UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
DOCTORADO EN CIENCIAS BIOMÉDICAS
INSTITUTO DE ECOLOGÍA

CONSERVACIÓN, DIVERSIDAD FUNCIONAL Y RIESGO DE EXTINCIÓN EN MAMÍFEROS NEOTROPICALES A MÚLTIPLES ESCALAS

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

PRESENTA:

M. en C. JOSÉ F. GONZÁLEZ MAYA

DIRECTOR DE TESIS
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MÉXICO, D. F. MAYO DE 2015.

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MÉXICO, D. F. MAYO DE 2015.

La presente tesis se desarrolló en el Laboratorio de Ecología y Conservación de Fauna Silvestre del Instituto de Ecología de la Universidad Nacional Autónoma de México como parte del Programa de Doctorado en Ciencias Biomédicas.

Dedicatoria

A mi familia,
por darme todo,
la fuerza y ganas, y
por enseñarme
lo que es valioso.

Agradecimientos

La presente tesis fue realizada como parte del Programa de Doctorado en Ciencias Biomédicas de la Universidad Nacional Autónoma de México y desarrollada en el Laboratorio de Ecología y Conservación de Fauna Silvestre del Instituto de Ecología de la UNAM.

Agradezco al Posgrado en Ciencias Biomédicas-PDCB y al Instituto de Ecología por el apoyo en la realización de mis estudios de Doctorado. Agradezco la beca otorgada para estudios de posgrado del Consejo Nacional de Ciencia y Tecnología – CONACyT y la UNAM (beca 255983). Así mismo, agradezco el estímulo de graduación otorgado como parte del Programa para el Apoyo al Posgrado (PAEP) del PDCB.

Adicionalmente, agradezco el soporte y financiamiento proporcionado por el Instituto de Ecología, ProCAT Colombia y el Programa de apoyo a proyectos de investigación e innovación tecnológica (No. IN211811) de la UNAM.

Agradecimientos a mi comité tutoral, Dr. Gerardo Ceballos, Dr. Enrique Martínez-Meyer y Dr. Rodrigo Medellín por su apoyo e indudable aporte a mi tesis y a mi doctorado en general. Un agradecimiento especial a mis asesores externos, Dr. Jerrold Belant y Dr. Jan Schipper, por su invaluable y constante apoyo personal y profesional.

A mi jurado de candidatura Dr. Carlos Montaña (QEPD), Dr. Enrique Martínez-Meyer, Dr. Rafael Lira, Dra. Ana Mendoza y Dr. Gerardo Suzán y a mi jurado de grado Dr. Gerardo Suzán, Dr. Gerardo Ceballos, Dr. Joaquín Arroyo, Dr. Rurik List y Dra. Ella Vasquez por sus valiosísimos aportes y discusión que aportaron significativamente a mi desarrollo doctoral.

Agradecimientos

Desarrollar un doctorado es por naturaleza una labor de colaboración en la que numerosas personas aportan desde lo intelectual, operacional y emocional, por lo que unas pocas palabras siempre serán insuficientes para la enorme contribución de valiosísimas personas al crecimiento y formación personal de quien la desarrolla. Sin embargo, es necesario mencionar algunas que hicieron parte fundamental de este maravilloso proceso sin dejar de lado todas aquellas que de una u otra forma hicieron parte de este sueño.

Agradezco en primer lugar a mi tutor y amigo, Gerardo Ceballos, quien con su visión completa, su apoyo, su humor y su indudable dedicación hicieron posible no sólo el desarrollo de este trabajo si no mi formación como persona e investigador. ¡Gracias carnal!

A Jerry Belant, mi asesor externo, quien ha sido una de las personas más influyentes en mi desarrollo profesional. Colega, colaborador y sobretodo infaltable amigo estuvo siempre dispuesto a ayudarme en todo momento, sin importar tiempos ni compromisos, y quién sin duda me ayudó a darle forma a esta tesis y quien ha sido mi apoyo y soporte para seguir adelante en cuanto proceso decido incursionar. Gracias amigo. A Jan Schipper, mi otro apoyo externo, quién desde hace años me acompaña y apoya en mi crecimiento y desarrollo profesional y personal; un amigo y colega con el que nos quedan años por caminar. A mi amigo Enrique Martínez-Meyer, quién desde mi comité tutoral aportó indudablemente al desarrollo de todo mi doctorado, haciéndolo sin duda una experiencia más agradable y enriquecedora. A Rodrigo Medellín, también miembro de mi comité, quien con su apoyo, sus discusiones y en general su confianza me ayudaron a crecer y desarrollar y concluir este proceso.

