiológicos y a las condiciones térmicas estresantes [10, 27, 46]. Esta capacidad de termorregulación desliga hasta cierto punto (dado que el cuerpo pierde o gana calor en el medio ambiente y debe mantenerse en equilibrio a través del metabolismo o la disipación) su temperatura corporal interna de la temperatura del aire, por lo tanto, a pesar de la exposición del cuerpo a temperaturas del aire muy fríos o muy calientes, estas respuestas aseguran que la temperatura corporal no varíe en más de unos pocos grados centígrados a lo largo de la vida del organismo. Sin embargo, los cambios drásticos y prolongados en el clima pueden afectar directa o indirectamente la sobrevivencia de los individuos, a través de modificaciones en las tasas metabólicas, que a su vez determina las necesidades de consumo de recursos y esto a su vez presenta una influencia directa en las poblaciones de las especies y por tanto en sus distribuciones geográficas [27, 62].

En este sentido, los organismos endotérmicos cuando se encuentran expuestos a temperaturas ambientales extremas, limitantes o prolongadas por encima o por debajo de su zona térmica neutra (región en la que la tasa metabólica no cambia con relación a la temperatura del aire), requieren del consumo de muchos más recursos, o de una mayor disipación de calor (en el caso de áreas con temperaturas altas) o generan estrategias como la hibernación o el torpor para seguir con vida, en contraste con otros endotermos que se encuentran expuestos a factores ambientales menos heterogéneos dentro de su zona térmica neutral. Esta exposición a temperaturas extremas conllevan a que la capacidad de termorregulación de los individuos se desestabilice, causando primero la hipo o hipertermia, y si la exposición continúa, a la muerte del organismo [20, 27]. Es importante anotar, que esto ilustra directamente la influencia directa del ambiente sobre los organismos, independientemente si es un depredador o un mamífero herbívero, por ejemplo.

Así mismo, podemos ver que el clima ejerce efectos adicionales a través de la disponibilidad de recursos y/o de presencia de competidores y depredadores, teniendo así un efecto fundamental en todos los procesos biológicos, por lo tanto la variación climática afecta profundamente, aunque de forma diferencial, a todos los organismos que comparten el mismo medio ambiente en un área geográfica determinada [20]. Si observamos más el sistema, pero ahora teniendo en cuenta un grupo de individuos de la misma especie, podemos observar que por lo general muchos de los aspectos de su biología e historia de vida se encuentran vinculados y responden a la influencia estacional y a sus características biológicas y ecológicas. Entre éstos podemos encontrar factores como el tamaño corporal, la edad, la organización y clase social, patrón de actividad, condición reproductiva, la migración o la hibernación [10, 54, 27]. Como resultado, una población de una determinada especie puede variar su sobrevivencia, reproducción y dinámica poblacional dependiendo de las condiciones climáticas locales, así como la diversidad genética que se transmite de generación en generación en el rango de distribución de la especie. En este sentido las especies por lo general con tamaños grandes, por sus requerimientos biológicos y fisiológicos, son las que presentan más riesgos de extinción.

Si hacemos un escalamiento en espacio y tiempo, podemos explorar que a través de largos períodos de tiempo estos efectos del clima se han integrado a través de la conectividad y flujo genético entre las poblaciones que ocupan el rango geográfico de las especies, los cuales pueden variar en tamaño, ubicación, forma y nivel de ocupación [16]. A medida que estas tendencias ambientales se prolongan, como por ejemplo, durante los períodos interglaciares o glaciares del Pleistoceno (figura 2), las poblaciones pueden afrontar diferentes cambios, resultando en alteraciones de los linajes. Estas respuestas pueden variar dependiendo de las especies y su capacidad de respuesta a estos cambios, a través de procesos de adaptación, dispersión, especiación y extinción. En este sentido, un gran número de extinciones, colonizaciones y/o especiaciones locales concurrentes, ilustrarían lo que se ha denominado como recambio biótico a través de un reemplazamiento de ensamblajes o de una comunidad a una escala espacio-temporal mucho más amplia [10]. En la figura 3 se ejemplifica los diferentes procesos ecológicos y las diferentes respuestas frente a los cambios en el clima desde el nivel específico hasta el nivel de ensamblajes o comunidades.

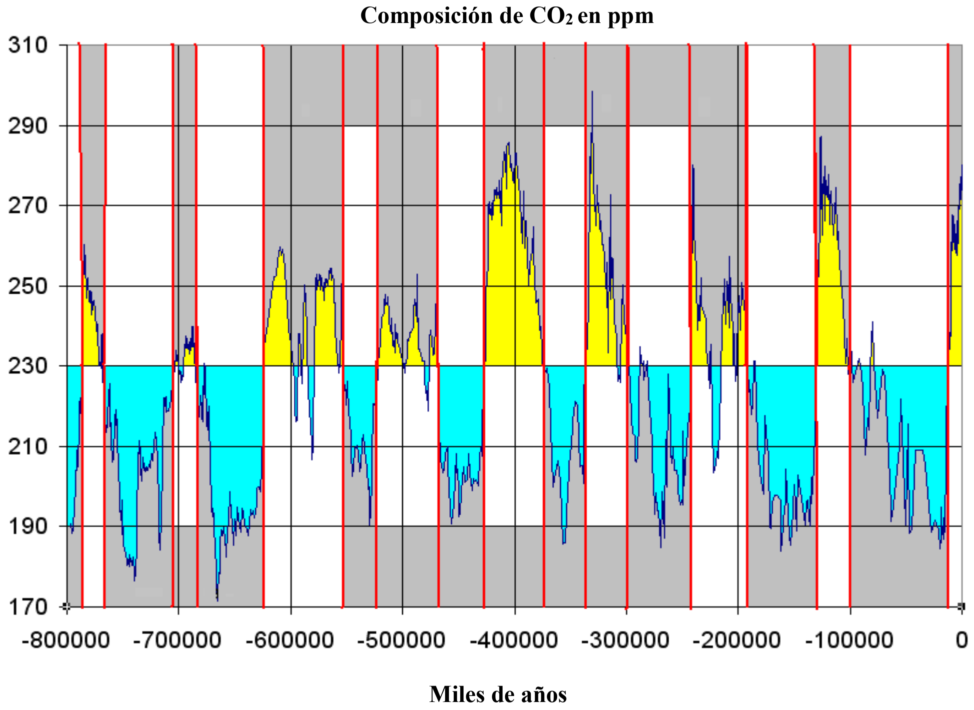

Figura 2. Periodos glaciales (azul) e interglaciares (amarillo) durante los últimos 800 mil años del Pleistoceno representados por el CO$_2$ atmosférico medido a partir de muestras de núcleos de hielo. (Tomado y modificado de NOAA http://www.ncdc.noaa.gov/).

Por otro lado, demostrar los impactos del cambio climático sobre las especies es un desafío grande tanto en términos evolutivos, como el alcance geográfico y metodológico, así como también la diversidad taxonómica que se quiera abordar. Como algunos de estos ejemplos podemos encontrar que ciertas especies podrían ser afectadas reduciendo sus poblaciones y fragmentando sus distribuciones, quedando así aisladas en o entre ambientes no favorables, lo que podría resultar en una eventual extinción local o total de la especie. Nogues-Bravo y colaboradores [47] exploraron el efecto del cambio climático (al igual que la influencia humana) durante varios períodos del Pleistoceno, sobre el mamut (*Mammuthus primigenius*), una especie que se distribuía desde Eurasia hasta Norte América durante el Pleistoceno medio hasta su desaparición a inicios del Holoceno (3.6 miles de años (ka)).

Encontraron que alrededor del 90% de la distribución con condiciones ambientales adecuadas desapareció entre los 42 ka y los 6 ka, quedando sólo unas pocas zonas adecuadas al norte de Siberia de donde provienen los últimos registros fósiles. Estos mismos autores sugieren que esta desaparición de su distribución se originó, en parte, como un colapso del nicho climático de la especie, lo que ocasionó una disminución significativa del tamaño poblacional, haciéndola mucho más vulnerable a otras amenazas, como la cacería por el hombre. Concluyen que tanto el clima, como el efecto antrópico (efecto multifactorial) jugaron un papel crucial en la extinción de esta especie a inicios del Holoceno.

Así mismo, entre estas modificaciones que han ocurrido en el clima pasado, podemos encontrar que la diferencia en la riqueza de especies entre las sabanas y los bosques neotropicales se debe, en parte, a la extinción de muchas especies de ungulados y otros megaherbívoros desde la última glaciación. Las grandes extinciones durante el Pleistoceno y el Holoceno redujeron significativamente la diversidad de ungulados en el continente americano, mientras que en África las comunidades de grandes herbívoros permanecieron relativamente intactas [14, 38, 41, 58]. Esto ilustra en parte como el componente climático juega un papel importante y tienen la mayor influencia sobre los rangos de distribución y sus límites a estas escalas geográficas grandes (regional, continental), el cual, igualmente define parte del nicho de las especies [16, 41, 34, 35 67]. Por lo tanto, las restricciones impuestas por el clima y la expresión de los nichos ecológicos a nivel geográfico, pueden limitar o promover los diferentes procesos ecológicos y así restringir o promover las respuestas de las especies y los cambios en las distribuciones frente a éstos. Al parecer estas respuestas son mucho más evidentes en los límites de distribución de las especies, donde las condiciones ecológicas ya se encuentran próximas a los límites de tolerancia y donde es previsible que las consecuencias sean mucho más severas [24, 68].

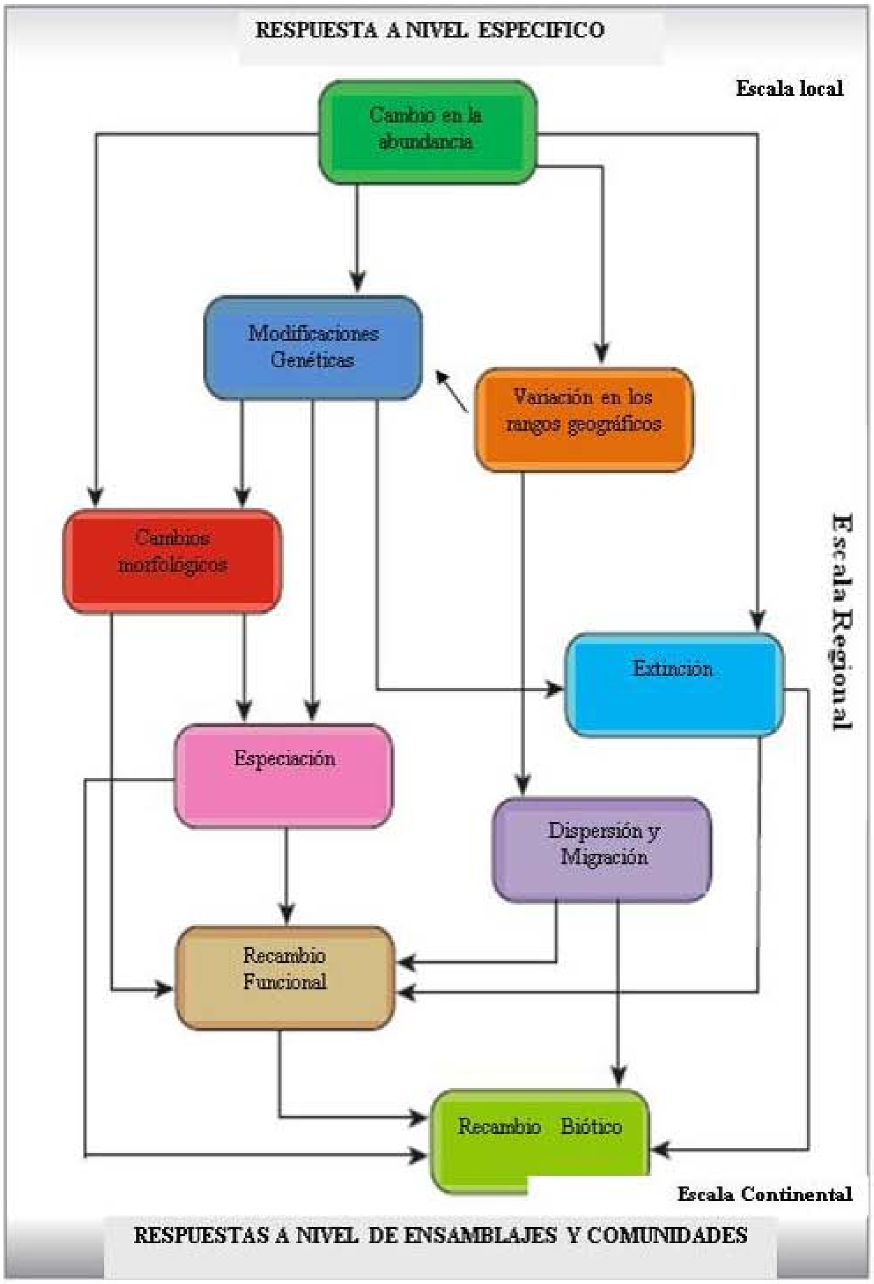

Figura 3. Procesos y respuestas frente a cambios ambientales a diferentes niveles jerárquicos desde especies hasta ensamblajes y comunidades, y a diferentes escalas geográficas. (Tomado y modificado de Blois y Hadly, (2009)).

Por otro lado, otras especies podrían verse beneficiadas por los cambios en el clima, aumentando sus poblaciones y sus áreas de distribución, como se ha propuesto principalmente para algunas especies vectores transmisoras de enfermedades [45, 48]. Por ejemplo, Peterson y Shaw [48], en un estudio con especies del género *Lutzomyia*, un insecto vector de la enfermedad de la leishmaniasis en Sur América, plantean la posibilidad de una ampliación en la distribución para una de estas especies (*Lutzomyia whitmani*) con relación a variaciones en el clima, y por tanto una potencial ampliación en el rango de transmisión de la enfermedad. No obstante, estos autores enfatizan en la importancia y precaución sobre la interpretación de estos resultados y de los errores que pueden presentar, ya que pueden conducir a predicciones inexactas.

En la actualidad se plantea igualmente que aquellas especies con umbrales de tolerancia ambientales bajos en cualquiera de las etapas del ciclo vital (por lo general en anfibios y reptiles), podrían ser más susceptibles a éstos cambios climáticos, con modificaciones drásticas en sus dinámicas poblacionales, lo que aumentaría la probabilidad de extinguirse en todo o gran parte de sus rangos de distribución [2, 4]. Sin embargo, estudios recientes usando métodos mecanísticos con especies del género *Sceloporus*, plantean la posibilidad de que algunas de estas especies podrían adaptarse a nuevas condiciones ambientales a través de modificaciones comportamentales en la termorregulación, dado que actualmente estas especies no han experimentado su límite térmico estresante y aún se encuentran en la zona térmica neutral [36].

Lo anterior ilustra nuevamente que no sólo estos patrones y sus cambios a través del tiempo son fundamentales para entender la evolución de la biodiversidad, junto con sus patrones ecológicos y geográficos actuales [35], sino también enseña que las respuestas de las especies frente a los cambios ambientales no siempre son negativos como generalmente se tiende a pensar. Por ello, en la medida que se realicen análisis cada vez más completos sobre estos temas y se logre entender la naturaleza de los factores a los cuales estuvieron y están expuestas las especies, se podrá avanzar aún más sobre la comprensión zoogeográfica, paleoecológica y ecogeográfica; áreas que aún están abiertas a interpretaciones e hipótesis alternativas.

Métodos y técnicas en el estudio de la distribución de especies.

Entender cómo las especies de fauna y flora se distribuyen en el planeta a través del espacio y el tiempo ha sido una pregunta crucial que ha tenido una larga historia y trayectoria. La mayoría de estas aproximaciones tienen sus raíces, como se mencionó anteriormente, desde las expediciones de naturalistas como von Humboldt [59], al igual que las realizadas durante el siglo 19 por Darwin [74] y Wallace [en 75]. No obstante, al parecer no es sino hasta la década de los 70s que se originan y surgen las primeras aproximaciones y planteamientos sobre los modelos de distribución basado en sistemas computacionales [5, 23]. Según Guisan y Thuiller (23) uno de los primeros intentos de un modelo de distribución de especies, parece ser las predicciones espaciales realizadas por Henry Nix y colaboradores en Australia. Posteriormente con el surgimiento y desarrollo de herramientas mucho más eficientes en los 90s [23, 49, 50] y el manejo de información de gran cantidad de bases de datos, permitieron abordar desde nuevas y diferentes aproximaciones el tema de las distribuciones geográficas de las especies [31, 49].

Actualmente este tema de distribución de especies y ecosistemas tanto en el espacio geográfico-ecológico en el pasado como en el futuro, se ha transformado en una de las áreas de mayor investigación en diferentes disciplinas, desde la biogeografía, macroecología, hasta la biología de la conservación [50, 63], impulsando cada vez más tanto la generación de nuevas técnicas y herramientas [23], como la implementación de técnicas estadísticas y algorítmicas cada vez más complejas para la obtención de "resultados significativos y más robustos". Sin embargo, es importante preguntarnos y no pasar por alto, hasta qué punto se está sacrificando el alcance y significancia real de estos patrones y procesos biológicos, por el hecho de obtener aproximaciones y modelos que podrían estar representando meramente un artificio estadístico-matemático.

Por ejemplo, hasta qué punto se está desviando la pregunta central (en términos biológicos) que se busca responder con estas nuevas aproximaciones metodológicas [31, 50, 69], ¿efectivamente si estamos respondiendo a estos interrogantes biológicos, ecológicos y evolutivos de cómo se organizan y cuáles son los factores que determinan la distribución espacial de las especies?. En este sentido algunos autores resaltan que estas limitaciones e interrogantes surgen cuando las decisiones de modelado de los nichos ecológicos y la distribuciones geográficas de las especies, no están siendo explícitamente motivadas por hipótesis y preguntas biológicas específicas, comenzando a dejar de lado la teoría ecológica y/o éstas no son plenamente integradas en el proceso, cualquiera que fuese el método abordado [23, 29, 44, 64].

Operacionalmente la distribución de una especie se define como el conjunto de zonas o cuadrículas (en términos operacionales) del espacio geográfico, en el que las presencias de individuos de una especie pueden ser detectadas. Desde la perspectiva biogeográfica y macroecológica la distribución se delimita generalmente a escalas amplias (ej. > 10 km^2) y de baja resolución espacial (ej. celdas de 104-105 km^2), las cuales normalmente son mucho más gruesas que las escalas autoecológicas (ej. escalas locales-regionales) [77]. Entre las técnicas metodológicas, podemos encontrar tres aproximaciones basadas según los datos de las especies: 1) de solo presencia; 2) de presencia/ausencia; y 3) de presencia/"background o de entorno"/ o de pseudoausencias [49]. Dentro de estas aproximaciones podemos encontrar una serie de algoritmos o procedimientos estadísticos, reglas y funciones matemáticas que nos permiten estimar cómo responden, se organizan y cuáles son los factores que determinan la distribución espacial de las especies [17, 49, 50, 82].

En términos generales, el reto de estimar la distribución de una especie dada, es caracterizar el área geográfica dentro de una región, en términos de valores cuantitativos relacionados con la probabilidad de ocurrencia (o pertenencia), en función de las variables de interés. Es decir, el propósito sea cual sea la técnica, es crear un modelo para caracterizar la variable dependiente (ya sea nicho ecológico, o rango de distribución) cuya función este dada por: $f = \mu(G_{data}, E)$, donde G_{data} representan los registros de presencia, ausencia, "background" o pseudoausencias; y E representa el área de estudio en términos de las variables de interés (ambientales, topográficas, etc.) [17, 49, 50, 82].

Técnicas de solo presencia

Aquí podemos encontrar desde las aproximaciones espaciales iniciales como el mínimo polígono convexo o las extensiones de ocurrencia. Estas unen linealmente los puntos de presencia más periféricos de una especie en un mapa, definiendo así el área entre ellos como una estimación cualitativa de la distribución de la especie. Estas aproximaciones son basadas y realizadas principalmente con base en opinión de expertos, y su aproximación intenta reflejar la distribución actual u ocupada de las especies. El inconveniente es que este mapa de puntos generalmente no tiene en cuenta las distinciones bióticas y abióticas de la zona que pueden estar influyendo en la presencia de la especie y su recolonización [3, 83]. Por tanto su distribución potencial historica no es considerada en estas aproximaciones.

Otra de las aproximaciones más simples y más recientes son los llamados envolturas bioclimáticas. Uno de los primeros en desarrollar esta aproximación fue BIOCLIM [15], el cual se basa en la creación de rangos mínimos y máximos a modo de rectángulo, envolviendo los valores ocupados por la especie a lo largo de las variables ambientales [15, 49]. Similar a BIOCLIM, está HABITAT [60, 49], técnica que por medio de un polígono mínimo convexo o de un poliedro, ajusta mucho más los datos de presencia con relación al espacio ambiental. Sin embargo, uno de los inconvenientes a estas dos aproximaciones, es que no toman en cuenta los tipos de interacciones entre las variables (ej. colinealidad) o el efecto de la distancia geográfica entre las presencias (autocorrelación espacial), supuestos que por lo general, al igual que con otros métodos, se tratan de evitar, los cuales quizás en la naturaleza del problema de las distribuciones de especies sean de mayor relevancia y más informativos de lo que se cree.

En este mismo grupo podemos encontrar las distancias de Mahalanobis y las distancias de Gower [22], las cuales miden por medio de distancias, las diferencias entre la información ambiental presente en los registros, con los valores promedio de cada una de las variables del área de estudio, así entre más cerca se encuentren las localidades de la media, menor será la distancia y por tanto más cerca al optimo ambiental. Es importante anotar que todos estos métodos hacen inferencias sin hacer referencia a ninguna probabilidad de presencia y/o de condiciones para las especies. Una mayor ampliación sobre éstos y otros métodos puede verse en Rotenberry et al. [56] y Peterson et al. [49].

Técnicas de presencia/ausencia verdaderas

La mayoría de estas técnicas se basan en modelos estadísticos de regresión. Un enfoque estadístico para relacionar una variable respuesta (dependiente) con los valores de las variables predictoras (independientes) [49]. Entre éstas podemos encontrar los modelos lineales generalizados (GLM por sus siglas en inglés), los cuales son una extensión de las regresiones de mínimos-cuadrados [49]. Estos están basados en una relación supuesta (o función de enlace) entre la media de la variable de respuesta y una combinación lineal de las variables explicativas. Ésta relación define la correspondencia entre la ocurrencia de la especie y la variable ambiental, y la distribución de error se puede seleccionar de entre varios tipos de distribución, incluyendo la distribución binomial, normal, Poisson, o binomial negativa [43, 49, 70]. Así mismo, podemos encontrar los modelos aditivos generalizados (GAM por sus siglas en inglés), los cuales son una extensión semi-paramétrica de los GLM, y de igual forma utilizan una función de enlace pero con un menor número de supuestos, permitiendo así ajustar relaciones no lineales y no monotónicas [49, 70].

En este mismo grupo podemos encontrar otras aproximaciones, tales como los árboles de regresión y de clasificación (CARTs por sus siglas en inglés). Se basan en particiones repetidas de los datos en pares de grupos mutuamente excluyentes, analizados por medio de árboles de regresión (si las variables son continuas) o clasificaciones (si las variables son categóricas) por medio de reglas, donde se asigna una clase para cada combinación de las variables predictivas que estimaran el modelo de distribución [12, 49, 50]. Random Forest es un ejemplo de estas técnicas CARTs [12]. Es importante anotar que estas aproximaciones estadísticas como los GAM y lo GLM pueden ser implementadas en este contexto de técnicas de presencia/background o presencia/pseudoausencias cuando no se cuentan con datos de ausencias verdaderas. Sin embargo, esto puede traer problemas a las estimaciones ya que por lo general estas pseudoausencias son inventadas aleatoriamente, por lo que resulta mucho más complejo la determinación de la probabilidad de ocurrencia, su poder predictivo disminuye y es necesario aplicar un factor de corrección a los estimadores, comparado cuando se tiene ausencias verdaderas (por lo general estos registros son escasos y difíciles de obtener) [2, 17, 49].

Técnicas de presencia/background o de entorno

Este enfoque se caracteriza por usar registros sobre la información ambiental a lo largo del área de estudio (datos de entorno), en lugar de usar datos de ausencia o pseudoausencias en el proceso de modelación, presentando así un mayor poder discriminante con relación a los métodos de solo presencia [49]. Uno de estos métodos heurísticos es el algoritmo de MaxEnt, este programa aplica un algoritmo matemático basado en la teoría de la máxima entropía y técnicas bayesianas, cuyo propósito es estimar distribuciones de probabilidad de máxima entropía o distribuciones de probabilidad de Gibbs (i.e., la distribución más uniforme), con base en registros de presencia de la especie y sujeto a restricciones dadas por la información ambiental y otras variables (ej., variables geográficas) (figura 4) [49, 71, 72]. En este sentido las predicciones realizadas representan hipótesis sobre condiciones similares a aquellas donde la especie en cuestión ha sido observada, y éstas posiblemente se encuentran entre el nicho fundamental existente (EA) y el nicho ocupado de la especie (EO) (ej., nicho biótico reducido [EP] correspondiente al área potencial de distribución [GP]) (tabla 1 y figura 5) [49]. Es de resaltar que posiblemente estas predicciones realmente no representan una probabilidad de ocurrencia de las especies *per se*, ya que con estos métodos no es posible estimar idealmente la probabilidad que una especie este presente dado el ambiente Pr(y = 1|z), donde ***y*** representa la presencia=1 y z los ambientes evaluados. Lo que realmente se estima es una aproximación a esa probabilidad Pr(y = 1|z) = f1(z) Pr(y = 1)/f(z) a través de dos parámetros conocidas, f1(z) Pr(y = 1), el cual representa la probabilidad de los ambientes dado que la especie está presente, y f(z) corresponde a todos los ambientes presentes en el área estudiada.

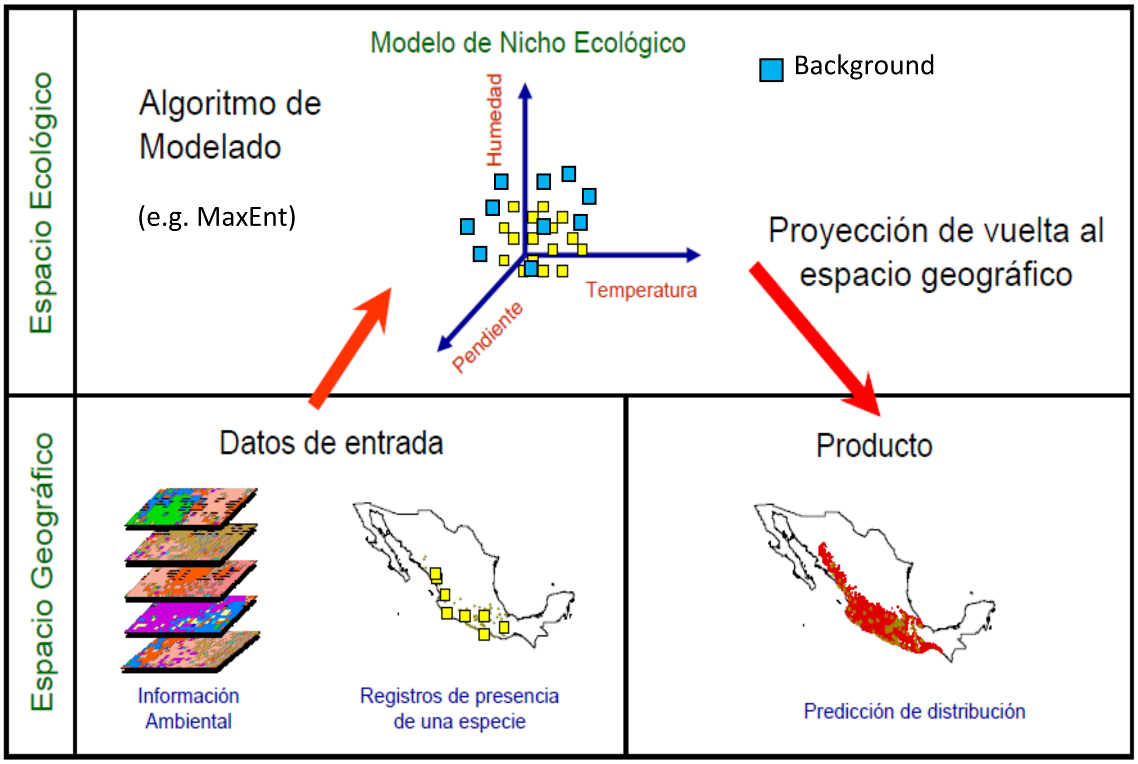

Figura 4. Esquema de modelación del Nicho Ecológico. **Hipótesis nula**: los patrones de distribución geográfica de las especies son aleatorios. (Tomando de Martínez-Meyer (2010)).

Otra aproximación en este grupo es el Análisis de Factores del Nicho Ecológico (ENFA) [26]. Este método aplica una técnica de ordenación (factores no correlacionados) similar al análisis de componentes principales (PCA en inglés) y compara en el espacio ecológico los registros de presencia con el “background” mediante dos aproximaciones: Marginalidad y especialización. La primera cuantifica, cuanto de la media de la información de las variables en los registros de presencia, difieren con la media de las variables (centroide) de toda el área de estudio, y la segunda cuantifica cuanto de la varianza de los registros se relaciona con la varianza total.

Tabla 1. Áreas de distribución y su correspondientes nichos ecológicos definidas por Peterson et al. (2011). (Ver figura 5 para una representación visual en el espacio geográfico (**G**).

Área de Distribución		**Nicho Ecológico**	
Símbolo	**Nombre**	**Símbolo**	**Nombre**
$\mathbf{G_A}$	Áreas con condiciones adecuadas	$\mathbf{E_A}$	Nicho fundamental existente
$\mathbf{G_I}$	Área geográfica invadible	$\mathbf{E_I}$	Nicho invadible
$\mathbf{G_O}$	Área de distribución ocupada	$\mathbf{E_O}$	Nicho ocupado
$\mathbf{G_P}$	Área potencial de distribución	$\mathbf{E_P}$	Nicho biótico reducido o potencial

Técnicas de presencia/pseudoausencias

Esta técnica es en esencia similar a la anterior, aquí en lugar de background, las pseudoausencias corresponden con un remuestreo de toda el área de estudio para proporcionar el contraste necesario con respecto de los datos de presencia. Uno de los algoritmos heurísticos más implementados es GARP (Genetic Algorithm for Rule-set Production). Este está inspirado en el proceso evolutivo de la selección natural, para obtener el modelo más informativo de una serie de posibles soluciones, a través de iteraciones de reglas establecidas tipo secuencia genética, métodos de regresión y envolturas climáticas [2, 17, 49].

Estas aproximaciones anteriores igualmente muestran sus limitaciones y presentan una amplia discusión a nivel metodológico, principalmente con relación al número de datos de presencia, el tamaño del área de estudio, y su evaluación estadística. Sin embargo, por lo general proporcionan resultados robustos comparados con otras técnicas [17, 44, 49, 40, 82].

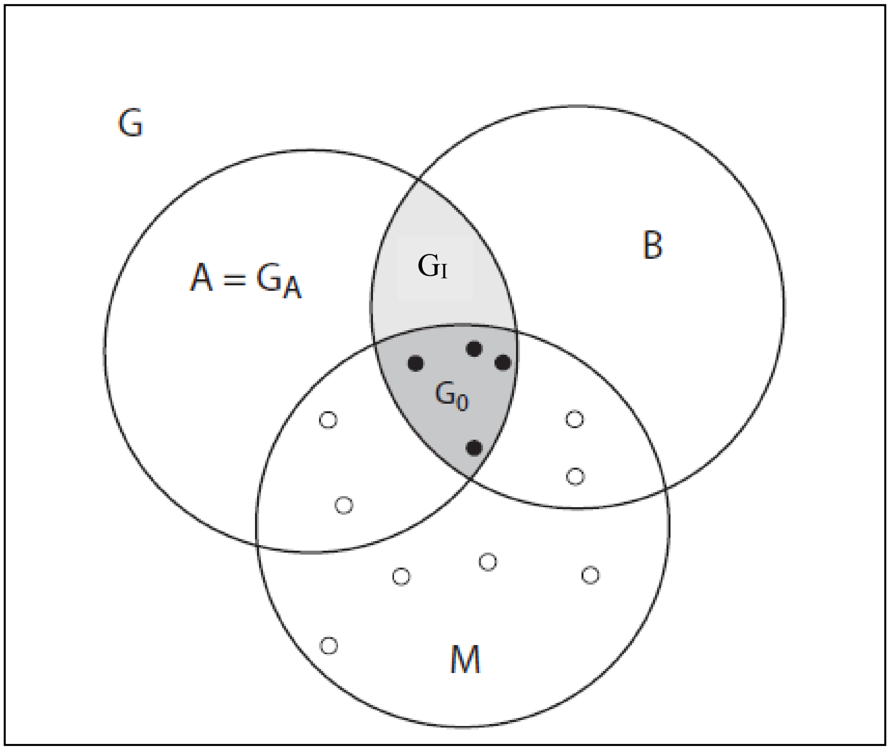

Figura 5. Diagrama BAM, conceptualización de la expresión del nicho ecológico en la geografía (G) y su relación con la distribución de las especies. **B**. factores bionómicos (principalmente interacciones bióticas); **A**. factores scenopoéticos (principalmente abióticos); **M**. Factores de movilidad y accesibilidad geográfica. $\mathbf{G_A}$ áreas geográficas con condiciones adecuadas; $\mathbf{G_O}$ área de distribución ocupada por la especie; $\mathbf{G_I}$, área de distribución invadible; $\mathbf{G_P} = \mathbf{G_O} + \mathbf{G_I}$, área potencial de distribución. Presencias, puntos negros; Ausencias puntos blancos (Tomado y adaptado de Peterson et al. (2011)).

Distribución y su transferencia a escala temporal

Finalmente uno de los pasos siguiente en este contexto de las distribuciones de especies es su proyección en el espacio-tiempo, ya sea en el pasado, presente o futuro. Principalmente este proceso de transferencia temporal representa grandes retos y desafíos para la macroecología y la biogeografía, ya que depende, por ejemplo, de los datos necesarios a nivel ambiental (ej. selección de variables adecuadas o importantes), fuentes de información de presencias (ej. registro fósil), diferencias entre técnicas, así como de su validez para poder estimar estos cambios en el tiempo y el espacio [17, 49]. Por ello, el abordar o hacer interpretaciones inadecuadas de la teoría y de los métodos subyacentes, puede llevar a errores e interpretaciones potencialmente erróneas como se ha mencionado anteriormente.

En este sentido a nivel temporal, existe una mayor incertidumbre asociada hacia las proyecciones futuras de cambio climático comparado con las retroyecciones, ya que por un lado, la validación de estos modelos es prácticamente improbable debido a la falta de registros, y por otro, las apreciaciones y predicciones a largo plazo podrían considerar la existencia de climas que no existen en la actualidad (ej. climas no análogos) y que posiblemente las especies no han experimentado a lo largo de su historia evolutiva [17,49,78, 82]. Así mismo, otros posibles problemas a estas transferencias es la no inclusión de las interacciones y del contexto a nivel de ensamblajes, por ejemplo, ¿cómo la distribución de una especie se vería afectada por el aumento de competidores con los cuales no ha coexistía previamente?, o como se vería influenciado por el cambio del uso del suelo, donde posiblemente la magnitud de sus efectos sean mayores a corto plazo (ej. en cuestión de pocos años) comparado con los cambios en el clima a largo plazo [17, 79].

Por otro lado, las transferencias en el pasado presenta menos dificultades, ya que, aunque escaso para algunas especies, se cuenta con el registro fósil para la validación de los modelos y la información ambiental ofrece una mejor apreciación, por ejemplo, las estimaciones realizadas a partir de sedimentos extraídos del fondo marino y a partir de muestras de núcleos de hielo, han permitido reconstruir y mostrar que durante el cuaternario han ocurrido cerca de veinte fases de enfriamiento y calentamiento con duración de decenas de miles de años [80, 81].

No obstante, a pesar de las incertidumbres, y en contraste con las técnicas anteriores, éstas aproximaciones ofrecen la posibilidad de abordar ya sea hacia el futuro o el pasado las áreas de distribución potencial de las especies (podrían considerarse como las distribuciones histórica) bajo el contexto del cambio climático. El reto es decidir hasta qué punto las inferencias están encaminadas en la dirección correcto con relación al problema biológico especifico que se está abordando. Es decir, el problema se hace mucho más explícito con relación a las definiciones conceptuales ecológicas, los alcances metodológicos y técnicos inherentes en el estudio de las distribuciones geográficas y sus cambios en el espacio-tiempo.

Consideraciones finales

Este contexto teórico y metodológico provee de un marco que permite abordar y entender los patrones espaciales y temporales de como las especies se distribuyen y sus procesos asociados. Este componente desde sus inicios ha sido una de las bases conceptuales en el desarrollo teórico del conocimiento biogeográfico y macroecológico. Por ello, los nuevos hallazgos, aproximaciones y el análisis sistemático de éstos, permitirán abordar de forma más detallada los procesos naturales y evolutivos subyacentes. Así como permitirán entender cada vez más las causas de cambio y extinción en las especies, tanto en el pasado como actuales, y quizás en el futuro, permitiendo así poder entender y anticipar hasta cierto punto las posibles consecuencias de los cambios en las distribuciones de las especies en términos de conservación y manejo de la biodiversidad. Así mismo, es importante resaltar que habitualmente éstas aproximaciones se han realizado a partir del nivel específico, pero vale la pena preguntarnos como podrían cambiar estos patrones de distribución si analizamos el sistema a partir de reconstrucciones espaciales de ensamblajes de especies, en los cuales se incorpore información relacionada por ejemplo con las interacciones, o las características ecológicas funcionales, así como información relevante relacionada a otros factores como la perdida de hábitat y el cambio del uso del suelo.

Igualmente en estas áreas del conocimiento como la ecología, la biogeografía y la macroecología, los modelos son una abstracción e interpretación del sistema (y no una verdad absoluta), éstos deben incluir aspectos de interés para un problema en particular, ya que no es posible contener todos los factores que pueden estar influyendo en el sistema. Por ello no existe una "receta particular" para desarrollar un método en específico en el proceso de estudio de las distribuciones geográficas y los nichos ecológicos, y quizás no existe un “método mejor que otro” como generalmente se suele discutir y enfatizar. Todo está en función del alcance y naturaleza de los datos, la caracterización del espacio ambiental o las variables de importancia, la incorporación o no de las interacciones biológicas y lo más importante la incorporación de los planteamientos y preguntas motivadas biológicamente por hipótesis específicas, las cuales por lo general comenzamos a dejar de lado cuando sólo vemos y nos enfocamos en el aspecto meramente metodológico y estos no son integradas por ende en el proceso cualquiera que fuese el método implementado para responder a la pregunta de cómo se organizan, y cuáles son los factores que determinan en influyen diferencialmente en la distribución geográfica de las especies.

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6. CAPÍTULO 2. Nicho ecológico y patrones de distribución geográfica en carnívoros (Mammalia: Carnivora) en América: pasado a presente

6.1. Environmental drivers and distribution patterns of carnivoran assemblages (Mammalia: Carnivora) in Americas: Past to present

Environmental drivers and distribution patterns of carnivoran assemblages (Mammalia: Carnivora) in Americas: Past to present.

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Abstract

Understanding species distributions and the variation of assemblage structure in time and space is a fundamental goal of biogeography and ecology. We used a database of fossil-and current records of extinct and extant carnivoran species in Americas from the Last Inter Glacial (LIG) to the present (C), combined with ecological niche and macroecological modeling to elucidate biogeographic patterns of carnivoran assemblages in the continent. Our results suggest a diverse distribution of carnivoran co-occurrences patterns at the continental scale as a result of spatial climatic variation as an important driver constrained by the ecological niches of the species. This influence was also an important factor restructuring assemblages at lower scales in the continent. Disruption of the niche during the environmental changes at the LIG-C transition show a considerable shift on assemblage richness and composition across the Americas, which suggests an environmental filtering mainly during the Last Glacial Maximum (LGM). LGM were likely to be critical on species functional adaptation and distribution and therefore on assemblages structuring and rearranging from continental to local scales through time in the continent.

Keywords: Assemblages, Carnivoran richness, Ecological Niche, Environmental filtering, Last Glacial Maximum.

Introduction

Understanding how species are distributed, their determinants and constraints, and how they are spatially structured in assemblages through time and space is a fundamental goal of macroecology and ecology (Brown et al. 1995; Ferraz et al., 2012; Tôrres et al., 2012; Agosta and Bernardo 2013). They can vary in size (in mammals, which span 12 orders of magnitude), location, shape, and occupancy (Gaston 2003; Davie et al. 2009; Jones et al. 2009) and are the result of species response to ecological rules such as climatic conditions, species dispersal abilities, historical events and biotic interactions (Steinitz et al., 2006; Davies et al 2006; Blois et al., 2013, 2014). Most studies have assessed these ecological patterns with a discreet taxonomic scope; an important question is whether similar processes structure assemblage and species distributions from continental to regional and/or continental local scales. However, accurate information on past and present distributional patterns for many species is often scarce at broad scales, and the mechanisms, determinants and constraints of these ranges at these scales are still poorly understood (Graham, 2001; Prevosti et al. 2005; Martínez-Meyer et al., 2004; Davies et al., 2009; Nogués-Bravo 2009). Nevertheless, our understanding of the relationship between the influence of environmental drivers and assemblages measures (i.e. richness and composition) have received more attention, especially when extreme climatic events (e.g. glaciations) can change the outcome of the ecological patterns and processes (Thibault and Brown 2008; Davies et al. 2011).

These patterns are largely governed by environmental factors (e.g., climatic conditions) which define part of the fundamental niche of the species, where the biotic interactions are usually less perceptible (Blois et al. 2014; Davis and Shaw 2001; Olson et al. 2001;

Martínez-Meyer et al. 2004; Soberón and Nakamura 2009; Levinsky, 2010; Arroyo-Cabrales et al. 2010; Morris et al. 2010; Levinsky et al. 2013; Lomolino et al. 2010; Lorenzen et al. 2011; Peterson et al. 2011). But, elucidating the influence of these processes on species coexistence and distribution is not straightforward because non-random species associations are not necessarily caused only by climatic factors, nor species interactions. All these processes can operate independently or in synergy to determine assemblages' patterns through time and space (Blois et al. 2014; Giarla and Jansa 2015; Martínez-Meyer et al. 2004). Therefore, the central issue is how to differentiate the influence produced by actual and biotic interactions or dispersal limitations, from those produced meanly by environmental filtering (Blois et al. 2014, Giarla and Jansa 2015). In this sense, the ecological niche played an important role to disentangle the combined effects of abiotic and biotic factors on assemblage's dynamics and coexistence at different scales (Davis and Shaw 2001, Bofarull et al. 2008; Martínez-Meyer et al. 2004; Levinsky et al. 2013; Soares 2013).

The order Carnivora with its high taxonomic, morphological, ecological niche diversity, and with a well-resolved phylogeny (Goswami & Friscia, 2010; Nyakatura & Bininda-Emonds, 2012), represents an excellent group for investigating questions of biogeography, evolutionary and ecological niche significance. Here we used an ecological niche modeling and macro-ecological approach in order to assess the influence of past climate change on carnivoran assemblage richness and composition patterns from continental to local levels over the last 130 K years in the Americas. It is important to note that relatively little attention has been given to understanding the underlying causes of non-random patterns as geographical distribution and assemblage structuring (Collins et al. 2011, Gotelli and

Ulrich 2012; Blois et al. 2014), therefore revealing these patterns and mechanisms would improve our knowledge on the macro-ecological history of carnivoran assemblages in the continent.

Methods

Species data

Following a geoinformatics approach (Arroyo-Cabrales et al. 2010), a database containing confirmed records of extant and extinct terrestrial carnivoran species in the continent was constructed (G+, sensu Peterson et al. 2011). We analyzed all species based on the assumption that all extant species were also present during the late Pleistocene, and the extinct species disappeared at the end of the Pleistocene-early Holocene epochs (approximately 10-12Kyr; Webb 2006; Davies et al. 2009). The criteria for selecting the species for our study included taxonomic validity, proper chronological dating and supporting information on the species' presence during the study period. We determined the list and the taxonomy for living species following Wilson and Reeder (2005), Wilson and Mittermeier (2009), and IUCN Red List of Threatened Species (version 2014.1.). For extinct species, the taxonomy was based on the fossil record and following Berta (1985), Barnett et al. (2005), Cisneros (2005), Cione et al. (2007), Soibelzon and Prevosti (2007), Arroyo-Cabrales et al. (2010) and Ferrusquía-Villafranca et al. (2010).

We obtained the records through a detailed revision of scientific literature and museum specimens from online databases of biological collections (i.e. American Museum of Natural History [AMNH], Field Museum of Natural History [FMNH], National Museum of Natural History Smithsonian Institution [NMNH]) and our own records from extensive field-work in the Americas. A literature review was performed based on online reference search engines (i.e. ISI web of science and Google scholar) through key words (i.e. Pleistocene, Carnivora, Felidae, Canidae and specific and scientific names) and included published and unpublished documents, including thesis, articles, books and technical reports, where species were recorded. Likewise, the search was complemented with online databases (i i.e. Mammal Networked Information System, Global Biodiversity Information Facility, FAUNMAP and Paleobiology Database portals). We only used those records that contained reliable taxonomic information, source/collector, identification validity, date and geographical coordinates or detailed information on locality.

Climatic data

We defined our study area as the entire American continent. This approach assumes that all historical and ecological processes of colonization and dispersal events related to the species of interest, occurred in the continent (i.e. the G.A.B.I.) and all studied species, both extant and extinct, are or were native to the Americas. Based on available past projections and current bio-climatic variables at the global scale, we specifically used three groups of climatic layers: 1) Last Inter-Glacial (LIG, ~120-140 Kyrs BP; Otto-Bliesner et al. 2006), 2) Last Glacial Maximum (LGM, ~21 Kyrs BP; Braconnot et al. 2007) and 3) Current period (C, Hijmans et al. 2005). We selected the resolution of our layers (0.08333 degrees, approximately 10 x 10 km) based on the scale of our analyses.

Ecological niche model (ENM) and geographical distribution patterns

Numerous methods are available for developing ENM, and they have been compared extensively (Austin et al. 2006, Tsoar et al. 2007; Elith and Graham 2009, Elith et al. 2011, Peterson et al. 2011). Thus as our objective is not focused on model comparison, we decided to select one method for our study. We performed a niche-based potential distribution models using a maximum entropy approach, (MaxEnt 3.3.3K; Phillips et al. 2006; Phillips and Dudík 2008). This algorithm has been found to have good performance (Elith et al. 2010; Peterson et al. 2011; Santika 2011). Ecological niche modeling (ENM) with MaxEnt estimates the probability of presence of the species across the landscape by contrasting the ecological conditions where the species has been recorded, against a sample of background pixels across the study area via a Bayesian procedure of model fitting under the maximum entropy principle (Phillips and Dudík 2008). The predictions represent hypotheses about similar conditions to those where the species has been observed, and these conditions are likely to be among the existing fundamental niche over geographical space (E_A), corresponding to the potential distribution of the species (*sensu* Peterson et al. 2011).

We built one-hundred replicate models (with five hundred iterations for each replicate) per species using a random 70:30 split (bootstrap method) of the total number of occurrence records (G+) for calibration and validation respectively at each replicate. We first generated the current range models using the current presence records over the current bio-climatic layers and hindcast the modeled niche over the past-periods climatic layers to generate the past ranges (LIG and LGM), and then validated with the fossil record of species. For extinct species, we generated the models using the fossil records over the Inter-Glacial climatic layer, and then we projected the niche model over the LGM layers. To test for model performance and discriminatory ability we used the AUC_{Test} (Area Under the ROC Curve based on the testing data) (Phillips et al., 2006; Muscarella et al. 2014). AUC_{test} has proved to be a useful measure for ordinal score models (McPherson 2004; Thuiller et al. 2005; Marino et al. 2011; Santika 2011; Muscarella et al. 2014). The statistical significance of models was evaluated with a binomial test, which determines whether the model differs and the extent of differences from null expectations (Muscarella et al. 2014). Afterwards, we generated potential distribution maps for each period for each species based on the probability threshold value that minimized omission error and the fractional predicted area, to avoid over-prediction (Phillips et al., 2006; Peterson et al., 2011; Muscarella et al. 2014). Detail explanations on ecological niche theory methodology can be found elsewhere (i.e.Phillips et al. 2006; Phillips and Dudík 2008; Soberón and Nakamura 2009; Peterson et al., 2011; Elith et al. 2011; Merow et al. 2013Muscarella et al. 2014).

Assemblage hot spots, composition and richness patterns

In order to assess the influence of environmental drivers over carnivoran assemblages measurments (hot spots, richness and composition), we generated a macroecological modeling approach for each measurement. Our question was to ask whether constraints patterns in richness and composition structures in replicated assemblages through time and space should reflect environmental filtering through ecological niche constraints. We generated a grid of 7760 cells of 1 x 1 degree over the continental scale for these three periods (LIG, LGM and C). With these grids for each time and with the species' potential distributions, an overlapping count analysis was performed using the Hawth tools (Beyer 2004), in order to extract the species co-occurrence as a proxy of the species assemblage richness and composition present in each cell at each time in the Americas. We then estimated the values for four environmental determinants in each cell for each period based on the aforementioned available global scale climatic variables. These variables have proved to be useful and informative as drivers mammalian biodiversity patterns and ecosystem functioning at global scale in previous studies (Safi et al. 2011; Gonzalez-Maya et al. 2015): i) mean precipitation, ii) precipitation seasonality, iii) mean temperature and iv) temperature range.