A Patricia Martínez y Erika Rodríguez, y en general todo el personal del Instituto de Ecología y el Programa de Doctorado en Ciencias Biomédicas por todo el apoyo en mi doctorado.

A los Dres. Gerardo Suzán, Joaquín Arroyo, Ella Vasquez y Rurik List por sus aportes y confianza en la revisión final de mi tesis.

A mi Laboratorio, actuales y egresados, por hacer mi estancia más agradable y construir un súper interesante grupo.

Sin duda un agradecimiento especial a mis amigos y colegas Eduardo Ponce, Daniela Yepes, Andrea Gallardo, Luli Martínez, Rodrigo Sierra-Corona, Jesús Pacheco, Cuauhtémoc Chaves, Antonio de la Torre, Marilyn Bejarano, Rurik List, Octavio Monroy, Julián Velazco y en general todos los cuates que hicieron mucho más agradable mi estancia y con los que además construimos procesos personales y académicos valiosísimos e inolvidables, pero sobretodo amistades interminables. ¡Salud!

Armando Escobedo, hermano, gracias a usted he hecho muchas cosas, por usted hace años terminé aquí y no alcanzo a agradecerle todo lo que ha significado, nos quedan muchos años por delante. A mis roomies y hermanos Andrés Arias-Alzate, Luis Víquez-R y Heliot Zarza por acompañarme, por la amistad sin falla, por la colaboración, y en general por la familia extendida que construimos en nuestro paso por este maravilloso país. Colombia, Costa Rica y México hermanadas.

A mi equipo de ProCAT Colombia/The Sierra to Sea, Diego Zárrate-Charry, Mauricio González, Mauricio Vela-Vargas, Alexandra Pineda-Guerrero, Diego Gómez-Hoyos y Sebastián Jiménez quienes me acompañaron y aguantaron mis tiempos, pero que aun así se mantienen firmes en construir lo que creemos vale la pena.

A mi familia, Pastor, Dolly, Mauro, Paula, Cami, Cata, Maia, Ceci y Eli, sin duda mi soporte angular, mi apoyo, mi base y todo lo que soy y por lo que trabajo. Les debo más que la vida, este logro para ustedes, sin duda, mi base fundamental.

Angela, ya sabes lo que significas y significarás y tu apoyo y soporte fueron fundamentales para terminar esta etapa y para dar el salto a todo lo que sigue en mi vida profesional y personal.

José F. González-Maya
México D.F.
8 de junio de 2015

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Resumen

Los mamíferos son uno de los grupos de mayor importancia en el funcionamiento de los ecosistemas, y representan uno de los grupos bajo mayor amenaza por el cambio global y las presiones humanas en general. Considerando que cerca del 25% de los mamíferos se encuentran amenazados a escala global, la pérdida de sus poblaciones y su consecuente pérdida de funciones, representan potencialmente una de las mayores amenazas a escala global sobre el funcionamiento y la provisión de bienes y servicios de los ecosistemas. Diferentes aproximaciones para evaluar la diversidad de especies han sido utilizadas a diferentes escalas, siendo históricamente la riqueza de especies la principal medida utilizada para entender procesos macroecológicos o como herramienta para la planificación y priorización en conservación. Avances recientes, sin embargo, han abordado diferentes dimensiones de la diversidad, principalmente desde los puntos de vista funcional y evolutivo.

La diversidad funcional es una medida de la diversidad de funciones que cumplen las especies dentro de una comunidad, y que por ende tienen implicaciones para el funcionamiento y capacidad de resiliencia de los ecosistemas. Originalmente desarrollada para plantas, hasta años recientes esta medida no había sido ampliamente utilizada en grupos de fauna, y en especial para mamíferos no se había abordado el tema en función de sus patrones, procesos y determinantes. El objetivo de la presente tesis fue el de evaluar los patrones de la diversidad funcional a diferentes escalas, el efecto de la escala espacial y biogeográfica, su variación espacial y los principales determinantes a escala global, regional y nacional, así como su relación con la intervención humana y las especies amenazadas.