To assess the assemblages richness and composition shifts patterns over the continent for the transition between periods (LIG-LGM and LGM-C), we first generated an Ordinary Least Squares (OLS) in order to select the best explaining models (shifts in assemblages richness and composition patterns) using the variable combinations (González–Maya et al., 2016a; González–Maya et al., 2016b). For each measurement (richness and composition) we generated all possible variable combinations with no replacement, resulting in 15 possible models, and then selected the best competing models based on the lower Akaike Information Criterion values (AIC) (Wagenmakers & Farrell, 2004; González–Maya et al., 2016a; González–Maya et al., 2016b). We used the R^2 as an indicator of the proportion of variation that is explained by the resulting models (higher R^2 values were preferred). After selecting the best models we assess multicollinearity to see which variables are potentially redundant in influencing model patterns by extracting the estimated coefficients and Variance Inflation Factor (VIF); VIF values greater than 7.5 are considered suspicious and redundant, so both should not be used (O'brien, 2007; Fotheringham et al., 1998). Once the best model was selected we tested for spatial differences from random expectation, we used the Moran's I spatial autocorrelation test of the residuals (Brunsdon et al., 2010), in order to assess if other important variables are potentially missing in the model. We also estimated the Koenke studentized Breusch-Pagan statistic (K(BP)) and its probability, in order to assess the reliability of standard errors when heteroscedasticity is present. In cases where the K(BP) was significant, we used the robust probability instead of the raw probability estimation. Significant heteroscedasticity and stationarity indicates that the relationship between the dependent variable (assemblage richness and composition shifts) and the drivers (environmental drivers) would vary with changes in the magnitude of the drivers, and that changes and the relationship is not equal along geographic space.

Likewise, we explore where spatial mismatching for each period occurred and where selected models did not perform adequately (i.e., showing at least one important variable was missing from the model). We performed a hot–spots analyses using the residuals of selected models based on the Getis-Ord Gi* test by estimating Z-values (i.e. standard deviations) and its associated probability for each cell (Getis & Ord, 1992; Ord & Getis, 1995; González–Maya et al., 2016a; González–Maya et al., 2016b) on the continent. This analysis identifies where clusters of high or low richness values are more marked and are significant ($p > 0.05$) than one from theoretical complete random expectation as the null hypothesis (Ebdon 1991). Mapping these high and low values allowed us to highlight if these carnivoran species clusters were different for each period in the continent and thus indicating if one or more explanatory variables are missing in the model for that cell, in turn indicating spatial mismatch overall model and the explanatory variables. Thus indicating that others important factors could mediate and play an important role on this patterns (Getis & Ord, 1992; Ord & Getis, 1995; González–Maya et al., 2016a; González–Maya et al., 2016b).

Afterwards we performed a geographically weighted regression (GWR) to identify the spatial influence of the environmental factors within the continental grid cells over each assemblage measurement, allowing us to identify a spatial heterogeneity (e.g. heterocedasticity and stationarity) due to heterogeneous environment influence over the continent for the transition between periods (LIG-LGM and LGM-C) (González–Maya et al., 2016a; González–Maya et al., 2016b). As the influence of different variables is likely spatially defined, we selected GWR as an appropriate method capable of identifying heterogeneity patterns at our spatial scales (Fotheringham 2002; Brunsdon et al., 2010; González–Maya et al., 2016a; González–Maya et al., 2016b). All analyses and statistical tests (using the spatial statistics tools, considered significant at 95%, $p < 0.05$) were performed on a Geographic Information System using ArcGIS 9.3 software (ESRI 2009).

Results

Ecological niche model (ENM) and geographical distribution patterns

For 8 carnivoran species out of total of 88 species, no potential distribution models for each period were estimated due to lack of records (*Mustela africana, Cuon alpinus, Speothos pacivorus and Enhydra macrodonta*), ranges restricted to islands (*Urocyon littoralis* and *Procyon pygmaeus*, which are recently separated from two continental species that were isolated after the last glacial maximum) and recently described as new species and separated from *Nasuella olivacea* (*Nasuella meridensis*) and *Leopardus trigrinus* (*Leopardus gutullus*). In terms of model performance for all species, AUC_{Test} values were all higher than 0.81, indicating a good performance and model discriminatory ability. With respect to the model validation, all species models presented a statistical significance ($p< 0.05$), except for the past range models of *L. guigna*, *L. jacobitus* which no fossil records were found. However, this does not mean that these models are not informative for subsequent analysis.

Assemblage hot spots, composition and richness patterns

We found a diverse distribution of carnivoran co-occurrence patterns at the continental scale as a result of spatial climatic variation constrained by the ecological niches of the species (Figure 1). Climatic niche coincidences among species and therefore on ranges variations (expansion and contraction) were the main reason of taxa co-occurrences. The spatial hot spots analysis allowed us to identify statistically significant and noticeable changes in assemblage's structure during the LIG-LGM-C transitions. We found a high assemblage of hot spots at low to mid latitudes in North America and in the Andes of South America during the LIG, and a significant assemblages disassemble in the north of North America occurred during the LGM, suggesting an environmental filtering (Figure 2). The areas with more stable climatic conditions of the Neotropic over these periods suggests that these conditions enable the persistence of some assemblages to present time.

Carnivoran assemblage richness show a latitude-structuring pattern and a significant shift from the LIG to C period across the Americas (Figure 3). The best model (model with the lower AIC value, Table 1) that accounted and explained richness shifts include mean temperature, temperature range and precipitation seasonality as important drivers for richness patterns at continental scales (LIG-LGM OLS R^2=0.328; LGM-C OLS R^2=0.433, Table 1; Figure 3). The LIG had a greater carnivoran species richness concentrated from low to mid latitudes in North and South America in the subtropical regions, however, during the LIG-LGM transition, due to glacial conditions, low temperatures and drier environments, this pattern changed with high loss of species from north and central North America (Figure 3). During the LGM-C transition the biogeographic assemblages richness patterns tend to recover toward the temperate areas of North America (i.e. Grasslands, Savannas, Temperate Coniferous Forests, Temperate Broadleaf and Mixed Forests), but with species loss in the Neotropics (Figure 3).

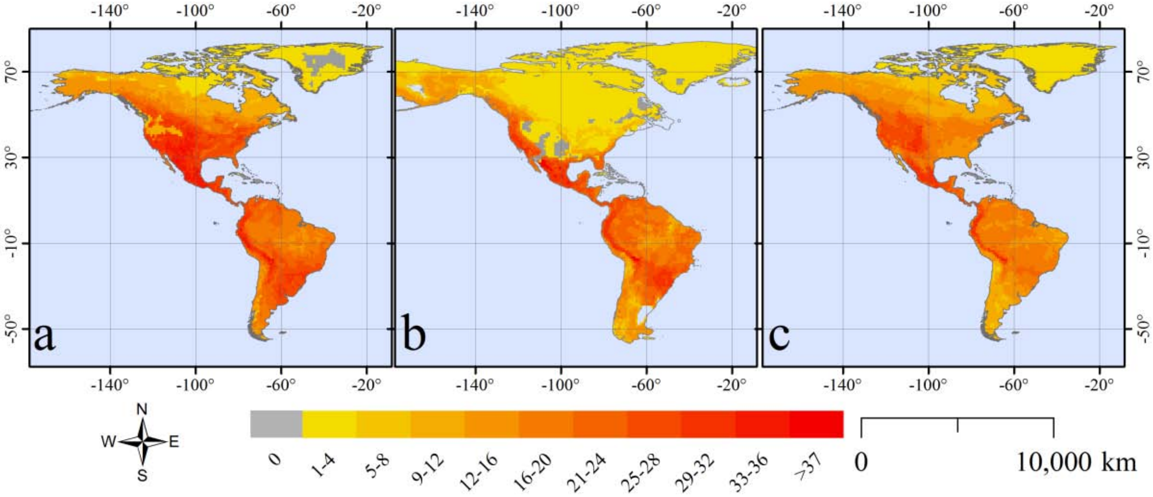

Figure 1. Carnivoran assemblage richness patterns over the last 130 K years in America. a. LIG, b. LGM and c. C.

K(BP) Statistic indicated heteroscedasticity and stationarity of the model, indicating that the changes on the relationship between the assemblages richness patterns and the environmental drivers change when the magnitude of drivers change and this relationship is not constant across geographic space and time (Table 1). These patterns suggest a greater association and a heterogeneous environment influence on carnivoran richness patterns at local-regional levels within the continent for the transition between periods (LIG-LGM GWR R^2=0.67; LGM-C GWR R2=0.75, Table 1) (Figure 4).

Carnivoran assemblage composition structure shows a different pattern. The best model that accounted for and explained composition shifts included mean temperature, temperature range, mean precipitation and precipitation seasonality as main drivers (LIG-LGM OLS R^2=0.274; LGM-C OLS R^2=0.346, Table 2) (Figure 3). During the LIG-LGM the environmental drivers caused greater shifts in carnivore composition at mid to high latitudes in North America, and at mid latitudes and in the western coasts of South

America. During the LGM-C transition, the environmental effects were in the Neartic region and austral zone of South America (Figure 3).

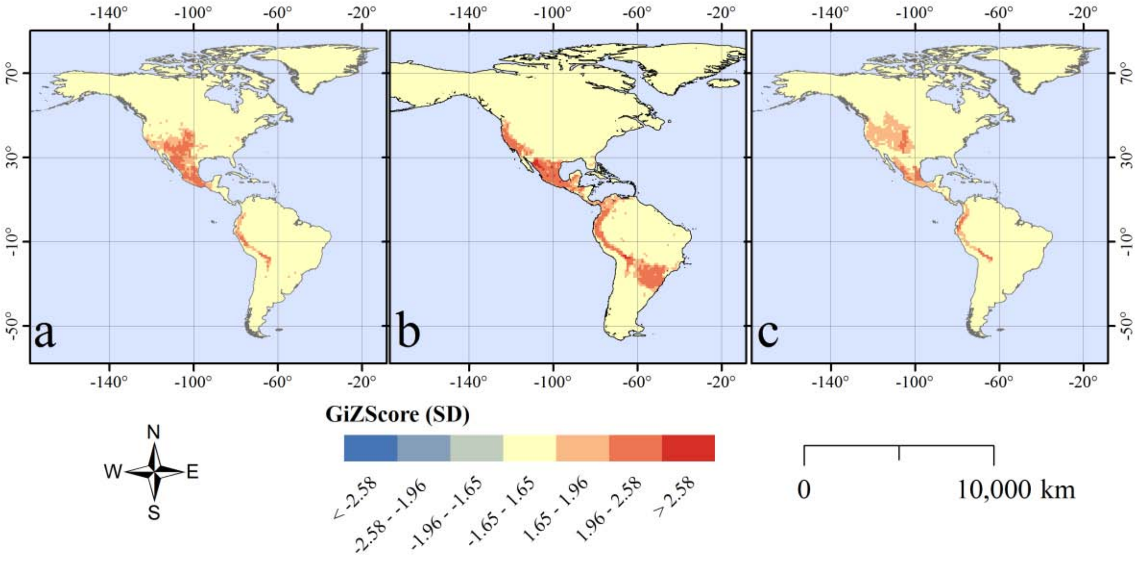

Figure 2. Hot spots of carnivoran assemblages across Americas over the last 130 K years. a. LIG; b. LGM and c. C periods. Z-scores accounts for standard deviations of the Getis-Ord Gi test. Red dots indicate significant ($p<0.05$) and more marked associations.

Likewise, K(BP) Statistic indicated heteroscedasticity and stationarity of the model, indicating that this relationship is not constant across geographic space and time in America, suggesting a moderate environmental influences at local-regional levels (Table 2). However, due to the low variation explained by the model compared with the richness pattern (LIG-LGM GWR R^2=0.57; LGM-C GWR R^2=0.62), some other important variables could be missing in the model (i.e. species interaction, human influence, resources,) that could help to explain the remaining proportion of variation in the composition shifts during this transition (Figure 4).

Discussion

Understanding the carnivoran species distributions and how they are spatially structured has received greater attention in recent years (Goswami and Friscia 2010; Lenvinsky 2013). Most of carnivoran lineages in the Americas were holartic species with a lower diversity during the Miocene-Pliocene compared with the Pleistocene (Marshall et al. 1982; Prevosti & Reguero 2000; Webb 2006; Prevosti and Soibelzon 2012). This group was one of the most successful in mammalian species to participate in the biotic interchange (GABI as a complex process that persist today) (Dundas 1999; Graham, 2001Webb 2006; Johnson et al. 2006; Prevosti et al. 2011; Rincón et al. 2011; Bacon et al 2015). However, some of these species and other terrestrial fauna faced the "Megafauna Extinction", which apparently affected mostly the mammalian faunas of the Nearctic, Neotropics and Australasia regions (Bofarull et al. 2008; Prevosti and Soibelzon 2012). Evidence on these events, reveal a more complex biogeographical history of this group than previously thought.

Carnivoran co-occurrence patterns at continental scales in the Americas are, in part, the result of important environmental drivers constrained by the ecological niches stability of the species. The significant climatic variation was critical in range contractions, meanly from high to mid latitudes in North America during the LIG-LGM transition, causing substantial changes on assemblage richness and composition at the continental scale. These environmental factors (mean precipitation, precipitation seasonality, mean temperature and temperature range) have been recognized as some of the primary drivers with significant effects on the distribution and diversity patterns of other vertebrate assemblages and communities in other regions (Graham & Mead 1987; Root 1988; Lundberg et al. 2000; Lyons 2003; Eronen & Rook 2004; Svenning & Skov, 2004; Blois and Hadly 2009).

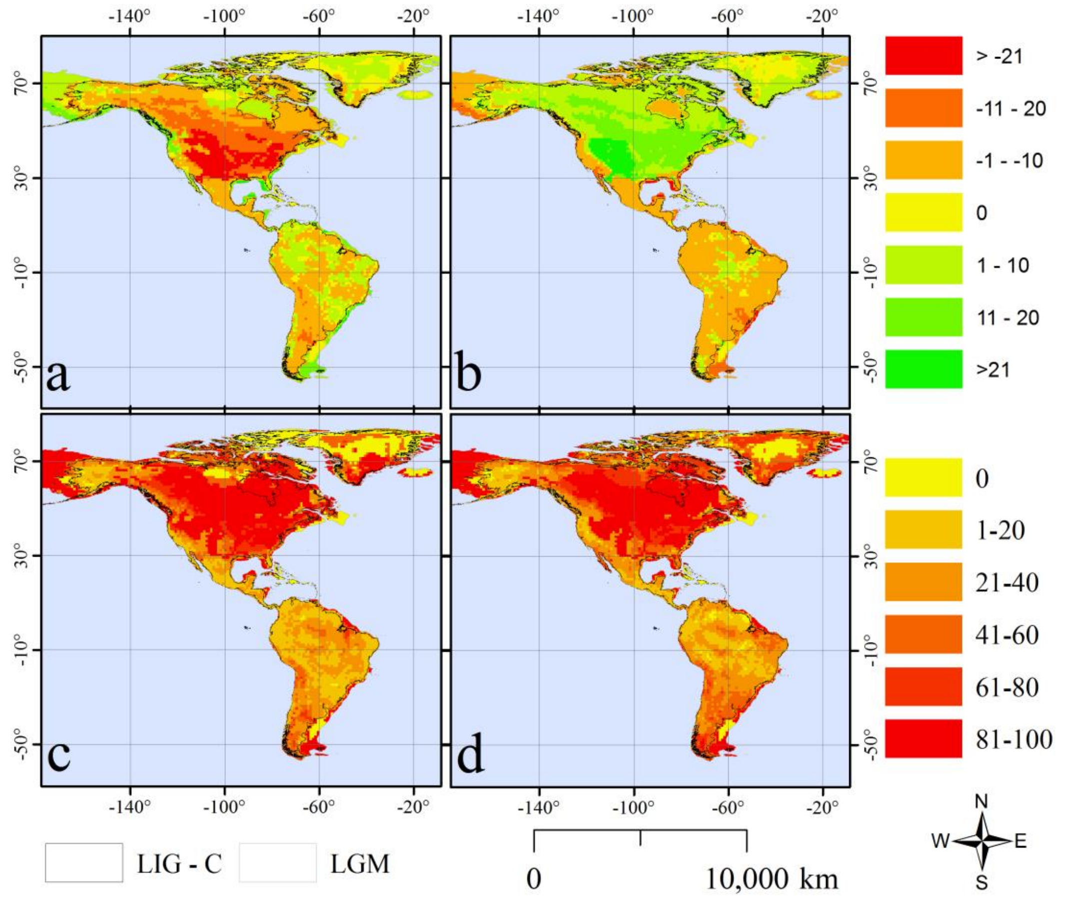

Figure 3. Influences of environmental drivers on carnivore assemblages **Richness shifts patterns** a. LIG-LGM, b. LGM-C; **composition shifts patterns** c. LIG-LGM, b. LGM-C. (The a. and b. legend represents number of species loss and gain and c. and d. represents the percentage of change during the transition between periods).

Our results show important latitudinal gradients consistent with other approaches at continental scale (Gittleman and Gompper 2005; Schipper, 2008; Polly 2010), the smallest carnivoran ranges are mostly present in the tropical region, and the largest ranges are found from low to high latitudes. These patterns evidently follow the Rapport's rule, which reflects the seasonal variability of high latitude environments (Stevens 1989; Davies et al. 2011). This rule also could explain the greatest assemblage richness pattern towards the tropics, since greatest ranges confluence with the narrower ranges at more equatorial latitudes. This was also evident at the last glacial maximum (LGM) where more stable ranges tend to be larger and more stable where rainfall and temperatures patterns were much less variable (Davis and Shaw 2001; Davis et al. 2011). This high richness pattern in the late Pleistocene is consistent, as previously suggested, as one of the highest worldwide in proportion to the continental area, and significantly higher than the richness during middle Holocene (Cione et al. 2003; Prevosti & Vizcaino 2006) and the current time as shown herein.

Table 1. Results for best competing and selected models testing for environmental drivers influence on carnivoran assemblages richness shifts patterns using a 7760 1 x 1 degree cells in Americas. AIC: Akaike Information Criterion, SE: Standard Error, VIF: Variance Inflation Factor, ORL: ordinary least squares; GWR: Geographic weighted regression, K(BP): Koenker's studentized Breusch-Pagan Statistic.* indicates the selected models.

LIG-LGM Models												
Model	**Variable**	**Coefficient**	**SE**	**P**	**Robust t**	**Robust p**	**VIF**	**ORLR^2**	**GWR R^2**	**AIC**	**K(BP)**	**K(BP)-Prob**
1*	Intercept	-0.599	0.132	<0.05	-6.256	0.000		0.328	0.67	53117.48	495.590	<0.05
	Mean Temperature	0.443	0.010	<0.05	42.345	0.000	1.282					
	Temperature range	0.063	0.005	<0.05	14.336	0.000	1.284					
	Precipitation seasonality	0.115	0.003	<0.05	32.499	0.000	1.011					
2	Intercept	-0.617	0.133	<0.05	-6.421	0.000		0.328		53118.28	513.678	<0.05
	Mean Temperature	0.437	0.011	<0.05	36.850	0.000						
	Temperature range	0.062	0.005	<0.05	14.047	0.000						
	Mean precipitation	0.000	0.000	0.274	1.116	0.264						
	Precipitation seasonality	0.113	0.003	<0.05	28.301	0.000						
3	Intercept	0.250	0.114	<0.05	2.420	0.016		0.315		53265.06	152.355	<0.05
	Mean Temperature	0.373	0.010	<0.05	37.468	0.000						
	Mean precipitation	0.001	0.000	<0.05	2.960	0.003						
	Precipitation seasonality	0.114	0.004	<0.05	29.189	0.000						
4	Intercept	0.336	0.110	<0.05	3.194	0.001		0.314		53272.2	104.903	<0.05
	Mean Temperature	0.386	0.009	<0.05	43.973	0.000						
	Precipitation seasonality	0.119	0.003	<0.05	34.603	0.000						
LGM-C Models												
1*	Intercept	-1.679	0.096	<0.05	-17.387	0.000		0.433	0.75	49996.54	207.303	<0.05

	Mean Temperature	0.465	0.007	<0.05	66.180	0.000	1.024						
	Temperature range	0.127	0.008	<0.05	13.063	0.000	2.626						
	Precipitation seasonality	0.059	0.006	<0.05	7.727	0.000	2.612						
2	Intercept	-1.667	0.096	<0.05	-17.511	0.000			0.433		49996.6	158.532	<0.05
	Mean Temperature	0.460	0.008	<0.05	57.452	0.000							
	Temperature range	0.126	0.008	<0.05	13.121	0.000							
	Mean precipitation	0.000	0.000	0.16	1.235	0.217							
	Precipitation seasonality	0.057	0.006	<0.05	7.154	0.000							
3	Intercept	-1.887	0.094	<0.05	-21.374	0.000			0.426		50088.73	535.589	<0.05
	Mean Temperature	0.460	0.008	<0.05	58.442	0.000							
	Temperature range	0.183	0.005	<0.05	42.762	0.000							
	Mean precipitation	0.001	0.000	<0.05	3.484	0.001							
4	Intercept	-1.948	0.093	<0.05	-21.881	0.000			0.425		50102.07	690.205	<0.05
	Mean Temperature	0.475	0.007	<0.05	67.932	0.000							
	Temperature range	0.191	0.005	<0.05	51.072	0.000							

On the contrary, it appears that the composition shifts at these scales were less influenced by these climatic drivers. However, glaciers covered most of North America during the LGM, and carnivore ranges responded accordingly with most species characteristics, shifting greater distances southward and westward to more suitable areas (Dyke 2005), causing important changes on richness than composition patterns, more pronounced in the Neartic region. Nevertheless, species with both temperate and tropical distributions where less affected by drastic climatic changes, and this shift pattern was apparently less severe in South America during LIG-LGM transition mainly from low to mid latitudes. Which are consistent with the impact of Quaternary climate oscillations on others mammals (Davies et al. 2011; Lorenzen et al. 2011; Levinsky et al. 2013; Blois et al. 2014). The loss of jaguar populations distributed at higher latitudes (*P. onca augusta* from North America and *P. onca mesembrina* from South America) and range constriction from high latitudes towards the tropics is an example. It is important to note that this minor effect on composition patterns were, perhaps, because during this last period there was no considerable carnivoran species turnover as previously occurred. For example through a glacial-interglacial transition during the middle Pleistocene in the Americas, where replacement emergence, apparently by competition, with the appearance of new carnivoran species with similar ecological trait-space niches (Prevosti y Soibelzon 2012).

Table 2. Results for best competing and selected models testing for environmental drivers influence on carnivoran assemblages composition shifts patterns using a 7760 1 x 1 degree cells in Americas. AIC: Akaike Information Criterion, SE: Standard Error, VIF: Variance Inflation Factor, ORL: ordinary least squares; GWR: Geographic weighted regression, K(BP): Koenker's studentized Breusch-Pagan Statistic.* indicates the selected models.