Se evaluó la diversidad funcional de mamíferos, medida a partir del concepto de riqueza funcional, evaluando sus patrones a tres niveles: a escala global a partir de regiones biogeográficas, biomas y ecoregiones, a escala regional para el Neotrópico y el continuo del istmo de Panamá-Chocó, y a escala nacional para Colombia y Costa Rica. Se obtuvo la distribución espacial de todas las especies de mamíferos del mundo de la Lista Roja de Especies Amenazadas de UICN y se construyó una base de datos de atributos funcionales para cada especie abordando aquellos que tuvieran mayor relación con el uso de recursos de las especies y por ende con mayor influencia en el funcionamiento a nivel del ecosistema. A partir de esto se utilizó el índice de Diversidad Funcional de Petchey y Gaston, definido como Riqueza Funcional, y se estimó para cada escala de acuerdo a la unidad de evaluación. Para la escala global se evaluaron los patrones y gradientes de distribución, su variación espacial y su relación con la escala ecológica y el área a nivel de ecoregiones; adicionalmente se evaluó la influencia de las especies amenazadas sobre esta diversidad funcional, identificando las ecoregiones más susceptibles a la pérdida funcional y su variación espacial. A escala regional se evaluó la distribución de la diversidad funcional para el Neotrópico y la influencia de la intervención humana y las especies en riesgo a esta escala; así mismo se evaluó la variación de atributos ecológicos y los gradientes para el continuo Panamá-Chocó, identificando las áreas de recambio en la conexión de Centro y Suramérica. Para la escala nacional se evaluó la distribución de la diversidad funcional y sus principales determinantes biológicos, ambientales y antropogénicos para Costa Rica; a su vez se probó la subrogación de la diversidad funcional, la riqueza de especies y la

diversidad filogenética para Colombia con el fin de evaluar si el uso de una sola medida podría representar las otras como base para priorizar y planificar acciones de conservación.

Se encontró que la diversidad funcional de mamíferos varía a escala global con claros patrones similares a la diversidad de especies, pero influenciada por la escala ecológica y por la riqueza de especies y el área geográfica de las ecoregiones; a su vez, se pudo determinar que la riqueza de especies y la diversidad funcional no se ajustan a escala global, por lo que para ciertas regiones existen procesos subyacentes que deben ser considerados, a la vez que una sola medida no es suficiente para planificar medidas de conservación. Adicionalmente se encontró que las especies amenazadas son fuertes determinantes de la diversidad funcional a escala ecoregional, explicando el 60% de esta diversidad a escala global, y variando espacialmente a más del 70% en ciertas regiones del globo. A nivel regional se encontró que la intervención humana y las especies en riesgo están entre los principales determinantes de la diversidad funcional actualmente, donde ciertas regiones ya han sufrido fuertes cambios a nivel funcional y otras son más susceptibles a perderla por la pérdida de las especies más vulnerables. En términos de la variación de atributos funcionales se encontró una fuerte variación entre Centro y Suramérica, donde la convergencia de atributos genera gradientes continuos funcionales, a la vez que permite identificar donde se dan cambios abruptos en la composición funcional de los ensamblajes. A escala nacional se determinó que la diversidad funcional sigue un gradiente diferente a la riqueza de especies y esta está fuertemente influenciada por la composición (*i.e.*, murciélagos y roedores); así mismo se identificaron para Costa Rica tres regiones claras en términos funcionales y sus determinantes ambientales, biogeográficos y antropogénicos, los cuales afectan de forma diferencial dependiendo de la región. Se encontró además que las tres medidas (*i.e.*, funcional, filogenética y taxonómica) varían espacialmente, a escala de Colombia, y ciertas zonas muestran un desajuste entre las tres medidas, identificando la necesidad de planificar áreas prioritarias considerando las tres medidas para abordar las tres dimensiones asegurando la preservación de la historia evolutiva, el funcionamiento de los ecosistemas y la diversidad de especies a escala nacional.