LIG-LGM Models												
Model	**Variable**	**Coefficient**	**SE**	**P**	**Robust t**	**Robust p**	**VIF**	**R^2**	**GWR R^2**	**AIC**	**K(BP)**	**K(BP)-P**
1*	Intercept	0.353	0.006	<0.05	73.82	0.00		0.274	0.57	4446.84	513.678	<0.05
	Mean Temperature	-0.008	0.000	<0.05	-15.39	0.00	1.636					
	Temperature range	0.005	0.000	<0.05	23.57	0.00	1.317					
	Mean precipitation	0.000	0.000	<0.05	9.71	0.00	1.504					
	Precipitation seasonality	0.005	0.000	<0.05	27.03	0.00	1.195					
2	Intercept	0.360	0.006	<0.05	74.52	0.00		0.265		4538.55	495.590	<0.05
	Mean Temperature	-0.006	0.000	<0.05	-11.85	0.00						
	Temperature range	0.005	0.000	<0.05	25.74	0.00						
	Precipitation seasonality	0.005	0.000	<0.05	32.58	0.00						
3	Intercept	0.339	0.006	<0.05	66.23	0.00		0.188		5312.81	391.469	<0.05
	Mean Temperature	-0.009	0.000	<0.05	-16.24	0.00						
	Temperature range	0.005	0.000	<0.05	22.73	0.00						
	Mean precipitation	0.000	0.000	<0.05	20.37	0.00						
4	Intercept	0.423	0.005	<0.05	82.54	0.00		0.226		4941.16	152.355	<0.05
	Mean Temperature	-0.013	0.000	<0.05	-28.84	0.00						
	Mean precipitation	0.000	0.000	<0.05	12.54	0.00						
	Precipitation seasonality	0.005	0.000	<0.05	27.29	0.00						
LGM-C Models												
1*	Intercept	0.367	0.004	<0.05	77.63	0.00		0.346	0.62	2231.26	158.532	<0.05
	Mean Temperature	0.015	0.000	<0.05	35.91	0.00	1.314					
	Temperature range	0.001	0.000	<0.05	2.07	0.04	2.634					
	Mean precipitation	0.000	0.000	<0.05	-14.26	0.00	1.537					
	Precipitation seasonality	-0.007	0.000	<0.05	-22.01	0.00	2.786					
2	Intercept	0.374	0.004	<0.05	75.20	0.00		0.323		2497.7	207.303	<0.05

	Mean Temperature	0.012	0.000	<0.05	29.50	0.00				
	Temperature range	0.001	0.000	0.15	1.17	0.24				
	Precipitation seasonality	-0.009	0.000	<0.05	-24.55	0.00				
3	Intercept	0.395	0.004	<0.05	74.92	0.00	0.284	2935.16	535.589	<0.05
	Mean Temperature	0.015	0.000	<0.05	30.57	0.00				
	Temperature range	-0.006	0.000	<0.05	-26.40	0.00				
	Mean precipitation	0.000	0.000	<0.05	-18.05	0.00				
4	Intercept	0.368	0.004	<0.05	79.24	0.00	0.345	2235.08	133.698	<0.05
	Mean Temperature	0.015	0.000	<0.05	36.46	0.00				
	Mean precipitation	0.000	0.000	<0.05	-14.17	0.00				
	Precipitation seasonality	-0.007	0.000	<0.05	-34.60	0.00				

This Glacial history has long been thought important in shaping diversity patterns worldwide (Davies et al. 2011, 2009), where the last glacial period is not the exception. The environmental factors and their disturbances events (e.g. glaciations) are the most important drivers that influence these ecological and evolutionary carnivoran distribution responses. Which are likely to be more detectable at broader spatial scales (Martínez-Meyer et al. 2004; Soberón and Nakamura 2009; Morris et al. 2010; Davies et al. 2011; Lorenzen et al. 2011 Levinsky et al. 2013; Blois et al. 2014). Nerveless, here we provide support that the environmental drivers dynamically and differentially affected these patterns in the Americas more directly on richness than composition, not only at the continental level, but also from regional and local scales as recently suggested (Blois and Hadly 2009; Wisz et a. 2013). Evidence on composition of European mammalian communities of the past 20 million years suggests that this composition structure remained constant despite the significant richness shifts of the dominant assemblages herbivores, as it is also proposed for the mammalian communities in Australia (Jernvall and Fortelius 2004; Prideaux et al. 2007; Blois and Hadly 2009).

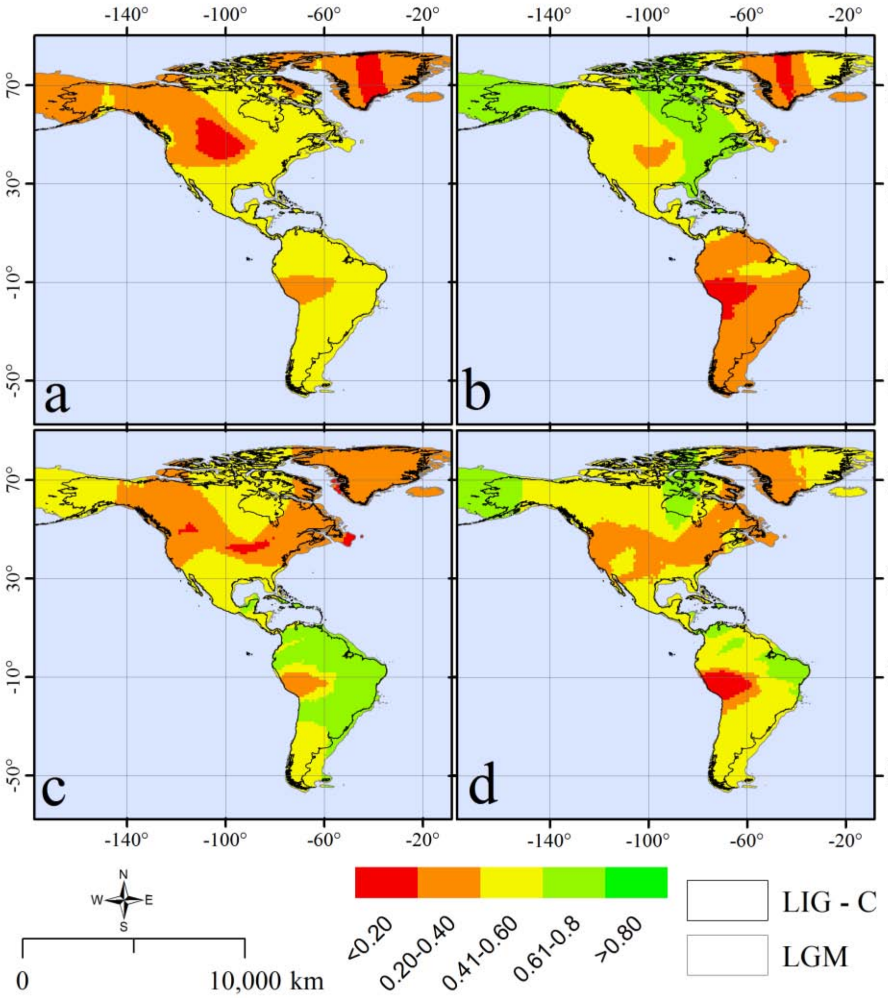

Figure 4. Geographically weighted regression for carnivore assemblages as influenced by local environmental drivers during the transition between periods. **Richness shifts patterns** a. LIG-LGM, b. LGM-C. **Composition shifts patterns** c. LIG-LGM, b. LGM-C. (Legend represents Local R^2 values).

These large-local scale carnivoran patterns that emerges herein can be viewed as a description of the environmental and ecological niches constraints that have contributed to shape geographical distribution lineages, suggesting an environmental filtering during the LIG-LGM-C transition (Cardillo et al. 2006; Davies et al. 2009; Palombo et al. 2008; Agosta and Bernardo 2013). It is possible that many of these carnivoran species that persisted through the last climate change "extinction filter" represent the current set of species best suited to face natural environmental changes. However, since the models assessed herein where not explained entirely by environmental drivers, past climate change and filter effects apparently played just a part over carnivoran assemblage structure patterns and extinction event in America. Others important forces, mainly associated with some well-defined ecological niche functional attributes related with biotic interactions could mediate and play an important role on these patterns from local and regional to continental levels (De Vivo and Carmignotto 2004; Araújo & Luoto 2007; Croitor and Brugal 2010; Davies et al. 2011Oliveira and Pereira 2013; Wisz et l 2013).

Here we provide new insights regarding history and spatial patterns of American carnivoran species during the last 130 Kyrs. Climatic variation and the ecological niches constraints are, in part, the main reason of taxa co-occurrences and important assemblage restructuring from continental to local scales in the Americas. Environmental filtering is likely a leading factor to species susceptibility to extinction and carnivoran assemblages persistence is likely attributable to those species that are best biologically and ecologically suited for facing environmental changes.

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6.2. Cross-validation of carnivoran assemblage's patterns: species niche-based potential distribution and extent of occurrences approaches

Cross-validation of carnivoran assemblage's patterns: species niche-based potential distribution and extent of occurrences approaches

Running title: Comparing niche-based and extent of occurrence distributions

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Introduction

Understanding how species are distributed, and how are spatially structured in ecological assemblages is a fundamental goal of biogeography, macroecology and ecology (Brown et al. 1995; Ferraz et al., 2012; Agosta and Bernardo 2013). Considering that extreme climatic events (e.g. glaciations), species dispersal abilities, historical events and biotic interactions, can change the outcome of the ecological patterns (i.e. richness and composition) through time and space (Thibault and Brown 2008; Davies et al. 2011). Therefore exploring species distributions is of special interest in the context of global change and mass extinctions (Martinez-Meyer 2002; Blois et al. 2014). Species coexistence patterns is the basis for theoretical and applied research, and more recently have gained more attention for conservation planning (Guisan and Zimmermann 2000; Soberón and Peterson 2005; Graham and Hijmans 2006; Guisan and Thuller 2005; Peterson et al. 2011). In this sense, species niche-based potential distribution modeling has become a tool of great importance and a valuable strategy to assess these and other biogeographic hypotheses (Martinez-Meyer et al. 2004; Aranda and lobo 2011; Peterson et al. 2011).

Estimating geographical gradients of diversity such as species' communities or assemblages' patterns (i.e., richness and composition) is not straightforward. Accurate information on past and current geographical distributions for many species is often scarce, and estimating these patterns via species distribution modeling is a big challenge (Aranda and lobo 2011; Peterson et al. 2011). In general, these approaches (richness and composition estimations) are generated from overlaying directly the individual species ranges derived from niche-based potential distribution models or overlapping expert criteria or to count the number of species present on a grid cell based only on punctual occurrence records (Hijmans & Spooner, 2001; Graham and Hijmans 2006). However, these approaches usually are made without following any particular macroecological analysis. The central issue is how to obtain useful and validated assemblages characterizations and to identify the strengths of these approaches that could be informative in ecology, biogeography, conservation planning and others applications.

Here we used a species niche-based potential distribution modeling and macroecological approach in order to assess if ecological assemblages species generated from individual species distribution could provide accurate richness and composition patterns compared with those ranges generated by other methods. For this study, we used the terrestrial carnivoran species of Americas, a diverse group with available extent of occurrences assessments, and legitimately as important models in structuring ecological communities in the face of global extinction crisis. Furthermore, we provide a free, open-access database on carnivore distribution modeled polygons for future reference or use in macroecological analyses.

Material and methods

Species data

Following a geoinformatics approach (Arroyo-Cabrales et al. 2010) a database containing confirmed records of 76 extant terrestrial carnivoran species in America was constructed (G+, sensu Peterson et al. 2011). We obtained the records through a detailed revision of scientific literature and museum specimens from online databases of biological collections (i.e. American Museum of Natural History [AMNH], Field Museum of Natural History [FMNH], National Museum of Natural History Smithsonian Institution [NMNH]; Instituto Alexander von Humboldt [IAvH]; Instituto de Ciencias Naturales [ICN]; Colección Teriológica Universidad de Antioquia [CTUA]; Colección Nacional de Mamíferos del Instituto de Biología-UNAM [IBUNAM]; Mammal Networked Information System, Global Biodiversity Information Facility and our own records from extensive field-work in different countries. Literature review was performed based on online reference search engines (i.e. ISI web of science and Google scholar) through key words (i.e. Pleistocene, Carnivora, Felidae, Canidae and specific scientific names) and included published and unpublished documents, including thesis, articles, books and technical reports, where species were recorded (e.g Aragona & Setz 2001; Prevosti, and Pardiñas 2001; Vila et al. 2004; Beisiegel and Zuercher 2005; Bueno & Motta-Junior 2006; De Azevedo & Murray 2007; Escobar & Vásquez 2007; Matsuda & Izawa 2007; Zeller 2007; De Azevedo 2008; Dematteo & Loiselle 2008; Balaguera-Reina et al. 2009; Randa et al. 2009; Benítez 2010; Arias-Alzate et al. 2011; Lemos & Facure 2011; Payan & Gonzalez-Maya 2011; Marino et al. 2011; Beisiegel et al. 2012; Briones-Salas & Lira-Torres 2012; De Oliveira et al. 2012; Luque et al. 2012; Tôrres et al. 2012; Ramírez-chaves et al. 2012; Bornholdt e al. 2013; Helgen et al. 2013; Carretero-Pinzón 2013; D'Elía et al. 2013; Srbek-Araujo & Chiarello 2013; Arias-Alzate et al. 2014). We only used those records that contained reliable taxonomic information, source/collector, identification validity and geographical coordinates or detailed information on locality. We determined the list and the taxonomy following Wilson and Reeder (2005), Wilson and Mittermeier (2009), and IUCN Red List of Threatened Species (version 2015.1; IUCN 2012)

Ecological niche models (ENM) and geographical distributions

Numerous methods are available for developing ENM, and they have been compared extensively (Austin et al. 2006, Tsoar et al. 2007; Elith and Graham 2009, Elith et al. 2011, Peterson et al. 2011). Thus as our objective is not focused on model comparison, we opted to select a good performance method (Elith et al. 2011; Peterson et al. 2011; Santika 2011; Merow et al. 2014) for our study. We performed niche-based potential distribution models using a maximum entropy approach, (MaxEnt 3.3.3K; Phillips et al. 2006; Phillips and Dudík 2008). Ecological niche modeling (ENM) with MaxEnt estimates the probability of presence of the species across the landscape by contrasting the ecological conditions where the species has been recorded, against a sample of background pixels across the study area via a bayesian procedure of model fitting under the maximum entropy principle (Phillips and Dudík 2008). Detail explanations on ecological niche theory and methodology can be found elsewhere (i.e., Phillips et al. 2006; Phillips and Dudík 2008; Soberón and Nakamura 2009; Peterson et al., 2011; Elith et al. 2011; Merow et al. 2014; Muscarella et al. 2014).

We built one-hundred replicate models (with five hundred iterations each replicate) per species using a random 70:30 split (bootstrap method) of the total number of occurrence records (G+) for calibration and validation respectively at each replicate. To generate the models we specifically used the 19 current bio-climatic variables (Hijmans et al. 2005). We selected the resolution of our layers (0.08333 degrees, approximately 10 x 10 km) based on the scale of our analyses. To test for model performance and discriminatory ability we used the AUC_{Test} (Area under the ROC Curve based on the testing data) (Phillips et al., 2006; Muscarella et al. 2014). AUC_{test} has proved to be a useful measure for ordinal score models (McPherson 2004; Thuiller et al. 2005; Marino et al. 2011; Santika 2011; Muscarella et al. 2014). Statistical significance of models was evaluated with a binomial test, which determines whether the model differs from null expectations (Muscarella et al. 2014). Afterwards, we generated geographic distribution maps based on the probability threshold value that minimized omission error and the fractional predicted area, to avoid over-prediction. As our aim was to approach to the occupied distribution rather than the potential distribution, we eliminate the areas which are suitable for the species but are not occupied due to potential dispersal limitations (i.e. species interactions or limited dispersal ability) (Phillips et al., 2006; Peterson et al., 2011; Muscarella et al. 2014).

We also obtained geographic distributions for the 76 extant carnivore species from the IUCN Red List of Threatened Species (IUCN 2015; Schipper et al. 2008). These distribution polygons are based on observations and expert criteria obtained through workshops held as part of the IUCN/SSC Global Mammal Assessment (Schipper et al. 2008). To date, these distribution polygons are considered among the most reliable and complete distribution polygons, built following a standardized methodology and corrected by expert criteria, making it a reliable source of information for most mammals (González-Maya et al. 2015, González-Maya et al. 2016).

Assemblages' patterns

In order to characterize the carnivoran assemblages' measures (i.e., richness and composition), we generated a macroecological modeling approach for each measure. We generated a grid of 7760 1 x 1 degree cells over the continental scale. With this grid and with the carnivoran geographical ranges and the extent of occurrences (EOO) of the IUCN, we performed an overlapping count analysis using the Hawth tools (Beyer 2004) in order to extract the species co-occurrence as a proxy of the species assemblage richness (number of species per cell) and composition (identity of species per cell) present on each cell and therefore generate the matrices (species per space) for the analysis. Afterwards, we validated and estimated the accuracy of these approaches comparing both assemblages patterns using a Pearson correlation test and the Jaccard index with a statistically significance of 99% ($p< 0.001$). All geographic analyses were performed on a Geographic Information System using ArcGIS 9.3 software (ESRI 2009) and the statistical analysis were performed using the Infostat software (DiRienzo et al. 2011).

Results

We obtained a total of 35310 occurrences for 76 extant terrestrial carnivoran species. For all but five carnivoran species, no potential distribution models were estimated due to lack of sufficient records (*Mustela africana*), those restricted to islands (*Urocyon litoralis* and *Procyon pygmaea*) and recently described new species (*Nasuella meridensis* and *Leopardus gutullus*). We obtained distribution models for the 76 species (SI 1), with high values of models´ performance; AUC_{Test} values were all higher than 0.81, indicating a good performance and model discriminatory ability. With respect to the model validation, all species models were statistically significant ($p< 0.05$).

Correlation among assemblage richness patterns was high (Pearson= 0.90, $p< 0.001$) (Figure 1). Both analyses showed relatively high richness from mid to low latitudes in the tropical zone and in the Andes region and low richness toward high latitudes in the continent. On the other hand regarding to the composition patterns, both approaches provided relatively accurate characterizations across the majority of the grid cells with high Jaccard values (Figure 2). Even though little spatial differences among approaches persist, possibly related to the way in which the distribution ranges are estimated (i.e., niche-based potential distribution models on ENM, and minimum convex polygon on EOO, differences in the accepted taxonomic names and species validity, for example spices of the genus Bassaricyon).

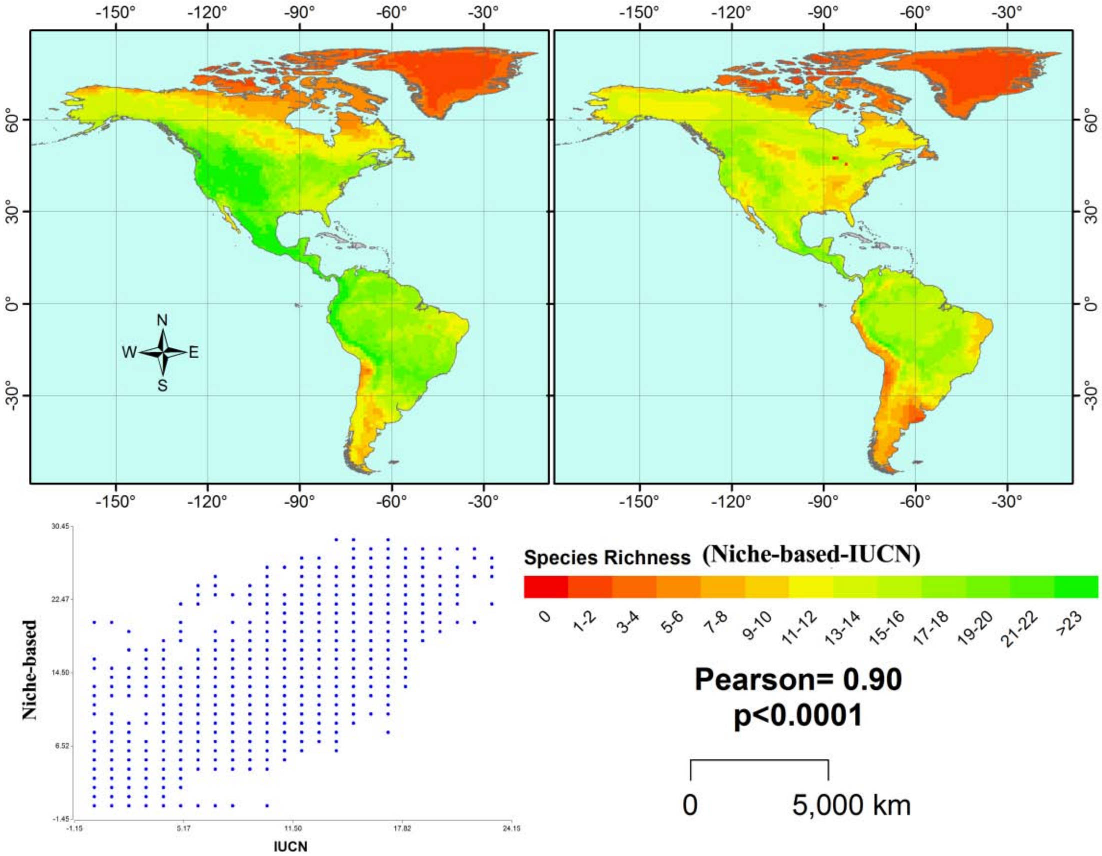

Figure 1. Carnivoran assemblage richness patterns in Americas generated from niche-based potential distribution models (left) and IUCN extent of occurrences (right).

Discussion

Understanding how species are spatially structured in assemblages through time and space is a fundamental goal to improve our knowledge on the ecological and biogeographic history and have gained very special attention in recent years, highlighting its potential usefulness for conservation purposes and several ecological and evolutionary applications (Peterson et al. 1999; Graham et al. 2004; Graham and Hijmans 2006). Here we propose a strategy combining niche-based potential distribution with a macro-ecological approach, which may provide a reliable assemblage´s characterization of richness and composition patterns. Generally, these estimations patterns have been based on assemble or sum the niche-based potential distribution directly, which could over-predict and show higher levels of species richness as a result of a methodological artifact.

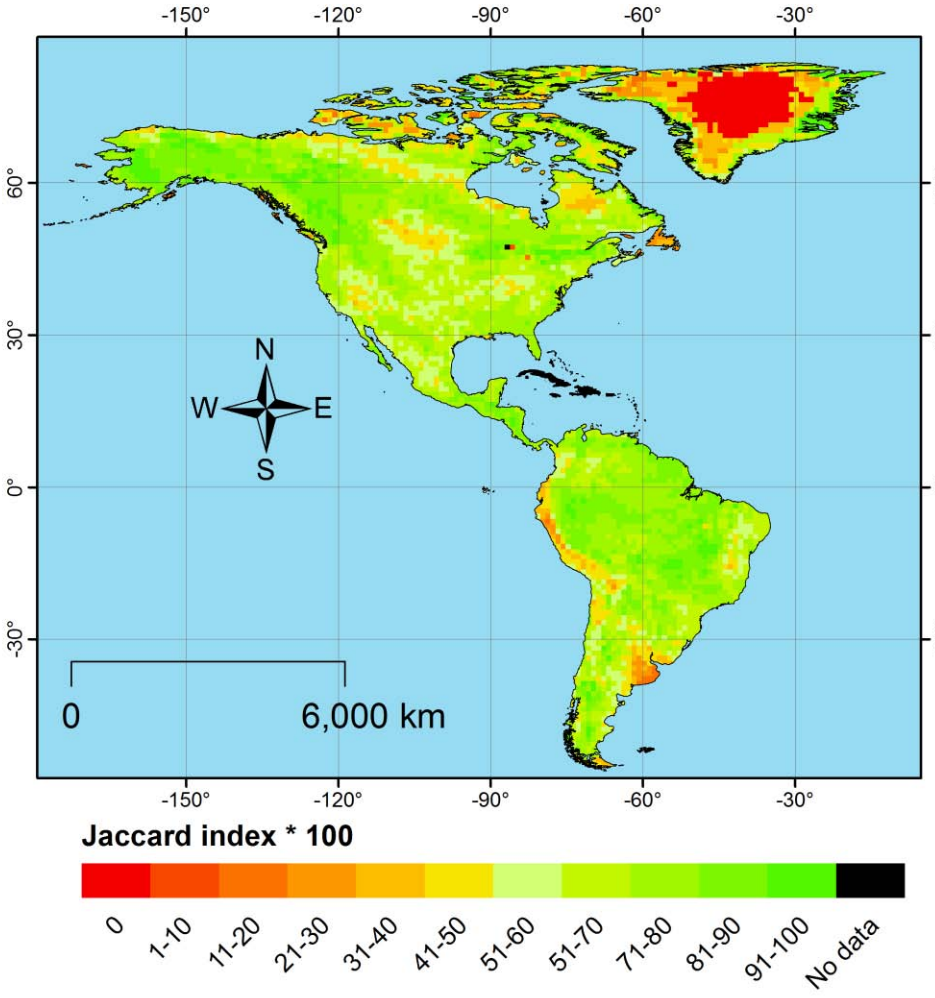

Figure 2. Composition similarity (cell by cell) between carnivoran assemblages generated from niche-based potential distribution models and IUCN extent of occurrences.

On the other hand, the sum of the expert EOO could under-predict since the species in some places are considered locally extinct, but they are currently present due to lack of available records or also could over-predict due to the include of big areas where the species really are not present (Graham and Hijmans 2006). Herein we showed that this macro-ecological approach for both expert extent of occurrences and niche-based potential distribution models could produce reliable inference on assemblages' richness and composition. For example, both richness patterns estimations are consistent with other approaches, with particularly high levels of species richness in the Andes and the tropics and declining toward high latitudes in the continent (Gittleman and Gompper 2005; Schipper et al. 2008; Polly 2010; Fergnani and Ruggiero 2015). This carnivoran high richness pattern towards the equatorial zone seems to follow the Rapaport's rule (Hawkins, 2001; Davies et al. 2011), since species with largest ranges present at both temperate and tropical zones confluence with the species with narrower ranges at more tropical areas and in the Andes region.