En términos generales, la diversidad funcional es una medida reciente que permite avanzar no sólo en el entendimiento ecológico de la diversidad pero a la vez permite planificar considerando la relación especie-ecosistema, con implicaciones para el funcionamiento y resiliencia de los ecosistemas. La variación y convergencia a escala global permite identificar factores como el filtramiento ambiental así como la convergencia de caracteres en el ensamble de comunidades asociado al tipo de ecosistema y la regionalidad ecológica. Los resultados del análisis a múltiples escalas permiten evidenciar la variación que existe en esta medida de la diversidad, y la necesidad de entender los patrones a diferentes escalas ecológicas y de planificación. En términos de conservación, los resultados tienen implicaciones para la priorización y planificación de áreas críticas para conservación, el impacto diferencial de la intervención humana y la necesidad de explorar la variación espacial de la relación especie-ecosistema y sus principales conductores. La diversidad funcional deberá ser una medida considerada en los futuros esquemas de conservación y su entendimiento permitirá una mejor resolución para explorar patrones ecológicos y como soporte a la toma de decisiones en conservación y manejo de la biodiversidad.

Abstract

Mammals are one of the most important groups in the functioning of ecosystems, and represent one of the groups under greater threat from global change and human pressures in general. Considering that nearly 25% of mammals are threatened on a global scale, the loss of their populations and consequent loss of functions can potentially represent a major threat to global scale ecosystem´s functioning and for goods and services provision. Different approaches to evaluate species diversity have been used at different scales, with species richness historically the main measure used for understanding macroecological processes or as a tool for conservation planning and prioritization. Recent developments however have addressed different dimensions of diversity, mainly from the functional and evolutionary perspective.

Functional diversity is a measure of the diversity of functions that species play within a community, and thus have implications for the functioning and resilience of ecosystems. Originally developed for plants, until recent years this measure had not been widely assessed in animals, especially mammals, and its related patterns, processes, and determinants had not yet been addressed. The aim of this thesis was to evaluate patterns of functional diversity at different scales, the effect of spatial and biogeographical scale, its spatial variation and main determinants at global, regional and national levels, as well as its relationship with human intervention and endangered species.

Mammals´ functional diversity, measured from the concept of functional richness, was evaluated by assessing patterns at three levels: globally from biogeographic regions, biomes and ecoregions, at regional level for the Neotropics and the Isthmus of Panama-Choco continuum, and at national levels in Colombia and Costa Rica. We obtained the range distribution for all mammal species from the IUCN Red List of Threatened Species and built a database of functional attributes for each species by addressing those more related with resource use and therefore exerting greater influence on ecosystem´s functioning. We estimated a functional diversity measure based on Petchey and Gaston index for each scale based on different sampling units. For global patterns we assessed functional diversity global gradients, spatial variation and its relation to the ecological and area scales across the world´s ecoregions; further we assessed the influence of threatened species on functional diversity identifying the most susceptible ecoregions to functional loss and its spatial variation. At regional scale we assessed the distribution of functional diversity for the Neotropics and the influence of human intervention and species at risk on this scale; likewise we evaluated the variation of ecological attributes for the Panama-Chocó continuum identifying gradient areas in the connection of Central and South America. For the national scale, we evaluated the distribution of functional diversity and its major biological, environmental and anthropogenic determinants for Costa Rica; furthermore, we tested the surrogacy and mismatch of functional, taxonomic and

phylogenetic diversity in Colombia to assess whether the use of a single measure could represent the other as a basis for prioritizing and planning conservation actions.

We found that mammal functional diversity varies globally with clear patterns similar to species diversity, but influenced by ecological scale, species richness and geographic area in the world´s ecoregions; in turn, we determined that species richness and functional diversity do not match at global scale, so that for certain ecoregions there are underlying processes that must be considered, while a single measurement is not enough for conservation planning. Additionally, we found that threatened species are strong influencers of functional diversity at ecoregional resolution, explaining 60% of this diversity on a global scale, and varying spatially with ecoregions influenced in more than 70% of their functional diversity by threatened species. Regionally, we found that human intervention and species at risk are the main determinants of current functional diversity, where certain ecoregions have already suffered from drastic functional loss and others are more likely to suffer this loss from vulnerable species extinction. In terms of the functional attributes variation we found strong variation between Central and South America, where the convergence of functional attributes generates continuous gradients, while identifying where abrupt changes occur in assemblages´ functional composition. Nationally, we determined that functional diversity differs from the species richness gradient and is strongly influenced by the composition (*i.e.*, bats and rodents), identifying three functionally distinct regions for Costa Rica, and that environmental, biogeographic and anthropogenic determinants influence varying depending on the region. Furthermore, we found that the three measures (*i.e.*, functional, phylogenetic and taxonomic) vary spatially in Colombia, indicating spatial mismatch between them, also highlighting the need to select priority areas considering these three dimensions and thus ensuring the preservation of evolutionary history, ecosystems´ functioning and species diversity nationally.

Overall, functional diversity is a recent measure that advances not only in the ecological understanding of diversity but also allows to do conservation planning considering the species-ecosystem relationship, thus with implications for ecosystems functioning and resilience. Global variation and convergence can be the response to environmental filtering as well as an extraordinary trait convergence in assembling communities associated with ecosystem type and ecological regions. The results of the analyses at multiple scales allow highlighting the variation that exists in this measure of diversity, and the need to understand the patterns at different ecological and planning scales. In terms of conservation, the results have implications for the prioritization and planning of critical conservation areas, the differential impact of human intervention and the need to explore the spatial variation of the species-ecosystem relationship and its key drivers. Functional diversity should be a measure considered in future conservation schemes and its understanding will allow better resolution for exploring ecological patterns and how to support decision-making for biodiversity management and conservation.

1. Introducción general

Los mamíferos son uno de los grupos de especies más importantes para el funcionamiento de los ecosistemas del planeta (Asquith et al. 1997; Bakker et al. 2006; Ceballos & Ehrlich 2002), y a pesar de ocupar casi la totalidad de estos, aún muchos aspectos de su ecología, estado de conservación y papel en los ecosistemas se mantienen desconocidos (Schipper et al. 2008). Actualmente cerca del 25% de todas las especies de mamíferos del planeta se encuentran en riesgo de extinción (Schipper et al. 2008), y esta tendencia es aún más marcada y delicada a nivel de poblaciones (Ceballos & Ehrlich 2002; Ceballos et al. 2005; Ceballos et al. 2010). A pesar de las múltiples iniciativas a múltiples escalas para asegurar su conservación (Ceballos et al. 2005; Hoffmann et al. 2011; Hoffmann et al. 2010), la mayoría de esfuerzos aún no han logrado detener la pérdida acelerada de especies y poblaciones a escala global, siendo incluso esta época llamada la sexta extinción en masa global (Barnosky et al. 2011; Ceballos et al. 2010; Dirzo et al. 2014). La conservación de la biodiversidad impone retos supremamente grandes para la ciencia, y en general para la humanidad, con el fin de mantener la mayor biodiversidad posible ya que de esta depende la provisión de bienes y servicios de los cuales dependemos como sociedad (Armsworth et al. 2007; Costanza et al. 1997; Daily et al. 1997).