It is important to highlight that different biogeographic hypotheses and ecological questions could led to different distribution predictions based on niche-based potential distribution modeling (i.e. potential distribution, occupied or realized distribution, potentially invaded distribution, effects of climatic change, niche conservatism) (Thuiller et al. 2005; Graham and Hijmans 2006; Martínez-Meyer et al. 2004; Aranda and Lobo 2011; Davies et al. 2011; Peterson et al. 1999; Peterson et al. 2011). Therefore, using inadequate estimations and ignoring other potential factors that may constrain species' distributions, such as dispersal limitation, or biotic interactions and the expert knowledge (Guisan and Thuiller, 2005; Soberón and Peterson, 2005; Graham and Hijmans 2006) could led to inadequate characterization and inferences in biogeography and macroecological analysis. Lower spatial resolutions grid cells than higher spatial resolutions seems to be a valid and powerful approach to account for reliable inference on assemblages richness and composition patterns in macroecological analysis solving the arbitrary species' characterizations (Guisan and Zimmermann 2000; Graham and Hijmans 2006; Aranda and Lobo 2011). Even though the attempt to capture assemblages distributions patterns will provide some differences between approaches derived from expert extent of occurrences and niche-based potential distribution models, this may explain the little differences between booth approaches found herein. The usefulness will depend on the goals for which the characterization is performed and the study goals and contexts.

Since nature is too complex and heterogeneous, and inferences deepens on the particular goals (Guisan and Zimmermann 2000), we highlight the importance of evaluating appropriately the ecological species assemblage patterns either for a given application or particular regions of interest in order to make accurate inferences and assessments on biogeography, ecology or evolutionary history about a certain group of interest.

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7. CAPÍTULO 3. Nicho ecológico y riesgo de extinción en los felinos silvestres de América

7.1. Wild felid range shift due to climatic constraints in the Americas: a bottleneck explanation for extinct felids?

Wild felid range shift due to climatic constraints in the Americas: a bottleneck explanation for extinct felids?

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Abstract

Theoretical and empirical evidence suggests that the ecological niche of species tend to be conservative over evolutionary time in many taxonomic groups, thus representing long-term stable constraints on species geographic distributions. Using an ecological niche modeling approach, we assessed the impact of climatic change on felid species potential range shifts over the last 130 K years in the Americas and the potential of such shifts as an extinction driver. We found a significant range shift for most species (both living and extinct) across their distributions driven by large-scale environmental changes. Proportionally, the most drastic range increase for all species occurred in the Last Glacial Maximum (LGM: 18 K years)-Current transition, while for the Last Inter-Glacial (LIG: 130 K years)-LGM transition occurred an important range reduction, being larger for extinct North American species. In conclusion, the reduction of climatically suitable areas for many species in the transition LIG-LGM may have produced population reductions, which, in turn, may have played an important role in species' extinction throughout the continent.

Keywords: Bottlenecks, Ecological Niche, Felidae, Late Pleistocene, Range shift, Extinction

Introduction

One of the main goals of ecology and biogeography is to understand the spatial patterns and structure of species' assemblages (Brown 1995; Lorenzen et al. 2011; Peterson et al. 2011; Agosta and Bernardo 2013), and recently, the study of species distributions and co-occurrence in the context of their ecological niches has gained a fair amount of attention (Farlow and Pianka 2002; Mikkelson 2005; Raia et al. 2012; Levinsky et al. 2013; Li et al. 2014). So far, most studies have assessed these ecological patterns at local geographical scales and with a limited taxonomic scope; an important question is whether similar processes structure species' distributions at larger scales (e.g., regional and continental). Theoretical studies suggest that at these scales biotic interactions are less perceptible (but not less important) and distributions are largely governed by climatic conditions that define part of their fundamental niches (Davis and Shaw 2001; Martínez-Meyer et al. 2002, 2004; Davies et al. 2009; Soberón and Nakamura 2009; Lomolino et al. 2010; Lorenzen et al. 2011; Peterson et al. 2011).

Recent advances in ecological niche theory allow exploring further the historical distribution patterns of species or lineages, providing an important framework to address diverse paleontological, biogeographical and macroecological questions (Olson et al. 2001; Martínez-Meyer et al. 2004; Peterson et al. 2004, 2011; Arroyo-Cabrales et al. 2010; Morris et al. 2010; Levinsky et al. 2013). Thus, the ecological niche concept has served as a theoretical foundation for explaining species' coexistence and distribution patterns (Mikkelson 2005; Peterson et al. 2011). For instance, the effect (or absence) of certain ecological constraints over time may restrict or allow range shifts (i.e., shrinks or expansions), thus restructuring species' ranges, and therefore influencing the vulnerability to extinction (Palombo et al. 2009; Lomolino et al. 2010; Lorenzen et al. 2011).

The geographic distribution of a species is the response of populations to different factors, from climatic and historical events, to dispersal abilities and biotic interactions (Dundas 1999; Steinitz et al. 2006; Croitor and Brugal 2010; Blois et al. 2013). Ranges can be measured in terms of their size, location, shape, and level of occupancy (Gaston 2003; Davies et al. 2009; Jones et al. 2009); understanding the main drivers of change in such parameters can also shed light in terms of local and global extinctions. Since climate is an important determinant of species' ecological niche and its geographic expression, it can also help to understand extinction processes through range shifts and bottleneck events (Martínez-Meyer et al. 2004; Nogués-Bravo et al. 2008; Davies et al. 2009; Levinsky 2010; Lomolino et al. 2010). Historical patterns of species' geographic responses to climatic variations may indicate how some species have passed through climatic "extinction filters" (Cardillo et al. 2006; Davies et al. 2009; Palombo et al. 2009). In this sense, extinction processes are the result of many interacting factors that affect species differentially, where climate is just one part of the picture (Cione et al. 2003, 2007; Thomas et al. 2004; Araújo et al. 2006; Blois and Hadly 2009). When climate changes, it generates shifts, expansions or reductions on available suitable areas for the species, which in combination with other factors may reduce or increase the probability of extinction (Blois and Hadly 2009; Levinsky et al., 2013). Therefore, expansion and contraction of a species' geographical range is the result and a proxy of population dynamics (Dundas 1999; Graham 2001; Martínez-Meyer et al. 2004; Prevosti et al. 2005; Webb 2006; Nogués-Bravo et al. 2008; Lorenzen et al. 2011).

Felids (family Felidae) are one of the most well-studied mammal groups in terms of evolutionary history (e.g., phylogenetic patterns, Mattern and McLennan 2000; Goswami and Friscia 2010; Nyakatura and Bininda-Emonds 2012; Christiansen 2013); however, extinction processes, both historical and current, are probably some of the least known aspects of felid evolution. Because felids in general play critical roles as predators in ecosystems (both past and present) (Barnett et al. 2005; Goswami and Friscia 2010; Nyakatura and Bininda-Emonds 2012; Christiansen 2013), understanding extinction drivers and their geographic patterns represents an important piece in the historical ecosystem dynamics puzzle. Furthermore, understanding these historical patterns and determinants of felid evolution and extinction, could also inform about current threats to this group, especially when facing the current climate change and other habitat stressors (Millennium Ecosystem Assessment 2005).

Using an ecological niche modeling approach, here we assessed the impact of climatic variations on felid species' potential geographic ranges over the last 130 Kyr in the Americas and the potential of such range shifts as an extinction driver. We specifically analyzed range shifts that occurred in all felid species present in the Americas over the past 130 Kyr (late Pleistocene to current time) by comparing the projected geographic expression of the niche (i.e., species' potential range) at three different time periods, namely Last Interglacial (LIG; ~130 kyr BP), Last Glacial Maximum (LGM; ~18 kyr BP), and Present. Then, we identified the potential bottlenecks that occurred for all species caused by range shifts, and finally, we hypothesized on the possible extinction driving factors for each species.

Materials and methods

Species data

A database containing past (late Pleistocene) and current occurrence records (G+ sensu Peterson et al. 2011) of all living and extinct felid species in the Americas was constructed. We analyzed all felid species based on the assumption that all extant species were also present during the late Pleistocene, and that extinct species disappeared at the end of the Pleistocene-early Holocene (approximately ~12-10Kyr; Webb 2006; Davies et al. 2009). The criteria for selecting the species for our study included taxonomic validity, correct chronological dating and supporting information of their presence during the study period. We determined the list and the taxonomy for living species following Wilson and Reeder (2005), Wilson and Mittermeier (2009), Johnson et al. (1999, 2006), Eizirik et al. (1998), and the IUCN Red List of Threatened Species (version 2015.1). For extinct species, taxonomy was based on the most updated revisions (Berta 1985; Kurtén and Werdelin 1990; Barnett et al. 2005; Cisneros 2005; Cione et al. 2007; Soibelzon and Prevosti 2007; Arroyo-Cabrales et al. 2010; Ferrusquía-Villafranca et al. 2010).

We obtained occurrence records through a detailed revision of scientific literature and museum specimens from biological collections (i.e., American Museum of Natural History [AMNH], Field Museum of Natural History [FMNH], National Museum of Natural History Smithsonian Institution [NMNH]; Instituto Alexander von Humboldt [IAvH]; Instituto de Ciencias Naturales [ICN]; Colección Teriológica Universidad de Antioquia [CTUA]; Colección Nacional de Mamíferos del Instituto de Biología-UNAM [IBUNAM], Mammal Networked Information System, Global Biodiversity Information Facility, FAUNMAP, and Paleobiology Database portal). Literature review was carried out online (i.e., ISI web of science and Google scholar) through key words (i.e., Pleistocene, Carnivora, Felidae, and specific names) and included published and unpublished documents, including thesis, articles, books and technical reports where species were recorded, and where detailed information of records was provided. We only used those records that contained reliable taxonomic information, source/collector, identification validity, and geographical coordinates and/or detailed information on locality that were later manually georeferenced.

Climatic data

We defined our study area as the entire American continent (M sensu Peterson et al. 2011), because all historical and ecological processes of colonization and dispersal of the species of interest occurred in the continent (after the Great American Biotic Interchange; GABI), and all studied species, both extant and extinct, are native to the American continent. Based on the available global scale past climatic scenarios and current bioclimatic variables, we specifically used 18 bioclimatic layers that represent averages for three periods drawn from the General Circulation Model of the Community Climate System Model-CCSM version 4: 1) Last Inter-Glacial (LIG, ~140-120 Kyrs BP; Otto-Bliesner et al. 2006), 2) Last Glacial Maximum (LGM, ~20-16 kyrs BP [representing ~21 Kyr BP in astronomical years]; Farrera et al. 1999; Braconnot et al. 2007) and 3) Current (C, ~1950-2000 period representing current conditions; Hijmans et al. 2005; http://worldclim.org/current) (for bioclimatic details and description see http://www.worldclim.org/bioclim). All layers were resampled to a 0.08333° resolution (approximately 10 x 10 km). We consider that these variables at this time scale studied herein have biological relevance for the species being modeled, as they represent annual, seasonal, and extreme climatic trends, which have proven limiting environmental factors for many species from different taxa, including felids (Tôrres et al. 2012).

Ecological niche modeling (ENM) and range estimation

Numerous methods are available for developing ENM, and they have been compared extensively (e.g., Austin et al. 2006; Tsoar et al. 2007; Elith and Graham 2009; Elith et al. 2011; Peterson et al. 2011). Thus, as our objective was not focused on model comparison, we opted for one modeling method. We generated niche-based potential distribution models using a maximum entropy approach (MaxEnt 3.3.3K; Phillips et al. 2006; Phillips and Dudík 2008), because this algorithm generally has shown good performance, and is robust with small sample sizes (Elith et al. 2011; Peterson et al. 2011; Santika 2011; Muscarella et al 2014). Ecological niche modeling with MaxEnt estimates the probability of presence of the species across the landscape by contrasting the ecological conditions where the species has been recorded, against a sample of background pixels across the study area via a Bayesian procedure of model fitting under the maximum entropy principle (Phillips and Dudík 2008). Detailed explanations of MaxEnt can be found elsewhere (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011; Merow et al. 2013). The map produced during the niche modeling procedure is frequently interpreted as the potential distribution of the species (Gp, sensu Peterson et al. 2011), i.e., the areas where ecological conditions are suitable for the establishment of the species.

We built 100 replicate models using a bootstrap method with 500 iterations per replicate for each species using a random 70:30 split of the total number of occurrence records (G+) for calibration and validation, respectively. During this procedure if more than one record was found in each of the 10 x 10 km pixel, duplicate records were removed. MaxEnt has an internal procedure of variable evaluation and selection that balances between overfitting and model generality. Also in MaxEnt, we selected the option of running a jackknife test to identify the informative variables. To generate range models of living species for the Inter- and Maximum Glacial periods, we first generated models using the current presence records on the current bioclimatic layers; then, these niche models were retrojected onto the past climatic layers and validated the resulting map with the fossil records of each species (Martínez-Meyer et al. 2004). For extinct species, we generated the models using the fossil records from all periods over the Inter-Glacial climatic dataset (assuming that the species was present since this period), and then we projected the niche model onto the Last Glacial Maximum and Current climatic layers. To test for model discriminatory ability and performance we used the AUCTest (Area under the ROC Curve based on the validation data) implemented in MaxEnt (Phillips et al. 2006). Despite that AUC has been criticized as a method for evaluating model quality (Lobo et al. 2008,), we still considered the AUCtest as a useful measure for ordinal score models in agreement with previous works (McPherson 2004; Thuiller et al. 2005; Elith et al. 2011; Marino et al. 2011; Santika 2011; Muscarella et al. 2014). Statistical significance of models was evaluated with a binomial test, which determines whether the model differs from null expectations (Peterson et al. 2011). More detail explanations on ecological niche modeling and MaxEnt methodology can be found elsewhere (i.e., Phillips et al. 2006; Phillips and Dudík 2008; Soberón and Nakamura 2009; Peterson et al., 2011; Elith et al. 2011; Merow et al. 2013; Muscarella et al. 2014).

MaxEnt output probability maps –which represent the potential distribution of species– were converted into binary maps based on the probability threshold value that minimized both the training and testing omission error (< 5%) and the fractional predicted area to avoid under- and over-prediction, and with a statistical significance evaluated with a binomial test ($p < 0.05$) (Peterson et al. 2011). Afterwards, for each species we calculated the extent of the potential distribution area (km^2) and estimated a range change proportion (the most recent range divided by ancient range minus 1) for each pair of periods (LIG-LGM, LGM-C).

For a more clear presentation, species distributed only in North America are considered as Nearctic species, South American species as Neotropical, and species with both distributions as Continental. All geographic analyses were performed on a Geographic Information System using ArcGIS 9.3 software (ESRI 2009) and all mean values are presented followed by standard deviations (±SD) unless otherwise stated.

Results

We obtained a total of 7835 records of wild felids species across the continent with *Lynx rufus* (2466) and *Leopardus guigna* (24) the species with the highest and lowest number of current records, respectively, and *Puma concolor* (41) and *Smilodon fatalis* (21) the species with the highest and *Miracinonyx trumani* (4) and *Leopardus guigna* and *L. jacobitus* (0) the lowest number of fossil records (Table 1).

According to the jackknife analysis, the most important variables common to all species were: mean precipitation, precipitation of the warmest quarter, mean temperature, isothermality (ratio of average diurnal range with respect to the average annual range), temperature seasonality, mean temperature of the coldest and the wettest quarter, minimum temperature of the coldest month, and maximum temperature of the warmest month.

In terms of model performance, AUC_{Test} values for all species were all above 0.81, indicating a good performance and model discrimination ability (Table 1). Regarding model validation, all species' models were statistically significant ($p < 0.05$) according to the binomial test, except for the past range models of *Leopardus guigna* and *L. jacobitus* for which no fossil records were found, thus no validation test could be carried out.

Table 1. Number of current and fossil records for extant and extinct (†) felid species during the last 130,000 years. Area Under the ROC Curve values of validation data (AUC_{Test}) and standard deviation (SD) for ecological niche models. Ho: Holocene; LGM: Last Glacial Maximum; LIG: Last Inter-Glacial, and E: Entire period.

			Pleistocene Periods					
Species	**Common name**	**Current**	**Ho**	**LGM**	**LIG**	**E**	**Total**	**AUC_{Test} ± SD**
Smilodon populator †	Sabre-tooth Cat	0	0	9	3	3	15	0.95 ± 0.016
Smilodon fatalis †	Sabre-tooth Cat	0	0	6	1	14	21	0.89 ± 0.0386
Panthera atrox †	North American Lion	0	0	6	2	9	17	0.87 ± 0.0568
Miracinonyx trumani	American Cheetah	0	0	2	0	2	4	0.84 ± 0.035
Homotherium serum †	Scimitar Cat	0	0	0	1	4	5	0.81 ± 0.0051
Leopardus colocolo	Pampas Cat	28	0	1	2	1	4	0.94 ± 0.0208
Leopardus geoffroyi	Geoffroy's Cat	113	0	0	1	0	1	0.97 ± 0.0053
Leopardus guigna	Kod kod	24	0	0	0	0	0	0.99 ± 0.0019
Leopardus jacobitus	Andean Cat	42	0	0	0	0	0	0.99 ± 0.0016
Leopardus pardalis	Ocelot	857	5	1	0	3	9	0.92 ± 0.0065
Leopardus tigrinus	Oncilla	112	0	1	0	0	1	0.96 ± 0.02
Leopardus wiedii	Margay	267	1	1	1	2	5	0.95 ± 0.0075
Lynx canadensis	Canadian Lynx	428	0	0	2	1	3	0.95 ± 0.0064
Lynx rufus	Bobcat	2466	2	10	1	19	32	0.89 ± 0.0044
Panthera onca	Jaguar	923	6	12	3	10	31	0.90 ± 0.0061
Puma concolor	Mountain Lion	2265	9	13	3	16	41	0.89 ± 0.0079
Puma yagouaroundi	Jaguarundi	310	3	1	1	3	8	0.94 ± 0.0112
Total		**7835**	**26**	**63**	**21**	**87**	**197**	

We found significant range shifts (i.e., expansions or contractions) for most species, both living and extinct, across their distributions. The most drastic potential range proportional reductions occurred during the LIG-LGM transition, when all five extinct species and five living species suffered important potential range reductions (Table 2). This range shrinking occurred mainly for Nearctic species, with a mean proportional reduction across all species of 0.80 ± 0.15, whereas it was considerably lower for South American species, where only the extinct *Smilodon populator* suffered a small range proportional contraction of 0.018. Continental species suffered a mean proportional reduction of 0.14 ± 0.07 (LIG-LGM transition) but only for three species (*Panthera onca*, *Leopardus wiedii*, and *L. pardalis;* Table 2). Interestingly all the *Leopardus* species endemic to South America, increased their ranges in the same period, as well as two continental species (*Puma yagouarundi* and *Leopardus tigrinus*; Table 2, Fig. 1). For the LGM-C transition, some Nearctic species showed a tendency to expand their potential ranges (i.e., *Lynx canadensis* and *L. rufus*), but most species' ranges shrank with a decreasing net proportion of 0.70 ± 0.29 (LIG-C) (Table 2). For Neotropical and Continental species, no consistent pattern was observed as some species increased and others decreased their ranges. Throughout the whole period (LIG-C), the decreasing net proportion in South America was 0.20 ± 0.13 while the increase net proportion was 0.89 ± 0.93 (Table 2, Fig. 1).

Table 2. Potential geographic range size (km^2) of extant and extinct (*†*) felid species in the Americas at three different times: Last Interglacial (LIG), Last Glacial Maximum (LGM) and Current (C), and proportional range size change (Δ) during transitions. Current ranges for extinct species represent niche model projections from the past to the present.

Realm	Species	LIG	LGM	C	Δ LIG-LGM	Δ LGM-C
Nearctic	*M. trumani†*	7,269,614	145,418	21,889	-0.980	-0.849
	H. serum †	10,639,525	1,059,593	2,491,064	-0.900	1.351
	P. atrox †	6,729,375	1,512,929	1,262,226	-0.775	-0.166
	S. fatalis †	8,246,544	1,634,062	2,123,834	-0.802	0.300
	L. rufus	4,461,357	2,118,412	9,461,937	-0.525	3.467
	L. canadensis	11,322,515	2,231,341	8,847,198	-0.803	2.965
Continental	*L. wiedii*	13,767,496	10,623,909	13,179,571	-0.228	0.241
	L. tigrinus	7,510,790	10,927,447	4,416,770	0.455	-0.596
	P. yagouaroundi	13,777,666	13,805,377	15,350,759	0.002	0.112
	P. onca	18,744,503	16,573,486	14,916,510	-0.116	-0.100
	L. pardalis	19,611,895	18,063,411	17,405,046	-0.079	-0.036
	P. concolor	20,986,881	22,673,977	27,766,007	0.080	0.225
Neotropical	*L. guigna*	180,194	434,173	401,039	1.409	-0.076
	L. jacobitus	256,969	947,589	870,589	2.688	-0.081
	L. geoffroyi	2,803,520	3,522,452	3,983,932	0.256	0.131
	S. populator †	8,441,875	8,287,044	6,068,173	-0.018	-0.268
	L. colocolo	7,889,437	8,644,521	6,671,297	0.096	-0.228

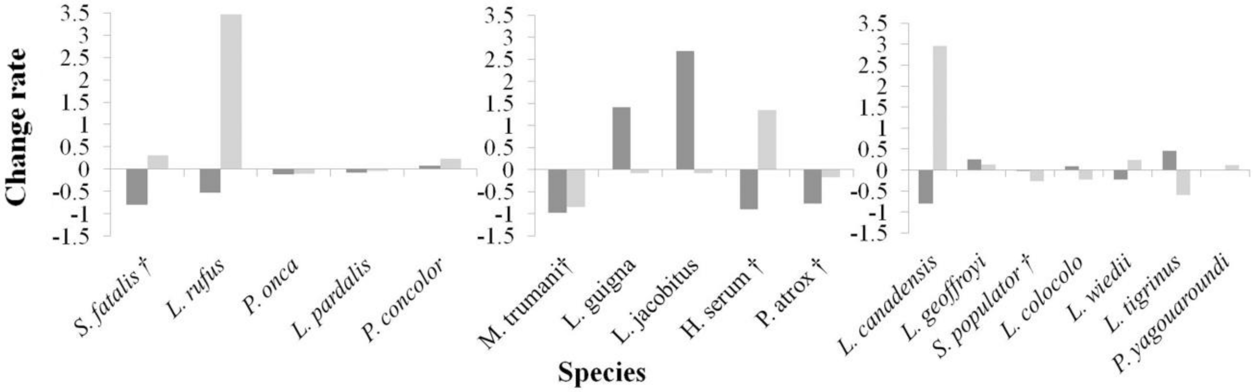

Figure. 1 Extant and extinct (*†*) felid species geographic range change rate in the Americas during the Last Interglacial-Last Glacial Maximum (LIG-LGM, dark gray) and Last Glacial Maximum-Current (LGM-C, light gray) transitions.

Range reduction and shifts were more drastic for extinct North American species (*Smilodon fatalis*, *Homotherium serum, Miracynonyx trumani*, and *Panthera atrox*) than for living species, mostly reducing their ranges towards western and southern North America and to small isolated patches of suitable climatic conditions from LIG to LGM (Fig. 2a-d). Interestingly, all species but *M. trumani* showed a regain of suitable areas (hypothetical areas) in the LGM-C transition (Fig. 2). On the other hand, *Smilodon populator* in South America also showed a significant range contraction and shift, with a more patchy potential distribution from LIG to LGM, but with the most significant and continuous distribution patches mainly to the east of the Andes, which continued until the Holocene-C transition (Fig. 2e).

[Figure 2]

Living species, with the exception of *Lynx canadensis* and *L. rufus*, and all species not in the *Leopardus* group (i.e., *Puma concolor, P. yagouaroundi*, and *Panthera onca*), showed no drastic changes in their distribution and suitable climatic areas during the LIG-LGM-C transition, but only with a small constriction from high latitudes towards the tropics (Figs. 3 c, d, e). *Panthera onca* was found at higher latitudes during the LIG and LGM, coincident with fossil subspecies (*P. onca augusta* from North America and *P. onca mesembrina* from South America). Conversely, both species of the *Lyn*x genus did suffer drastic range reductions during the LIG-LGM transition, but both species increased their ranges considerably for the LGM-C transition (Fig. 3 a, b).

For the *Leopardus* species, significant changes occurred for *L. jacobitus, L. guigna*, and *L. geoffroyi*, increasing their ranges over the LIG-LGM (Fig. 4c, e, f). Interestingly, *L. pardalis* reduced its range especially towards the northern limits of its distribution, while *L. wiedii* did not change significantly in any period (Fig. 4a, g). *Leopardus tigrinus* changed significantly for the LIG-LGM period, increasing 45.5% its range, but decreased its range considerably (59.6%) for the LIG-C period (Fig. 4b).