Con el fin de entender los grandes procesos relacionados con la diversidad biológica, la macroecología se ha encargado de evaluar los patrones de la diversidad a escalas globales y sus patrones subyacentes (Beck et al. 2012; Gaston & Blackburn 2006), siendo esta fundamental incluso para la definición de prioridades de conservación a estas escalas (Brooks et al. 2006; Brooks et al. 2010; Carwardine et al. 2008; Myers et al. 2000; Ricketts & Imhoff 2003). Numerosas medidas han sido utilizadas para entender diferentes aspectos de la diversidad biológica, siendo la riqueza de especies la medida más común e históricamente utilizada (Brown 1981; Buzas 1972; Gaston 2000; Hillebrand 2004; Kerr 1997; Klopfer & MacArthur 1960, 1961; MacArthur & MacArthur 1961; Myers et al. 2000; Reid 1998; Rovero et al. 2014; Sechrest 2003). Sin embargo, con el avance de la ecología, otra medidas han surgido, las cuales abordan diferentes aspectos relacionados no sólo con el número de especies si no también con aspectos evolutivos y funcionales (Blaum et al. 2011; Cardoso et al. 2011; Devictor et al. 2010; Pavoine et al. 2013; Safi et al. 2011; Stevens & Tello 2014). La diversidad funcional evalúa la diversidad de funciones que las especies cumplen en el ecosistema (Hooper et al. 2002; Petchey & Gaston 2002b) y por ende la relación con la capacidad de resiliencia y en general la funcionalidad de los ecosistemas (Hooper et al. 2002; Mayfield et al. 2005; Petchey & Gaston 2002a, b). Específicamente, la diversidad funcional puede ser dividida en tres niveles fundamentales: la riqueza, la equidad y la divergencia funcional, las cuales evalúan diferentes aspectos de la diversidad en función del espacio de nicho ocupado por las especies, la equidad en la distribución de la abundancia y el grado en el que la distribución del espacio de los nichos maximiza la divergencia entre los caracteres funcionales de la comunidad, respectivamente (Mason et al. 2005). Esta diferenciación ha permitido el entendimiento de múltiples aspectos de la diversidad funcional, aumentando el entendimiento de los ecosistemas desde la perspectiva del papel de las especies (Mason et al. 2012; Mouchet et al. 2010; Mouillot et al. 2011).

El estudio de la diversidad funcional, originalmente formulado para plantas (Tilman 2001), ha sido uno de los principales ejes para entender el funcionamiento de los ecosistemas y no es sino hasta años recientes que ha adquirido mayor atención y relevancia para animales (Blaum et al. 2011). Así, el número de iniciativas enfocadas en evaluar la diversidad funcional para otras especies diferentes de plantas ha venido en aumento, contando en la actualidad con aproximaciones para grupos tan variados como arañas, fitoplancton y vertebrados (Buisson et al. 2013; Cardoso et al. 2011; Edwards et al. 2013; Newbold et al. 2014; Safi et al. 2011). La mayoría de estas aproximaciones se han enfocado en entender los patrones macroecológicos subyacentes a esta medida de la diversidad, siendo para mamíferos aún escasas las aproximaciones en todas las escalas (Belmaker & Jetz 2013; Flynn et al. 2009; Rodríguez & Ojeda 2014; Safi et al. 2011). El entendimiento de la diversidad funcional en mamíferos puede servir como modelo para entender procesos ecosistémicos a escalas mayores, abordando uno de los grupos de mayor influencia en procesos de paisaje y proveyendo información sobre la funcionalidad relacionada con cadenas tróficas y otros aspectos en que los mamíferos juegan un papel fundamental (Belmaker & Jetz 2013; Farias & Svensson 2014; Flynn et al. 2009; Safi et al. 2011).

Considerando el alto riesgo de extinción que enfrentan los mamíferos a escala global (Schipper et al. 2008) y la creciente pérdida de poblaciones y extinciones locales (Ceballos & Ehrlich 2002; Ceballos et al. 2005; Ceballos et al. 2010), entender los procesos funcionales asociados a los mamíferos y su relación con el riesgo de extinción podría resultar en un mejor entendimiento de los procesos ecológicos y biogeográficos subyacentes, y consecuentemente informar con mejor resolución la toma de decisiones en conservación (Armsworth et al. 2007; Blaum et al. 2011; Buisson et al. 2013; Devictor et al. 2010; McMahon et al. 2011; Mouillot et al. 2013). Estudios recientes han indicado como la definición de prioridades debería incorporar las perspectivas evolutiva y funcional en los análisis (Barragán et al. 2011; Buisson et al. 2013; Devictor et al. 2010; Mouillot et al. 2013; Petchey & Gaston 2002a; Sundstrom et al. 2012). Adicionalmente, entender los factores subyacentes y determinantes de la diversidad funcional (Hoeinghaus et al. 2007;

McMahon et al. 2011), y la influencia de la escala (Bengtsson et al. 2002; Lennon et al. 2001; Schonewald-Cox et al. 1991; Whittaker et al. 2001), pueden mejorar considerablemente la definición de prioridades y en general los esquemas de conservación.

Con base en los conceptos anteriores, el objetivo principal de este trabajo es el contribuir al entendimiento de los patrones globales de la riqueza y diversidad funcional en mamíferos, identificar los principales determinantes de esta diversidad, el efecto potencial del riesgo de extinción y la influencia de la escala sobre estos patrones. Dada la naturaleza del trabajo, se usa la diversidad funcional bajo el concepto de riqueza funcional, entendida como la cantidad de nicho espacial ocupado por especies en la comunidad (Mason et al. 2005). El énfasis principal del trabajo es hacia los mamíferos Neotropicales, pero a manera de contexto se parte de una aproximación global al tema del trabajo. Este está estructurado a través de las escalas espaciales de lo global pasando por lo regional hasta lo local, usando diferentes aproximaciones espaciales con sentido ecológico. A través de estas escalas se evalúan aspectos relacionados con la divergencia funcional derivada de la escala ecológica (*i.e.*, similitud entre hábitats y ecoregiones), la influencia de diferentes determinantes ambientales, biológicos y antropogénicos sobre la riqueza y la diversidad funcional, la relación entre diversidad taxonómica, funcional y filogenética, la representatividad de las áreas protegidas sobre la diversidad y la influencia del riesgo de extinción sobre estos patrones. El trabajo pretende además de brindar algunos elementos para la definición de prioridades de conservación, responder algunos cuestionamientos ecológicos y biogeográficos sobre los patrones de la diversidad funcional. Como modelos de estudio se evalúan estos patrones a escala global, regional en el Neotrópico y local en Costa Rica y Colombia.

2. Estructura de la tesis

La presente tesis doctoral está estructurada en tres capítulos que abordan las diferentes escalas de análisis de lo global a lo nacional. Así mismo, la tesis 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 desde la perspectva global con análisis macroecológicos de patrones de distribución de la riqueza y la diversidad funcional y a medida que la escala disminuye, se explora la influencia de los diferentes determinantes ambientales y antropogénicos, esfuerzos de conservación y la incongruencia espacial entre estas medidas.

El primer capítulo aborda la perspectiva global usando como unidad de análisis las ecoregiones y su correspondiente clasificación en biomas (i.e., tipos mayores de hábitat) y ecozonas o regiones zoogerográficas, de acuerdo a la clasificación de Olson et al. (2002). Este primer capítulo está compuesto por dos artículos: un primer artículo aborda los patrones globales de variación de la diversidad funcional y sus implicaciones en conservación y un segundo artículo que aborda la influencia de las especies en riesgo de extinción sobre la diversidad funcional.

El segundo capítulo aborda la diversidad funcional de mamíferos a escalas regionales, enfocándose en la región Neotropical. Este capítulo está a su vez compuesto de dos artículos: el primer artículo aborda la distribución de la diversidad funcional para todo el Neotrópico, en especial evaluando la influencia de las coberturas naturales y las especies en riesgo de extinción; el segundo artículo evalúa la variación de la riqueza de caracteres funcionales para un área menor ubicada en la conexión entre Centro y Suramérica.

El tercer capítulo aborda las perspectivas de conservación y patrones ecológicos de la riqueza y la diversidad funcional a escalas de Colombia y Costa Rica. Este capítulo se compone de tres artículos en los cuales se evalúa la eficiencia de las áreas protegidas para proteger la diversidad de mamíferos en Costa Rica, los patrones de distribución de la riqueza, diversidad funcional y la influencia de determinantes ambientales, biológicos y antropogénicos sobre estos patrones también en Costa Rica y los determinantes ambientales e incongruencia espacial de diferentes medidas de diversidad de mamíferos en Colombia.

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

3. Objetivos

3.1. Objetivo general

Evaluar los patrones de distribución, determinantes de la riqueza y diversidad funcional de los mamíferos y su relación con el riesgo de extinción y conservación a diferentes escalas.