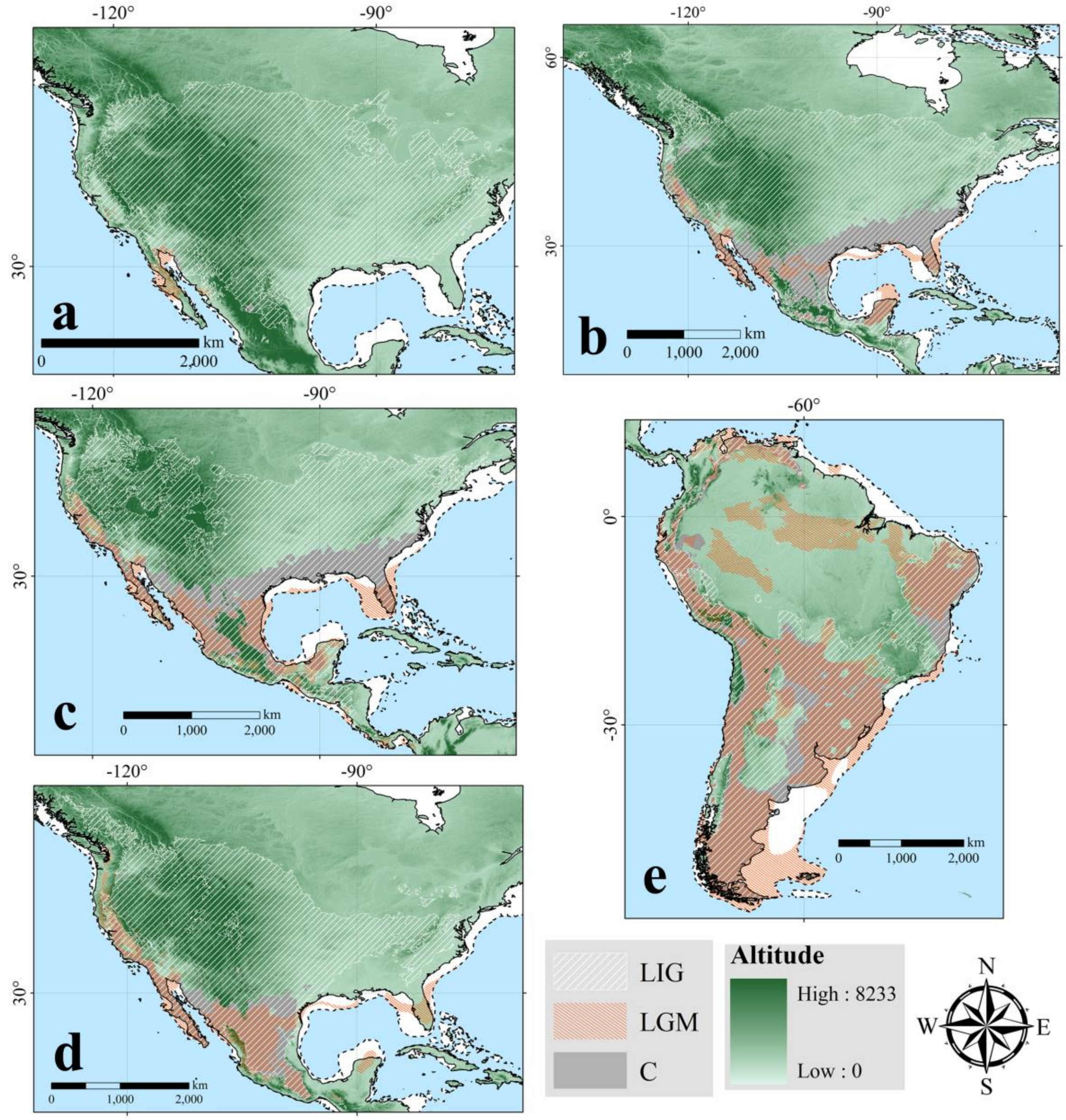

Figure. 2 Extinct (†) species geographic ranges in the Americas at three different times for **a**. *Miracinonyx trumani*, **b.** *Homotherium serum*, **c.** *Smilodon fatalis*, **d**. *Panthera atrox*, and **e.** *Smilodon populator.* Black continuous lines indicate continental limits for LIG and Current, and black dashed lines indicate continental limits for LGM.

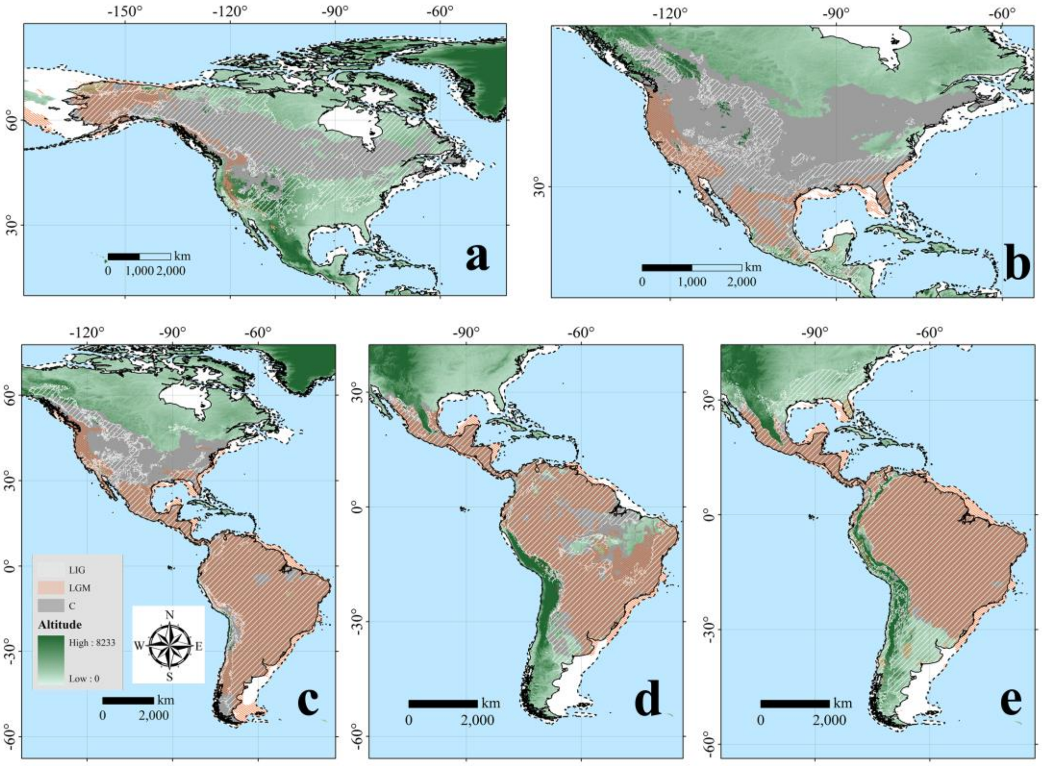

Figure 3. Extant *Lynx*, *Puma*, and *Panthera* species geographic ranges in the Americas at three different times. **a**. *Lynx canadensis*, **b.** *Lynx rufus*, **c.** *Puma concolor*, **d**. *Puma yagouaroundi*, and **e.** *Panthera onca.* Black continuous lines indicate continental limits for LIG and Current, and black dashed lines indicate continental limits for LGM.

Discussion

In recent years, the biogeographic history and phylogenetic relationships of felids have received increased attention (Mattern and McLennan 2000; Johnson et al. 2006; Goswami and Friscia 2010; Christiansen 2013). The Felidae was one of the most successful groups during the Great American Biotic Interchange (GABI) (Webb 2006; Johnson et al. 2006; Prevosti 2006; Prevosti et al. 2011; Bacon et al 2015), when numerous independent diversification and migration events occurred in both directions (Johnson et al. 2006; Prevosti 2006; Cione et al. 2007; Prevosti and Soibelzon 2012). Evidence on these events reveals a more complex biogeographic history of the American felids than previously thought (Prevosti 2006; Soibelzon and Prevosti 2007).

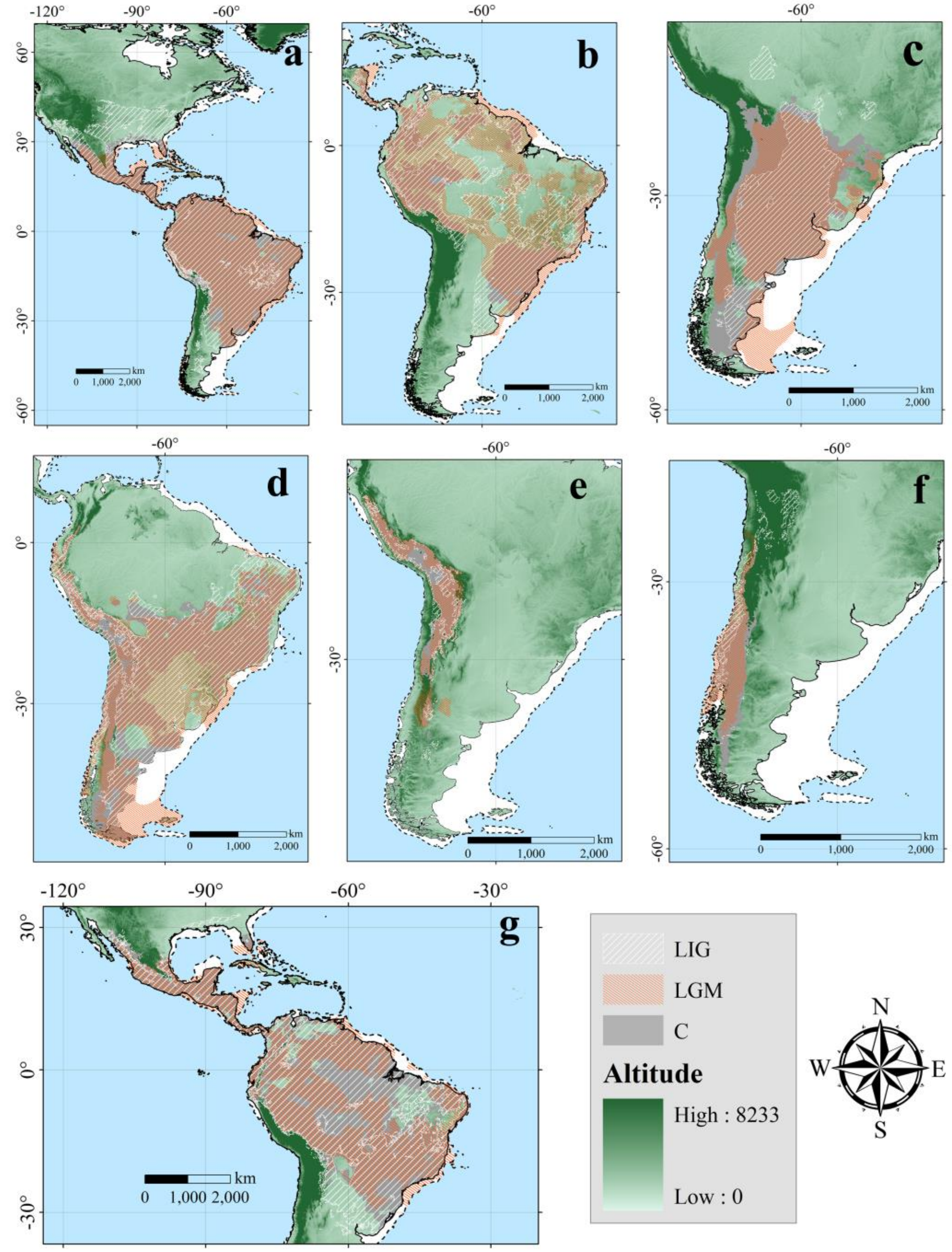

Figure. 4 Extant *Leopardus* group geographic ranges in the Americas at three different times. **a**. *Leopardus pardalis*, **b.** *L. tigrinus*, **c.** *L. geoffroyi*, **d**. *L. colocolo,* **e.** *L. jacobitus,* **f.** *L. guigna,* and ***g.*** *L. wiedii.* Black continuous lines indicate continental limits for LIG and Current, and black dashed lines indicate continental limits for LGM

According to our results, all extinct felids suffered a drastic contraction of suitable areas during the LIG-LGM transition across the continent, followed by a slight recovery during the LIG-C period. These reductions were significantly larger for the North American species than for the tropical ones, which lost most of the temperate portion of their suitable areas but maintained their tropical ranges. Interestingly, both *Lynx* species suffered drastic reductions, but unlike the large felids, they did not go extinct, the same as the species with tropical distributions. A word of caution is pertinent here. It is important to interpret these results under the reaches of data and the methodological approach. Fossil records are always limited by local conditions, taphonomy, thus sample size is generally small and spatial, and temporal distribution may be biased (Nogués-Bravo et al. 2008). The number of occurrence records is a key element in model calibration and performance (Peterson et al. 2011), thus, models for species with few records may not be as robust as models for species with plenty of occurrences. As well, climatic reconstructions of the Plesitocene are the average climatic conditions over a few thousand years, which inevitably present some unevaluated uncertainty. This is the reason why our analyses are not intended to present fine temporal or spatial resolution results, but general trends of responses of the species analyzed.

The majority of wild felids hold similar social systems where males and females are solitary and maintain intra-sexual non or little-overlapping home ranges, thus contraction of suitable areas necessarily brings population reductions. If this tendency continues chronically, extinction risk increases due to demographic bottlenecks, which become exacerbated if other stressors operate in the remaining ranges (Dundas 1999; Graham 2001; Webb 2006; Nogués-Bravo et al. 2008; Canto et al. 2010; Lorenzen et al. 2011; Davies et al. 2011; Agosta and Bernardo 2013). Large species are known to be more susceptible to geographic range reduction given their biological characteristics and area requirements, such as low population size, low reproductive rates, and large home ranges (Sunquist and Sunquist 2002). Therefore, these species are inherently more vulnerable to energetic constraint and range size reductions, the reason why most large species need to hold large distribution ranges in order to maintain viable populations to persist and to avoid bottlenecks events and extinction (Lessa and Fariña 1996; Purvis et al. 2000; Cione et al. 2003; Canto et al. 2010; Lorenzen et al. 2011; O'Regan et al. 2002; Agosta and Bernardo 2013; Levinsky et al. 2013). In our analyses, the largest species, such as the machairodontines (e.g., *Smilodon fatalis, Homotherium serum*) and pantherines (e.g., *Panthera athorx*), showed drastic reductions of their suitable areas (Table 2), thus were more susceptible to bottleneck processes. For instance, *Homotherium* and *Meganteron* in equatorial Africa and *Homotherium* in Europe became extinct at the middle of the Pleistocene, all apparently from suitable areas loss due to climatic constraints, whereas more ecologically tolerant, stable-range and smaller species, such as *Panthera leo*, *P. pardus, Lynx lynx,* and *L. pardinus,* survived these climatic changes (Croitor and Brugal 2010).

Range size has been previously related with climatic variability, where more stable ranges are the response to less variable climates (Davies et al. 2011). When climatic changes occur, it is likely that species' ranges change, either increasing, reducing, or shifting. Glacial-interglacial cycles during the Pleistocene certainly had profound consequences at the species ranges' level and dispersal patterns, particularly beyond the tropics. For instance, during the LGM most of North America was under ice; therefore temperate species responded accordingly restricting their distribution to the limited suitable areas in northwestern North America (Dyke 2005), as we also observed in our analyses of Neartic species (Fig. 3). Even though these climatic constraints were much less dramatic in the tropical regions, equatorial biomes also experienced great shifts (Davies et al. 2011), which likely impacted felids' biogeography. Interestingly, species with both temperate and tropical distributions were less affected by climatic changes and show relatively low variations along the whole study period. Species like the jaguar (*Panthera onca*) (e.g., *P. onca augusta* from North America and *P. onca mesembrina* from South America) and even the currently widely distributed puma (*P. concolor*) likely lost their higher latitudes populations but maintained the tropical ones (Culver et al. 2000); while tropical and subtropical species, such as the pampas cat (*Leopardus colocolo*), did not exhibit any significant range reduction or demographic bottlenecks during our study period as it has been suggested (Napolitano et al. 2008).

Here, we provide new clues on the history and spatial patterns of American felids for the last 130 Kyr. Our results suggest that climatic changes may have reduced suitable areas for several species, for which the largest ones suffered population reductions that may have played an important role in their extinction. Environmental filtering is likely a key factor that played a critical role in the extinction context, increasing the susceptibility of remaining populations, especially if other stressors were operating synergistically, such as habitat and prey loss (which could suffered the same climatic constraints), and human pressure (human migration and its effects was not uniform throughout the Americas) (Cione et al. 2003; De Vivo and Carmignotto 2004; Bofarull et al. 2008; Borrero 2008; Cione et al. 2009; Barnosky and Lindsey 2010; Croitor and Brugal 2010). In contrast, persistence in the face of environmental changes occurred for those species for which less drastic climatic alterations occurred across important portions of their geographic ranges (Cardillo et al. 2006; Palombo et al. 2008; Davies et al. 2009; Agosta and Bernardo 2013). These results have implications for extant species under current quick environmental change. Currently, habitat loss and fragmentation, poaching and climate change are the major threats for most felids in the Americas. Therefore, the two largest species –the jaguar (*Panthera onca*) and the puma (*Puma concolor*)– with extensive area requirements, also species under unstable, rapidly changing climates, such as *Lynx canadensis*, and those with small geographic ranges, as the Andean cats *Leopardus jacobita* and *L. guigna*-, are probably the most vulnerable to the current process of environmental change. It is important to learn the lessons from the past if we want to make the right decisions for the future.

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8. CAPÍTULO 4. El papel del nicho funcional en la estructuración de los ensamblajes de carnívoros y su simpatría a escalas geográficas locales

8.1. The role of morphological characteristics in structuring ecological assemblages: past to present coexistence of carnivorans (Mammalia: Carnivora) in the Americas

(Artículo será sometido a American Naturalist)

The role of morphological characteristics in structuring ecological assemblages: past to present coexistence of carnivorans (Mammalia: Carnivora) in the Americas

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Abstract

Mammalian Carnivoran are one of the most well-studied mammal groups in terms of evolutionary history and biogeographic patterns and is appropriated to understand the effects of species interaction (e.g. competition) in shaping assemblages, although the mechanisms that determinate species coexistence through time and space remain unknown. Here we use a macro-ecological and comparative ecological approach for assessing the influence of carnivoran ecological characteristics in structuring assemblages in the Americas at the Last Interglacial, Last Glacial Maximum and the Present time. Our analysis shows that the size ratio between species is likely involved as one of the main potential mechanism that limits the carnivoran species coexisting within assemblages and it tends to be conservative not only through different ecological trait groups but also through time and spaces in the Americas and this characteristic behaves like an economic system. This measure of functional diversity among species can be considered as a direct measure of species coexistence, as carnivoran species occupying the same geographic space tend to display differences in the ecological trait space, suggesting a functional niche filtering driven mainly by a size ratio relation from local to regional scales. The underlining Functional Diversity patterns exhibit low redundancy towards the tropics and the poles during the times evaluated. However, during the Last Glacial Maximum shifts occurred primarily in North America due to the climatic constraints causing local extinction of the hyper-size carnivoran species and large carnivoran populations at high latitudes, reducing the amount of Functional Diversity and affecting the size ratio distribution. Hence, functional niche constraints are in part the main reason of taxa co-occurrences and display an important role in structuring carnivoran assemblages through space and time in the Americas.

Key words: Size ratio, coexistence mechanism, Functional Niche, Glacial periods

Introduction

Quantifying and understanding species distributions and how they are spatially structured in assemblages as well as describing the main drivers of those structures are fundamental goals in macroecology and biogeography (Brown et al. 1995; Broennimann et al. 2012; Ferraz et al. 2012; Agosta and Bernardo 2013; Wisz et al. 2013; Godsoe et al. 2015). The structures of assemblages has been associated to ecological rules as climatic conditions, species dispersal abilities, historical events or biotic interactions acting at different scales (Steinitz et al., 2006; Davies et al 2009; Blois et al., 2013, 2014; Godsoe et al. 2015), although most studies have considered either climatic or environmental niche as the principal driver at large scale (Nogués-Bravo et al. 2008; Lorenzen et al. 2011; Blois et al. 2013; Martínez-Meyer et al. 2004; Soberón and Nakamura 2009; Lorenzen et al. 2011; Peterson et al. 2011). Understand how structure of assemblages is influenced by ecological characteristics or by the functional niche (Elton 1927) remain challenging (Linnell and Strand 2000; Pulliam 2000; Donaido and Buskirk 2006; Hunter and Caro 2008; Soberon 2010; Wisz et al 2013; Pellissier et al. 2013; Godsoe et al. 2015; Thuiller et al. 2015; Collins et al. 2011; Gotelli and Ulrich 2012; Blois et al. 2014; Woodward and Hildrew

2012; Oliveira and Pereira 2013; Blois et al. 2014) and requires approaches that allow the inclusion of interspecific interactions as an important part of biodiversity architecture and maintenance (Bascompte & Jordano, 2007).Therefore, providing insights into assemblages and meta-community structure such as species coexistence, richness and functional diversity (Thuiller et al. 2015). Elucidating elements that affect species coexistence is not straightforward and are not restricted to climatic factors. Actually, it is important to differentiate the influence of the different dimension of the species niche (Blois et al. 2014; Giarla & Jansa 2015; Martínez-meyer et al. 2004; Peterson et al. 2011), allowing to disentangle the combined effects of abiotic and biotic factors on assemblages dynamics and coexistence at different scales and times (Davis & Shaw 2001; Bofarull et al. 2008; Martínez-Meyer et al. 2004; Broennimann et al. 2012; Thuiller et al. 2015).

Traditional niche theory suggests that at local scales assemblages are structured primarily through the effect of the functional niche (mainly through trophic and reproductive habits), suggesting that only the differentiated species could coexist (Elton 1927; Huntchinson 1978; Mikkelson 2005; Steinitz et al. 2006; Peterson et al. 2011; Blois et al. 2013; Villalobos & Arita 2014). Thus, species that occupy the same geographic space should display non-similar ecological traits. Consequently, there must be a mechanism that limits the number of similar species that could coexist within assemblages (could be interpreted as an assemblages saturation) as a result of functional filtering associated with ecological traits that can be associated to attributes as body size, guild, activity patterns and habit (Hutchinson 1959, 1978; Brown & Nicoletto 1991; Farlow & Pianka 2003; Linnell & Strand 2000; Donaido & Buskirk 2006; Hunter & Caro 2008; Woodward & Hildrew 2012; Oliveira & Pereira 2013).

The order Carnivora has a high taxonomic diversity, a well-resolved phylogeny (Goswami & Friscia, 2010; Nyakatura & Bininda-Emonds, 2012) and share many ecological attributes that may predispose them to different forms of interspecific interaction (Farlow & Pianka 2003, Hunter & Caro 2008, Oliveira & Pereira 2013, Zimicz 2014). This is an excellent group for assessing questions of biogeography, evolutionary and ecological niche significance. This way, we used a macro-ecological and comparative ecological approach to evaluate the influence of carnivoran ecological characteristics in the structuring of assemblages over the last 130 K years in Americas. We hypothesize that carnivoran species present in replicated assemblages should exhibit great differences in the ecological trait-space (e.g. body size, as proxy of functional niches) in order to coexist and therefore show a high functional diversity patterns, thus being a mechanism for coexistence. Understanding how assemblages are structured and the mechanisms involved would improve our knowledge about carnivoran macro-ecological history and should also serve for conservation priorities of this group.

Methods

We generated first a macroecological approach with carnivoran distribution in the Americas in order to implement a comparative ecological analysis for assessing the influence of carnivoran ecological characteristics in structuring assemblages and their underlying functional diversity patterns (FD), as a proxy of the functional niche or trait space dimension. The idea was to find out whether in replicated assemblages a potential mechanisms would be involved in structuring the species coexistence through time and space. In this sense, several questions arise as how species with different or similar body size coexist within assemblages? How is the spatial functional diversity pattern across space and time? Are these structures conserved in time and space?.

Species geographical distributions were produced using a niche-based potential distribution models describe in Arias-Alzate et al. (2016). The models were produced to almost all continental carnivoran species (~88 spp.) based on the assumption that all extant species were also present during the late Pleistocene, and the extinct species disappeared at the end of the Pleistocene-early Holocene epochs, approximately 10-12Kyr (Webb 2006; Davies et al. 2009).

The criteria for selecting the species for our study included taxonomic validity, proper chronological dating and supporting information on the species presence during the study period. We determined the list and the taxonomy of living species by following Wilson and Reeder (2005), Wilson and Mittermeier (2009), and IUCN Red List of Threatened Species (version 2015.1). For extinct species the taxonomy was based on the fossil record and following Berta (1985), Barnett et al. (2005), Cisneros (2005), Cione et al. (2007), Soibelzon and Prevosti (2007), Arroyo-Cabrales et al. (2010) and Ferrusquía-Villafranca et al. (2010). For 8 carnivoran species no potential distribution models were used due to lack of rage models (*Mustela africana*, *Cuon alpinus*† [extinct in North America], *Speothos pacivorus*† and *Enhydra macrodonta*†), ranges restricted to islands (*Urocyon litoralis* and *Procyon pygmea*, which have been separated recently from two continental species that remained isolated after the last glacial maximum) and described as new species (*Nasuella meridensis* from *Nasuella olivacea* and *Leopardus gutullus* from *Leopardus trigrinus*).

In order to assess the influence of ecological characteristics in structuring carnivoran assemblages and the underlying functional diversity patterns (FD) we used six ecological traits: body size, dietary pattern, habit, activity pattern and social pattern (S1) that have been identified as drivers of ecosystem function and have proved useful in previous studies of functional diversity in mammals (Flynn et al 2009; Dalerum 2013; Fergnani & Ruggiero 2015; González-Maya & Ceballos 2015). Data come mainly from previously published works (Paleobiology Database, www.pbdb.org; Jones et al. 2009; González-Maya & Ceballos 2015).

Assemblages Structure

To estimate the assemblages we generated a grid with 159111 cells of 0.56 x 0.56 degrees (about 50 x 50 km) over the continent for three periods: Last inter Glacial (LIG), Last Glacial Maximum (LGM) and Current time (C). The size of the grid prevents generating false coexisting species due to grain size effects. Using an overlapping count analysis with the grids and the species potential geografical distribution we built for each period a species per space matrix indicating the occurrence of species in the cells. We assume that the co-occurrence of species in space defines direct or indirect interactions among species and is a proxy of the species assemblage present in each cell at time t. Afterwards, we join the species-ecological trait matrix with the species-space matrix in order to build a species-species matrix in which cells reflected the interaction quantity in which a pair of species was predicted together. The species-species matrix or the co-occurrence matrix was found by multiplying the species-space matrix by its transpose. In this way, the co-occurrence matrix A_{ij}^{t} represents the species coexistence in a time t, where i and j identify two different species.

Thereafter, for identifying the potential mechanism involved in structuring carnivoran co-occurrence, we implement a body size structure analysis which included a paired comparisons and analysis of weight distribution of all combination of i and j species in the matrix in terms of the Size Ratio (S_R) and its distribution probability for each cells $P(S_R)$. This could be interpreted as a body sizes spatial clustering effect mechanism. This Size Ratio was evaluated as $S_R = (SBS_i / BBS_j)$, where SBS_i represent the smaller size species and the BBS_j represent the bigger one. We estimated the all S_R assemblage distribution in space and on each time. These S_R distributions were also estimated for sympatric species within the same ecological trait group. Afterwards, these S_R distributions were then fixed as their complementary cumulative distribution (CCD) and were fitted with an exponential decay distribution as a way to obtain a better fitting, to reduce information loses and to observe the structuring pattern of the system (Newman, 2010). Is important to note, that as the body mass could vary throughout the species range but due to lack of particular information for many species and for more adequate analysis we used the mean size estimation as representing the body mass over the whole range of the species.

In order to establish whether S_R estimations are the result of species interactions rather than a random expectation we develop a null model contrasting analysis of 10,000 iterations with the Monte Carlo test following North et al (2002). In this analysis, the species identity was fixed and their links were randomized conserving the amount of interactions. It implies that in this model species size is conserved but their presence in space is randomized. For each iteration the empirical S_R was compared to the null models results. Likewise, in order to establish whether S_R estimations are not the result of methodological artifact, we perform an *a priori* model comparison as the simplest possible scenario (full species coexistence in all cells without spatial assemblages structuring pattern). This *a priori* analysis also allow us to validate the body sizes spatial clustering effect and the natural tendency of the observed S_R probability distribution. Since these two tests showed similar results, we chose to include only the *a priori* analysis as a more complete way to indicate the results.

Functional Diversity (FD) patterns

After estimating the interaction patterns between species, we mapped geographically the functional diversity of the carnivoran assemblages across space and time using a mean functional diversity index. We based our analyses on the functional diversity definition, which is the amount of functional niche trait space filled by the species in the assemblages or community (Mason et al 2005). This measure indicates spatially how different or similar among ecological trait-space (functional niche) the carnivoran species within the assemblages are and if these pattern is conservative across time and space. We generated a mean Functional Diversity (FD) index by each cell in the grid and for each time in Americas following Fergnani and Ruggiero (2015) and González-Maya & Ceballos (2015). We selected this metric since it does not depend on abundance data, performs adequately with multiple traits (Mason et al 2012) and as it is independent of the number of co-occurring species (species richness) per assemblages it can be used to compare FD values across grid cells (Fergnani and Ruggiero 2015).

Since assemblages necessarily involve co-occurrence, this index indicates the ecological dissimilarity between pairs of co-occurring interacting species (Podani and Schmera 2006; Fergnani and Ruggiero 2015). Thus, the index, which goes from 0 to 1, will show high similarity (values closer to 0) or high dissimilarity (values closer to 1) in the species ecological attributes and therefore reflect assemblages functional diversity patterns as a proxy of the influences of the functional niche in structuring assemblages across space and time.

All analyses and statistical tests (using the spatial statistics tools, considered significant at 95%, $p < 0.05$) were performed on a Geographic Information System using ArcGIS 9.3 software (ESRI 2009), R 3.0.3 (R core Team, 2015) with the package FD (Laliberté, Legendre and Shipley, 2014).

Results

Assemblage structure

We found a consistency of body size distributions trend across time and space for carnivoran co-occurrence patterns. Complementary cumulative probability distributions of S_R follow an exponential decaying distribution showing that within carnivores assemblages are more likely to find sympatric species showing small S_R values (large size differences) (Figure 1). Moreover, the distributions show a conservative quantity or a scale parameter that describe the system. It indicates that within the assemblages are more probable to find carnivoran species showing large size differences in order to coexist. If the S_R increases in magnitude the probability to find similar size species co-occurring decreases monotonically according to the scale.

This trend was evidenced in all the times evaluated LIG (R^2=0.971), LGM (R^2=0.976), P (R^2=0.997) showing a good fitting to exponential decay distribution according to the *a priori* model. For the three cases we evidenced a cut-off in the distribution close to S_R = 0.85 where the distribution tail decay more rapidly. It indicates that co-occurrence of species with similar body size (S_R values above the cut-off and near 1) have a low likelihood to be found within the same assemblages than other ratios and the expected by a perfect exponential decay. The scale parameter for S_R distribution corresponds to the expected mean S_R value per space unit or assemblages and mathematically is defined as the exponent of the decay distribution (LIG=0.232±0.003, LGM=0.226±0.003, C=0.432±0.003). It is important to note that according to the null model these values are significantly different than expected by chance (p value < 0.001) and even though this values not correspond exactly to the empirical mean S_R (LIG=0.246, LGM=0.251, C=0.331), they are highly correlated (Pearson=0.891, p< 0.001) and the difference corresponded to the distributions tail.

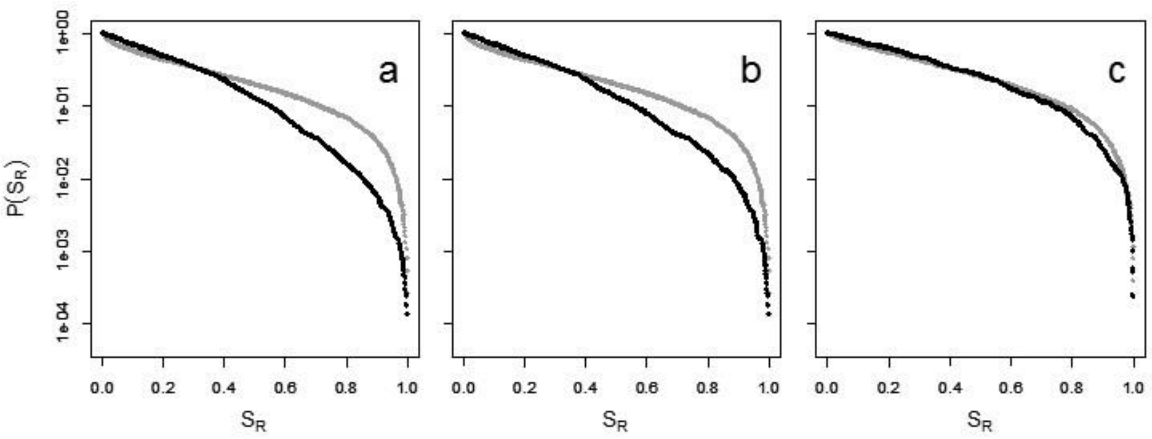

Figure 1. Complementary Cumulative Probability Distribution of carnivoran assemblages Size Ratio (S_R) in the Americas at three different periods. a) Last inter Glacial, b) Last Glacial Maximum, c) Present time. It is plotted using a *Log-Normal* scale. Black points are empirical data and grey points are a priori model results.

The *a priori* model evidence an exponential trend with a cut-off behavior as a natural effects of the size distributions interactions and the small number of species with similar body sizes. The differences observe between empirical results and the *a priori* model reflect that body sizes spatial clustering effect produces a clear mismatching between the distributions, particularly in the tail where empirical data are below the *a priori* model. This support the natural tendency of the empirical S_R probability distribution and the clustering effect, indicating that species with similar size are less frequent in the assemblages than expected if all species where in full overlapping. Thus, it is more common to find species showing large size differences. This trend is evidenced in all times but less powerful in P time, coinciding perhaps with the reduction in size differentiations by the extinction of the hyper-sizes species at the end of the LGM (Figure 1).

When we grouped carnivorous species present in the same assemblage according to their ecological traits (dietary pattern, habit, activity pattern and social pattern), the resulting structure show a similar S_R trend in exponential decay distribution (Figure 2) and also had a good fitting (Table 1). This means that species within the same ecological trait space in order to coexist within the assemblages must follow and behave as full assemblage with smaller S_R values. For all cases the observed cut-offs show that is less frequent to find similar size carnivoran species within the same ecological traits space. Thus, for ecological traits as dietary, diurnals and gregarious patterns the cut-off is remarkable. It implies that size difference and the S_R is a strong mechanism in structuring assemblages across space and time. This is consistent when comparing to the a priori model built according to the ecological traits, indicating that is less frequent to find within the same geographic space species with common size and with the same traits than the expected (see Supplementary materials).

For nocturnal and gregarious we evidenced that there is a high correspondence between empirical results and the model which implies that for these traits there is an additional mechanism that allow species a full spatial overlapping between them. Is important to note, that the scansorials, omnivorous, nocturnes species groups shows a larger empirical mean S_R during glacial period (Table 1) that is consistent with the hyper-size carnivoran extinction (e.g. *Smilodon populator*, *Panthera athorx*, *Arthodus simuns*, *Thremarcthos floridanus*, *Arthotherium spp*) meanwhile the other ecological trait groups (Carnivorous, Terrestrial, diurnal and solitaries) evidence that during the interglacial periods (LIG and C) the empirical mean S_R are lower than during glacial period.

Table 1. Summary of exponential fittings of S_R relation in carnivorans mammals at three periods of time, Current time (C), Last Glacial Maximum (LGM), Last inter Glacial (LIG). R^2 or fitting determination coefficient, scale parameter (*t*) error of scale parameter (*t*-error) and the empirical mean Size Ratio ($<S_R>$) of the interactions in the assemblage. Results are discriminated according to ecological traits groups.

Traits	**LIG**				**LGM**				**C**			
	$<S_R>$	*t*	t-error	R^2	$<S_R>$	t	t-error	R^2	$<S_R>$	t	t-error	R^2
Scanzorials	0.352	0.486	0.007	0.998	0.378	0.594	0.012	0.997	0.335	0.45	0.008	0.997
Terrestrials	0.245	0.27	0.005	0.991	0.236	0.169	0.004	0.97	0.256	0.27	0.005	0.991
Carnovorous	0.241	0.156	0.007	0.95	0.298	0.227	0.016	0.918	0.247	0.214	0.009	0.982
Omnivorous	0.271	0.265	0.005	0.979	0.274	0.287	0.004	0.985	0.283	0.381	0.008	0.986
Diurnals	0.292	0.314	0.016	0.984	0.31	0.328	0.012	0.992	0.253	0.151	0.018	0.953
Nocturnals	0.308	0.391	0.003	0.998	0.312	0.399	0.003	0.997	0.37	0.627	0.007	0.998
Gregarious	0.28	0.296	0.015	0.984	0.252	0.278	0.019	0.973	0.339	0.28	0.031	0.951
Solitaries	0.219	0.177	0.002	0.98	0.24	0.193	0.002	0.983	0.32	0.345	0.003	0.994

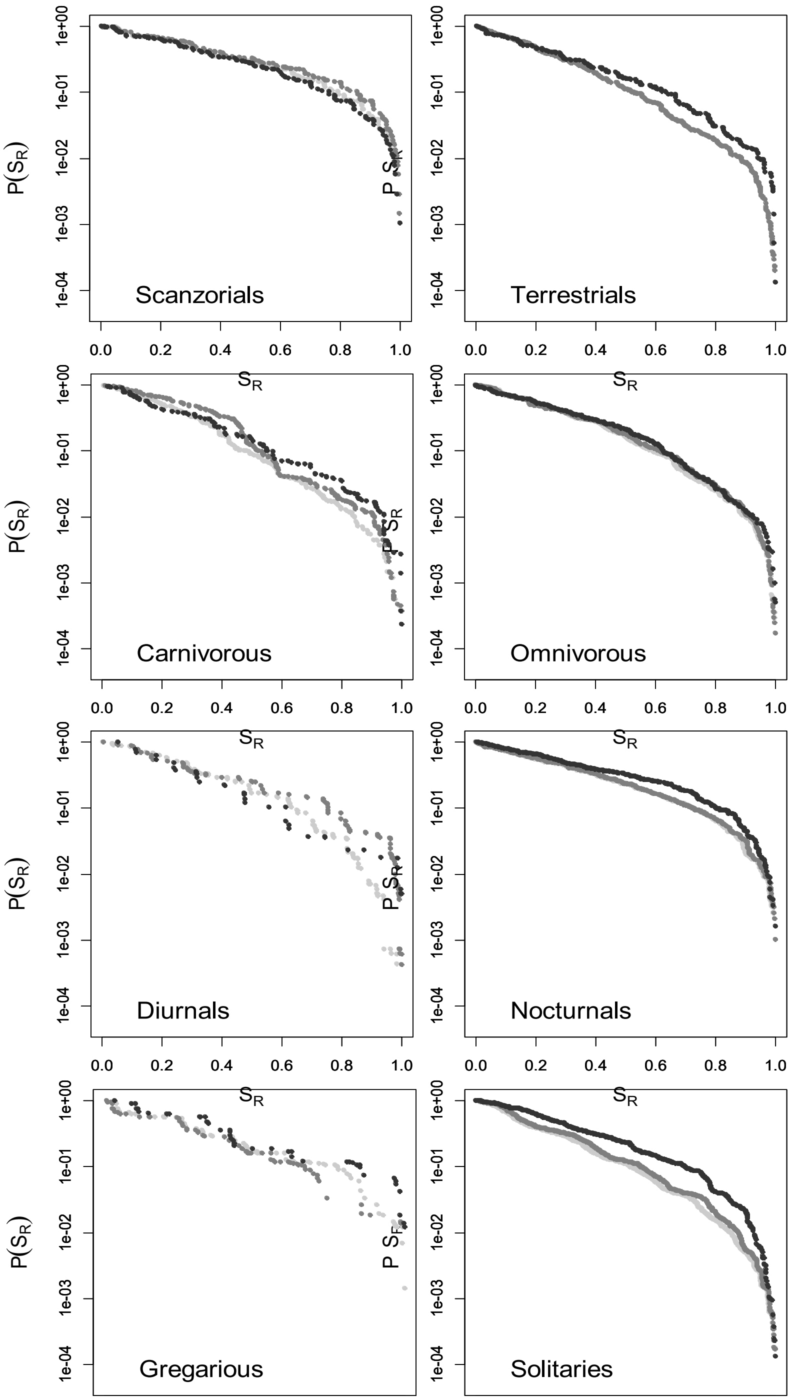

Figure 2. Complementary Cumulative Probability Distribution of carnivoran assemblages Size Ratio (S_R) in Americas at three different periods, and discriminated according to ecological traits groups. Light gray correspond to LIG, dark gray to LGM and black to P times.

Functional Diversity (FD)

The underlying functional diversity patterns of carnivoran assemblages in general exhibit a high functional diversity (low redundancy) towards the tropics, and the poles during the LIG and C times. This means that there is a tendency that carnivoran species occupy the same geographic space should display different ecological traits in order to coexist suggesting a functional niche filtering meanly driven by the size ratio (SR) relationship at local scales as show above. Also, this spatial analysis allowed us to identify dramatic changes in this measure occurred during the LGM occurred at North America due to the climatic constraints and not by functional constraints, causing the local extinction of many species and therefore on the reduction of the functional diversity patterns (Figure 3b). However, toward more tropical areas during the LGM this FD decreased perhaps showing an assemblages oversaturation, causing a greater probability of finding similar species (high values of S_R) and therefore a greater likelihood of competition between carnivoran species at mid-latitudes during this period (Figure 3b).

As expected, this FD measure can be considered as the expression of the underling carnivoran ecological characteristics as a mechanism in structuring assemblages across space and time. Carnivoran species present in replicated assemblages tent to exhibit great differences in their ecological characteristics (e.g. body size, as a proxy of functional niches), and therefore displaying high patterns of functional diversity in order to coexist at local to regional scales to avoid competitive exclusion. In this sense the trait space niche, represent an important role in structuring carnivoran assemblages through space and time in the Americas and body sizes spatial clustering effect between coexisting species appears to be a possible mechanism as a functional filtering for species coexistence.

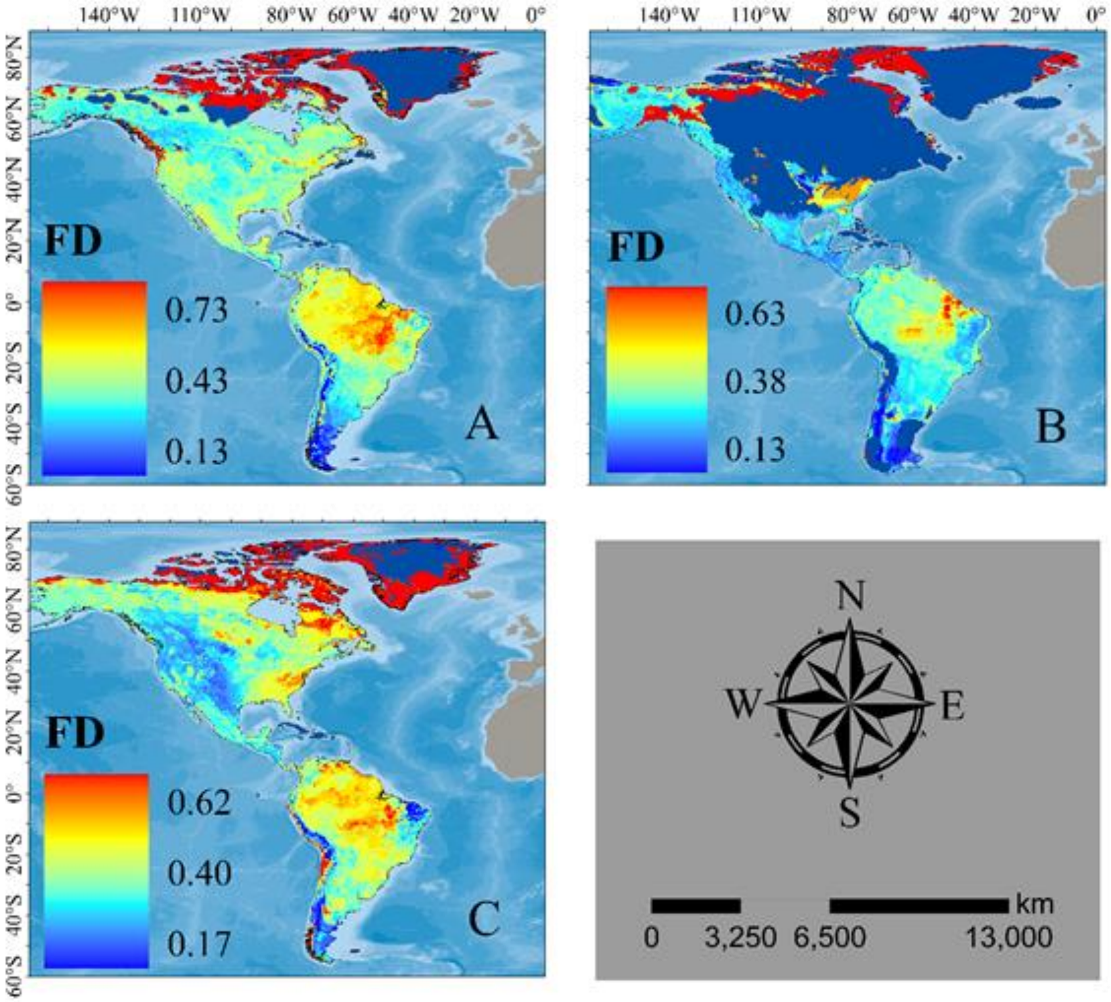

Figure 3. Functional diversity of carnivoran assemblages' patterns across space and time in the Americas. FD values goes between 0 (low functional diversity, maximum similarity within trait-space, high redundancy) and 1 (high functional diversity, high differences within trait-space, low redundancy). A. Last Inter Glacial (LIG), B. Last Glacial Maximum (LGM) and C. Current time (C).

Discussion

Elucidate the influence of the functional niche through the effects of ecological factors on the species coexistence and how these conform assemblages through time and spaces is a major focus on biogeography and macroecology. Historically, Hutchinson (1959) proposed the idea of body size ratios as a potential mechanism where species occupying the same geographic space at the same time should differ in size in order to coexist. Although, previous studies have found little support to this idea as a key in structuring assemblages and communities (Ernest 2005), we found that this size ratio (~1:3) is consistent not only thought space and time, but also within ecological traits groups. Likewise, here we found a consistency of body size ratio distributions trend in which species are following an exponential distribution of size ratio (S_R) in order to coexist. Therefore, the differences in body size in species with similar ecological traits are limiting the number of similar species that could coexist within assemblages. This may be interpreted as assemblage saturation as a result of functional filtering in order to avoid the competitive exclusion between the interacting or coexisting species and according to the a priori model it is a natural result of the sizes distributions trend.

Moreover, the exponential distribution evidenced in S_R reflects some important characteristics about the elements involved under the mechanisms that structure the carnivoran assemblage. The existence of a conserved scale parameter that describe the system as a whole and the presence of a limiting factor also controlling the structure as evidenced in non-biological systems (e.g. economical systems) (Drăgulescu & Yakovenko 2001). These elements correspond to the average S_R per pair of species that coexist per unit of space and the total sizes available to occupy the space. In this sense, regardless of body size of the carnivoran species, the assemblages maintain equals or lower values of the mean S_R in order to species coexist. If there is a tendency of the mean S_R to increase, the other ecological traits (e.g. habit, dietary and activity patterns) act as an extra rule in order to restore the S_R that govern this species sympatric patterns. Otherwise a strong violation of this mechanism occurs, which may conduce to the local-regional exclusion or extinction of one or more species in order to conserve this S_R. In this sense, our results show that there is a low probability to find carnivoran species occupying the same ecological trait spaces and coexisting within the same geographic space.

Thereby our results are consistent with the concept that relative stable coexistence requires important ecological differences between species, or in other words, differentiated niches to allow coexistence (in this case functional niches) (Brown and Wilson 1956; Hutchinson 1959; Chesson 1990; Leibold 1995). As we expected, these differences between coexistence species among the trait space can be considered as a direct measure of functional diversity. Carnivoran species present in replicated assemblages tent to exhibit great differences in their ecological traits, meanly driven by the body sizes spatial clustering effect and therefore show a high functional diversity at local to regional scales and also in continental scale as recently suggested (Blois and Hadly 2009; Wisz et al. 2013). The cut-off transition on the systems where S_R values begin to increase, seems to be a natural limiting factor that reflects the low likelihood of sympatric species with similar characteristics and thus the low redundancy in the FD patterns. As the S_R rate increases the likelihood of coexistence is reduced and the likelihood of competition is increased (Gittleman 1985; Donadio and Buskirk 2006). Therefore, it is expected that sympatric species should evolve discrete and segregated functional ecological attributes as the result of the evolutionary process in which species are differentiated in terms of adaptation to their environment. These heterogeneous environments have an epigenetic and buffering role over different phenotypes in space promoting phenotypic plasticity and clearly over body size which is strongly correlated with many physiological and fitness characteristics (Blanckenhorn 2000; Chesson 2000; Zhang et al. 2013; Verhoeven et al. 2016) and thus influencing the system and reducing the chance to similar species become together over space and time.

Glacial-interglacial cycles during the Pleistocene certainly had profound consequences for species ranges and dispersions patterns, particularly beyond the tropics. For instance, during the LGM most of North America was under ice (Dyke 2005). These environmental filtering affects mainly the hyper-large carnivoran species due to their energetic constraint, biological characteristics and area requirements (Lessa and Fariña 1996, O'Regan et al. 2002; Canto et al. 2010, Lorenzen et al. 2011; Agosta and Bernardo 2013; Levinsky et al. 2013). These changes are reflected in changes in the S_R and FD patterns between LIG-LGM-C periods consistent with the hyper-size carnivoran extinction (e.g. *Smilodon* spp., *Homotherium serum*, *Panthera atrox*, *Canis dirus*, *Arctodus simun*, *Arctotherium* spp.) at local and regional scales, showing a tendency towards a more homogeneous size ratios and a reduction in the FD pattern (displaying more redundancy) mainly in North America. These tendency of the S_R distribution implies that the sizes found in a particular place depends on local size ratio between the carnivoran species and the ratio present of overall sites, thus showing an effect from local to reginal scales, as it is showed in other phenomenon as richness distribution (Drăgulescu & Yakovenko, 2001).

As far as assemblages are functionally more saturated, the size ratio (S_R) and the body sizes spatial clustering effect appears to be a mechanism that controls the system regardless of the identity of the species within the assemblages. When the S_R decrease, the proportion of species coexist sites increased or are unsaturated, and at the same time it seems that the importance of competition between species decreases (Godsoe et al 2015) regardless whether they belong to the same ecological trait space. However, this rate of change in the

S_R would not be infinite and would be controlled by the carrying capacity (Lotka-Volterra competition models) through the availability resources in the system, which it is evidenced by the cut-off in the S_R distributions that reveals that species with almost the same size are less frequent than the expected. Therefore, the criteria for species coexistence in assemblages should be that intraspecific competition must be greater than interspecific competition, since species of similar size and/or the same energetically constrains (same functional niche) cannot coexist in the long-term in the same geographic space (Brown and Wilson 1956; Hutchinson 1959; Chesson 2000; Ernest 2005).

In these sense, the lack of character displacement in body-size makes that coexisting carnivores may face other mechanism constraints in other ecological trait spaces while seeking to maximize fitness and avoid competitive exclusion, which turns in a more diffuse interspecific interaction (Chesson 2000). It is noteworthy for example that in two South American foxes (*Lycalopex griseus* and *L. culpaeus*) that are morphologically and ecological similar and are mostly allopatric, present a tendency to segregate in size when are sympatric within a few geographical areas (Zapata et al. 2005; Gantchoff and Belant 2016). Likewise, in tropical similar size felids (e.g. *Leopardus wiedii* and *Puma yaguaroundi*) and foxes species (*Cerdocyon thous* and *Lycalopex gymnocercus*) coexistence appeared to be facilitated by temporal segregation or for example by fine-scale habitat segregation (e.g. *Puma concolor* and *Panther onca*). Likewise, other similar sized species may adjust their activity patterns alternating their peaks of activity in relation to the relative order of their body weights or have a finer dietary niche segregation to facilitate coexistence within assemblages (Di Bitetti et al. 2009, 2010; Barrull et al. 2014; Gantchoff and Belant 2016; Palomares et al. 2016). Thus supporting these results that body sizes spatial clustering effect and the ecological drivers play an important role in structuring carnivoran assemblages coexistence not only from local and regional scales but also from continental level and can mediate other interactions forms (e.g. Intraguild predation and interspecific killing) in Americas as recently suggested (De Vivo and Carmignotto 2004; Araújo & Luoto 2007; Croitor and Brugal 2010; Davies et al. 2011; Oliveira and Pereira 2013; Wisz et l 2013).

This mechanism that emerges herein can be viewed as a functional filtering that have contribute to shape the carnivoran assemblage structure patterns during the LIG-LGM-C transition. However, other important forces, meanly associated with past climate change played an important role as environmental filtering that have contributed also to shape the lineages geographical distribution in America (Cardillo et al. 2006; Davies et al. 2009; Palombo et al. 2008; Agosta and Bernardo 2013). This resembles the spatial storage effect mechanism (Chesson 2000), which is the interaction between the fluctuating environmental (climatic niche) and the ecological trait space (functional niche) operating differentially and synergistically at different times and space scales.

Here we provide new insights regarding history and spatial patterns of American carnivoran species during the last 130 Kyr. Functional filtering meanly driven by the mean size ratio (SR) as a potential mechanism that limited the number of carnivoran species that could coexist, are in part the main reason of taxa co-occurrences and play an important role in assemblages restructuring from local to continental scales in Americas

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Supporting Information

Table S1. Ecological characteristics description used to assess the carnivoran assemblages and the underlying functional diversity patterns (FD). The trait codification in the database was present (1), absent (0). The weight is given in grams for the case of body size

Body mass*:* this ecological trait can provide considerable information about the ecology and life history of the species and has proven to be one of the most fundamental characteristics of an organism in terms of adaptation to their environment and interaction with other species (Peters 1983; Farlow y Pianka 2003; Lyons and Smith 2008; Raia *et al.* 2012; Fergnani & Ruggiero 2015). The variability in body mass is a good predictor of the ecological niche of species, therefore is considered a proxy of functional diversity due to its relationship with ecosystem functioning (Peters 1983; Farlow y Pianka 2003; Hunter and Caro 2008; Lyons and Smith 2008; Raia *et al.* 2012; Fergnani & Ruggiero 2015).

Habit: this ecological trait can provide information about the locomotive adaptations to different substrate, indicating a relationship between the species and their environment. This is important because it reflects details of their feeding strategy (Van Valkenburgh 1985; Christiansen 2000; Fergnani & Ruggiero 2015). Depending on the species, one species may have one or more habits.

Social organization: this ecological trait represents the mean number of individuals of the species together during the most of the year outside of the breeding season. Group size is generally considered an anti-predator response, since larger groups reduce the risk of predation per capita, by increasing collective vigilance and predator detection, or by collective defense (Fergnani & Ruggiero 2015).

Activity pattern: this ecological trait represent the active period where the species is most active during a 24 hrs cycle. The active period is related to resource use and it is influenced by physiological constraints.

Trophic realm: this trait represent the main indicator of resources used and covers several dietary attributes that reflect amplitude of species diet (Jones et al. 2009).

Trophic guild: this ecological trait represent the main feeding specialization of the carnivoran species. It describes the different feeding types and allows us to distinguish more precisely between species (Van Valkenburgh 1985; Jones et al. 2009)

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9. DISCUSIÓN GENERAL

Entender los patrones de distribución de las especies y los procesos evolutivos subyacentes ha sido uno de los principales temas de interés de la ecología y la biogeografía desde hace décadas, y más recientemente ha tenido más atención en áreas como la biología de la conservación (Goswami and Friscia 2010; Levinsky 2013). Numerosas aproximaciones han mostrado el potencial de reconstruir patrones ecológicos y cambios importantes en la distribución pasada y actuales de las especies como resultado de diferentes eventos históricos (MacArthur 1972; Brown 1995; Blois y Hadly 2009; Steintz 2009; Lomolino et al. 2010) y más recientemente como efecto de las variaciones climáticas a escalas amplias (Martínez-Meyer et al. 2004; Soberón and Nakamura 2009; Morris et al. 2010; Davies et al. 2011; Lorenzen et al. 2011; Levinsky et al. 2013; Blois et al. 2014). Sin embargo, el explicar la manera en cómo las especies coexisten a nivel espacial y temporal, y que otros factores influyen en estos patrones no es una tarea fácil. Así, la evaluación de estos patrones, determinantes ambientales y funcionales a nivel espacial y temporal puede facilitar los procesos de análisis y reconstrucción de parte de la historia ecológica del continente con grandes implicaciones de conservación.

Hasta el momento, las hipótesis y reconstrucción de los patrones de distribución de las especies de carnívoros y como éstas se estructuran espacialmente en ensamblajes y sus factores asociados a nivel continental han tenido relativa poca atención. Nuestros resultados sugieren que diferentes mecanismos, actuando de manera combinada y con efecto diferencial, pueden influenciar estos patrones a nivel especial y temporal en América. Por un lado, el filtraje ambiental como se ha propuesto anteriormente para otros vertebrados

(Cardillo et al. 2006; Davies et al. 2009; Palombo et al. 2008; Agosta and Bernardo 2013) juega un papel clave e importante, operando a través de largos períodos de tiempo sobre la capacidad de adaptación y respuesta, conectividad y flujo genético entre las poblaciones de las especies de carnívoros, siendo crítico en sus rangos geográficos, los cuales variaron en tamaño y ubicación principalmente desde latitudes altas a medias en Norte América durante la transición LIG-LGM. Como consecuencia esta transición y el filtrado ambiental causaron cambios más marcados en los patrones de riqueza y composición (en menor grado) de los ensamblajes, tal y como se ha observado en otros grupos (Gittleman and Gompper 2005; Bonaccorso et al. 2006; Nogués-Bravo et al. 2008; Schipper, 2008; Blois and Hadly 2009; Mandujano y Naranjo 2010; Thomas et al. 2004; Polly 2010). Es importante señalar que estos patrones de alta riqueza de carnívoros a finales del Pleistoceno y la actualidad son consistentes como se ha sugerido previamente, siendo una de las más altas a nivel mundial en proporción al área continental, y significativamente más alta que los patrones de riqueza presentes antes del Pleistoceno y durante el Holoceno en América (Cione et al. 2003; Wroe et al. 2004; Prevosti & Vizcaíno 2006; Schipper 2008; Prevosti y Soibelzon 2012).

Igualmente, aquí evidenciamos que los factores ambientales afectan de forma dinámica y diferencial a los ensamblajes de carnívoros, más directamente sobre la riqueza que la composición, y no sólo a nivel continental, sino también a escalas regionales y locales como se ha sugirió recientemente (Blois y Hadley 2009; Wisz et al 2013). En este sentido los factores ambientales y sus cambios abruptos durante largos periodos de tiempo (e.g periodo glaciar), son uno de los impulsores más importantes que influyen en estas respuestas ecológicas y evolutivas, las cuales por lo general son más fácilmente detectables a escalas geográficas amplias (Martínez-Meyer et al. 2004; Soberón and Nakamura 2009; Morris et al. 2010; Davies et al. 2011; Lorenzen et al. 2011, Levinsky et al. 2013; Blois et al. 2014). Es importante señalar que durante este último periodo de tiempo esta respuesta mayor en la riqueza que se observa, quizás sea debido a que no ocurrió un recambio considerable de especies como ha ocurrido anteriormente.

Por ejemplo, Prevosti y Soibelzon (2012) señalan que durante el Pleistoceno medio en Sur América ocurrió una gran extinción de carnívoros entre las edades del Ensedandesne y el Bonarense (1.2-0.126 Ma), cambiando con ello de repente la composición, sin cambios abruptos en los patrones de riqueza de los ensamblajes. Desaparecieron algunas canidos hipercarnivoros (e.g. *Theriodictis tarijensis*, *Protocyon scagliarum*, *"Canis" gezi*, *Dusicyon ensenadensis*), dos osos gigantes de cara corta (*Arctotherium angustidens, Arctotherium vetustum*), algunos mustélidos de tamaño pequeño (e.g., *Lyncodon bosei*, *Galictis henningi*, *Stipanicicia Reig*), y un prociónido mediano (*Cyonasua merani*). Estos cambios principalmente en la composición al parecer fueron influenciados primero por cambios ambientales durante un periodo glaciar ocurrido durante estas dos edades (Ilinonian en Norte América y Santa María en Sur América 200-130 ka) y segundo por la competencia y recambio por la aparición de otros carnívoros con nichos funcionales similares a finales del Bonarense e inicios del Lujanense (130-126 ka) (e.g. Osos de cara corta de tamaño grande *Arctotherium tarijense*, *A. bonariense*, *A. wingei*; mustélidos pequeños *Galictis. cuja*, *Lyncodon patagonicus*, *Eira barbara*, *Pteronura brasiliensis*; canidos grandes *Canis dirus*, *Dusicyon avus*; prociónidos medianos *Nasua nasua*, *Procyon cancrivorus* y mefitidos pequeños *Conepatus semistriatus*, *Conepatus humboldtii*).

Es importante señalar que durante estos mismos periodos en Norte América (Ensedandesne-Bonarense, 1.2-0.126 Ma; Bonarense-Lujanense, 130-126 ka) también ocurrieron cambios, principalmente en la composición de especies, desapareciendo igualmente especies en proporción de tamaños (e.g. *Arctodus pristinus*, *Miracinonyx studeri*, *Smilodon gracilis*, *Brachyprotoma obtusata*, *Martes diluviana*) y recambio por especies ecológica y funcionalmente similares (e.g. *Arctodus simus*, *Ursus arctos*, *Miracinonyx trumani*, *Smilodon fatalis*, *Mephitis mephitis*, *Martes pennanti*). En este sentido, aunque nuestro estudio no incluyó estos otros periodos de tiempo, estos patrones son congruentes con nuestros resultados, donde la coexistencia relativamente estable entre las especies al interior de un mismo ensamblaje requiere de nichos ecológicos diferenciados (nicho ambiental y nicho funcional) (Brown y Wilson 1956; Hutchinson 1959; Chesson 1990; Leibold 1995; Thuller et al. 2015), donde el filtrado ambiental y el filtrado funcional juegan un papel clave como mecanismos no excluyentes de estructuración de ensamblajes a nivel espacial y temporal.

Así mismo, nuestros resultados indican que a medida que se baja de escala es posible identificar más claramente el papel del nicho funcional como unos de los mecanismos determinantes en cómo pueden coexistir las especies en una misma área geográfica. Mostrándonos así la existencia y en muchos de los casos subestimados de este filtrado funcional, actuando desde el nivel local hacia lo regional y continental, el cual es promovido principalmente por la relación de tamaño de peso promedio (S_R). Estos resultados son consistentes con lo propuesto por Hutchinson (1959) donde las especies que ocupan una misma área geográfica deberían diferenciarse principalmente en proporción a su tamaño corporal. Es de señalar que esto no sólo es coherente a través de grupos con los mismos atributos ecológicos, sino también a nivel espacial y temporal en el continente.

No obstante, si las especies se aproximan a un tamaño similar, es decir si no hay un desplazamiento considerable en esta característica, entonces estas despliegan una segregación en al menos uno de los demás atributos ecológicos. Esto se ve reflejado a nivel geográfico en la gran diversidad funcional expresada como un proxy de nichos funcionales diferenciados, que les permite a las especies coexistir dentro de los mismos ensamblajes. En este sentido, la falta desplazamiento en el tamaño corporal entre las especies coexistentes al interior de algunos ensamblajes, genera restricciones en otros atributos ecológicos, limitando así la similitud entre las mismas. De esta forma se maximiza la adecuación y se evita la exclusión competitiva, lo que resulta en una coexistencia con interacciones interespecíficas más difusas y en una baja redundancia funcional a nivel espacial (Chesson 2000; Ernest 2005; Petchey et al. 2007; Thuller et al. 2015). Esto es consistente como se ha sugerido recientemente para las especies de carnívoros actuales a escala continental (Farias y Svensson 2014; Fergnani and Ruggiero 2015).

Es importante señalar dado que la diversidad funcional es una medida del nivel de complementariedad entre los atributos ecológicos de las especies en un ensamblaje (Mason et al. 2005; Petchey & Gaston 2002; Safi et al. 2011; González-Maya 2015), ésta alta diversidad funcional en América aquí propuesta y su vulnerabilidad actual pueden representar un riesgo latente sobre la pérdida de la funcionalidad y capacidad de resiliencia de los ecosistemas. Su perdida podría traer efectos en cascada con posibles modificaciones en los procesos ecológicos a lo largo del continente. Farias y Svensson (2014) señal por ejemplo que, actualmente, muchas de las especies de carnívoros que aportan a esta alta diversidad funcional en Sur América, en su mayoría son especies que presentan un alto riesgo de extinción (categorizadas como vulnerables o amenazadas, IUCN 2016), proceso que puede agudizarse frente a la actual influencia de la intervención humana y el actual cambio climático. Es de resaltar que actualmente los mamíferos carnívoros son uno de los grupos entre toda la diversidad biológica que presentan la mayor fragmentación y reducción de su distribución geográfica, esto debido particularmente a su vulnerabilidad a la pérdida y fragmentación de los hábitats naturales por el cambio en el uso del suelo, reflejando así extinciones locales y regionales a nivel mundial (Di Minin et al. 2016).

En este sentido, si le damos una mirada integral a estas especies durante el periodo estudiado, podemos inferir que muchas de estas especies de carnívoros que pasaron por el "filtro de extinción" posteriormente al último máximo glaciar, representan el conjunto de especies con los atributos ecológicos más adecuados para hacer frente a los cambios ambientales naturales. Donde estas características y requerimientos biológicos juegan un papel clave en el riesgo de extinción. Las especies de carnívoros por lo general establecen áreas de dominio vital (Home Rnage) y patrones de actividad a nivel intrasexual (Conde et al. 2010), por lo tanto, las contracción y fragmentación de su distribución trae consigo reducciones de las poblaciones. Si esta tendencia continúa durante largos periodos de tiempo, el riesgo de extinción puede incrementarse debido los cuellos de botella demográficos, los cuales pueden volverse más críticos si otros factores estresantes (e.g. enfermedades, influencia humana, pérdida de presas, competencia interespecífica) actúan sobre las distribuciones remanentes (Dundas 1999; Graham 2001; Webb 2006; Nogués-Bravo et al. 2008; Canto et al. 2010, Lorenzen et al. 2011; Davies et al. 2011; Agosta and Bernardo 2013). Nuestros resultados sugieren que las reducciones en las distribuciones y restricciones en las áreas con condiciones adecuadas debido a los cambios ambientales pudo haber sido más crítico en la reducción de las poblaciones de las especies más grandes (e.g. *Smilodon fatalis*, *Panthera atrox*, *Homotherium serum*, *Arctodus simus*, *Tremarctos floridanus*), principalmente de aquellas especies y poblaciones ubicadas en grandes latitudes (i.e dos poblaciones de jaguares de tamaño grande se extinguieron, *Panthera onca augusta* en Norte América y *Panthera onca mesembrina* en Sur América), jugando así un papel importante en su extinción como se ha propuesto para otras especies de mega-mamíferos (Nogués-Bravo et al. 2008; Croitor and Brugal 2010).

De esta forma, las especies más grandes al presentan abundancia y densidad poblacional baja, bajas tasas reproductivas, áreas de domino vital muy grandes y a pesar de su alta capacidad de adquirir recursos, su capacidad de convertir estos recursos en descendientes es limitada (especialmente durante cambios estacionales más marcados y prolongados, ya que la probabilidad de sobrevivencia de las crías y la fertilidad es mucho menor) fueron las más susceptibles a estos procesos demográficos. Por ello, fueron inherentemente más vulnerables a restricciones energéticas y fragmentación de sus distribuciones, razón por la cual deben mantener amplias distribuciones a nivel espacial y temporal con el fin de mantener poblaciones viables y por ende disminuir el riesgo de extinción (Slaughther 1975; Martin y Neumer 1978; Lessa and Fariña 1996, Purvis et al. 2000; Cione et al. 2003; Canto et al. 2010, Lorenzen et al. 2011; O'Regan et al. 2002; Agosta and Bernardo 2013; Levinsky et al. 2013). Tal y como se plantea actualmente para las especies de carnívoros y sus implicaciones en conservación y permanecía a largo plazo en el planeta.

Con este trabajo proporcionamos nuevas luces sobre parte de la historia evolutiva y los patrones biogeográficos de las especies de carnívoros presentes durante los últimos 130 mil años hasta la actualidad en América. Las restricciones impuestas por el nicho ecológico, a través del filtrado en las dimensiones ambientales y funcionales, son en parte los principales mecanismos de coexistencia y estructuración de los ensamblajes a nivel espacial y temporal. Este mecanismo lo denominamos aquí como "***ecological niche clustering effect***", donde la coexistencia de las especies en parte es el resultado y un efecto combinado entre determinantes o las dimensiones ambientales y funcionales del nicho ecológico a diferentes escalas temporales y espaciales. Este mecanismo se asemeja al mecanismo de almacenamiento espacial propuesto anteriormente (*spatial storage effect mechanism*, Chesson 2000; Thuller et al. 2015). El entendimiento de esta influencia y de éstos y otros mecanismos puede permitirnos así la identificación y selección de prioridades de conservación en función de las amenazas actuales. Esto por medio de acciones dirigidas de conservación para las especies, y por que no, hacia la conservación de ensamblajes como una nueva estrategia de conservación, dada la importancia de estas especies en el funcionamiento y resiliencia de los ecosistemas. En este sentido es importante considerar y aprender las lecciones del pasado, si queremos tomar hoy las decisiones correctas para el futuro.

En la medida que conozcamos e indaguemos cada vez más sobre el por qué y cómo podrían cambiar o han cambiado estos ensamblajes a diferentes escalas espacio-temporales, podremos anunciar las posibles consecuencias sobre estas especies y su dinámica ecológica con implicaciones para la conservación de este grupo en América.

10. CONCLUSIONES GENERALES

Con este trabajo proporcionamos nuevas luces y perspectivas a cerca la historia, los procesos y patrones de ensamblaje de las especies de carnívoros presentes en el continente durante los últimos 130 mil años. El nicho ecológico y sus dos principales dimensiones, nicho ambiental y nicho funcional, juegan un papel esencial en los patrones de distribución y coexistencia de las especies de carnívoros, y esta influencia se observa dinámicamente a nivel temporal y espacial desde la escala continental hacia la local y viceversa.

Las especies de carnívoros simpátricos pueden presentar patrones similares en sus dimensiones del nicho, pero nunca en las dos dimensiones a la vez, esto con el fin de evitar la exclusión competitiva. Por lo general los carnívoros en América, a nivel especial y temporal, muestran tendencias de segregación con respecto a sus atributos funcionales (en algunas de ellas segregaciones muy finas como el patrón alimenticio), el cual es promovido principalmente por la relación de tamaño de peso promedio (S_R), reflejando así una gran diversidad funcional subyacente.

Factores como el filtrado ambiental y el filtrado funcional como dos de las principales dimensiones del nicho ecológico (nicho ambiental y funcional) juegan un papel clave y son unos de los principales mecanismos no excluyentes de coexistencia y estructuración de los ensamblajes de carnívoros en América. Mecanismo aquí denominado como "***ecological niche clustering effect***", donde la coexistencia en parte es el resultado y un efecto combinado entre estas dos dimensiones a diferentes escalas temporales y espaciales.

El último periodo glaciar jugo un papel importante en la sobrevivencia de muchas de estas especies. Cambios drásticos en el clima durante periodos continuos de más de 10 mil años, principalmente en Norte América, fueron críticos para las poblaciones de las especies, especialmente en las especies más grandes, lo que contribuyó en el riesgo de extinción y la reestructuración de los ensamblajes. Es importante anotar que en este trabajo solo abordamos algunos de los factores que conforman solo una parte en estos patrones geográficos, otros factores como los eventos históricos, la influencia humana y la pérdida de especies presa también pudieron jugar un papel clave en estos patrones en el continente.

Este abordaje de la simpatría de las especies de carnívoros y como éstas conforman ensamblajes podría considerarse actualmente en los futuros esquemas de conservación. Su entendimiento permitirá explorar la idea de proteger ensamblajes completos, considerando los posibles efectos del cambio climático actual, reintroducción de especies, especies invasoras, funcionamiento y resiliencia de los ecosistemas, y la influencia antrópica. Siendo así este enfoque de soporte para la toma de decisiones más integrales en conservación y manejo de la biodiversidad.

El éxito de poder anticipar los riesgos futuros estará dado cada vez más por la capacidad de comprender, reconstruir e interpretar muchos de estos patrones y aspectos evolutivos, que por lo general están siendo opacados y dejados de lado por una mayor importancia desmedida dada actualmente a aspectos meramente metodológicos.

Finalmente es de señalar que futuras investigaciones podrían incluir análisis a escalas de tiempo mucho más amplias, otros tipos de factores y junto con los nuevos hallazgos y el análisis sistemático permitirá tener cada vez más un mejor entendimiento de la historia evolutiva del continente. Igualmente estudios a escala del paisaje que involucren otro tipo de factores (i.e. antrópicos) podrían arrojar nuevas luces sobre los procesos de ensamblaje, la sobreposición de funciones y el recambio funcional de especies como respuesta a la intervención humana y al actual cambio climático. Estos trabajos futuros permitiran apoyar o rechazar estas y otras hipótesis que aún están y seguirán abiertas a interpretaciones e hipótesis alternativas.

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11. LITERATURA CITADA

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12. ANEXOS

12.1 Artículos publicados y derivados del doctorado

- **Arias-Alzate A**., Delgado-V C.A., Ortega J.C., Botero-Cañola S. & Sánchez-Londoño J.D. 2013. Presencia de *Puma yagouaroundi* (Carnivora: Felidae) en el valle de Aburrá, Antioquia, Colombia. Brenesia 79: 83-84.
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