3.2. Objetivos específicos

- Evaluar los patrones de distribución de la riqueza y diversidad funcional a escala global, sus determinantes y la influencia del riesgo de extinción.
- Determinar los patrones de distribución de la riqueza y diversidad funcional de mamíferos a escala regional, la influencia de la escala, sus determinantes y el riesgo de extinción.
- Evaluar los patrones de distribución y determinantes ambientales, biológicos y antropogénicos de la riqueza y la diversidad funcional e mamíferos y su conservación a escalas nacionales de planificación.
- Evaluar la coincidencia o divergencia espacial de diferentes medidas de diversidad de mamíferos a diferentes escalas.

4. Hipótesis

H1: La diversidad funcional de mamíferos sigue los patrones globales de distribución de diversidad de especies previamente propuestos y está influenciada por el área y el tipo de hábitat.

H2: Las especies de mamíferos en peligro de extinción influencian de forma significativa la diversidad funcional a escala de ecoregiones, afectando su funcionalidad y capacidad de resiliencia.

H3: A escala regional la diversidad funcional de mamíferos mantiene los patrones globales de distribución pero está fuertemente influenciada por las coberturas naturales y las especies en riesgo.

H4: La riqueza de especies y caracteres funcionales de mamíferos en el contínuo Panamá-Chocó denota un gradiente de reemplazo de caracteres en función del tipo de hábitat.

H5: Las áreas protegidas de Costa Rica protegen efectivamente la riqueza de mamíferos y sus ámbitos de distribución como aproximación a sus poblaciones.

H6: La distribución de la diversidad funcional en Costa Rica está influenciada por variables ambientales, biológicas y antropogénicas, permitiendo la regionalización funcional del territorio nacional.

H7: Existe congruencia entre las diferentes medidas de diversidad de mamíferos en Colombia (*i.e.*, taxonómica, funcional y filogenética) a escalas espaciales.

5. Capítulo 1. Diversidad funcional de mamíferos a escala global y la influencia de las especies en riesgo

5.1. Patterns of variation of mammal functional diversity at biogeographic scales and its implications for conservation

Classification: Biological Sciences–Ecology

Global mammal functional diversity

Patterns of variation of mammal functional diversity at biogeographic scales and its implications for conservation

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Abstract

Biodiversity loss is one of the most severe global problems caused by humans; for example, at least 25% of mammal species are threatened with extinction. Despite their role as key components of ecosystem dynamics, the functional roles of mammals have not been well explored and assessed, especially from the macro-ecological perspective. Incorporating functionality as a criterion for priority selection would potentially better inform and preserve different aspects of biodiversity also related to ecosystem function and resilience. Here we evaluate mammal functional diversity (FD) patterns at global scale and subsequent lower biogeographical (larger) spatial scales using an ecoregional approach. We specifically addressed distribution of mammal functional diversity and hot spots and how species richness and area explain mammal functional diversity at multiple biogeographical scales and the geographic mismatches between these metrics. We found at least five significantly clustered hot spots across the globe. Also, ecoregion species richness and area significantly explain functional diversity, but is also influenced by the realm and major habitat types (biomes). We noted that while functional diversity varies between realms, similar biomes have similar functional diversity and are clustered independent of its location. Species richness positively influences functional diversity for the entire globe, while area showed some stable influence in certain realms. We also identified at least five realms where spatial mismatch occur between species richness, area and functional diversity. Mismatch between this measures likely occur when local variables influence species´ assemblage processes instead of macroecological patterns. Our results contribute to the understanding of the determinants of mammal functional diversity and to conservation planning by providing further insights on diversity metrics distribution and priorities definition considering the evolutionary and functional components. Future analyses for biodiversity conservation should incorporate functional diversity at multiple spatial (biogeographical) scales.

Introduction

Loss of biodiversity is one of the most severe global environmental problems caused by human activities (1). Human-related extinction rates are so high that it is likely that Earth has entered the sixth mass extinction (2). For example, more than 25% of the world's mammal species are threatened with extinction, and many populations are declining due to human activities (3, 4). Recognition of global patterns of species distribution is useful for understanding large-scale trends that have conservation implications (5-7). For example, knowledge of global patterns of species distribution of land mammals has allowed us to evaluate population extinction trends, the overlap of species richness hotspots, endemism, and endangerment, and to define sites critical for conservation (4-6).

It is well known that mammal ecological traits such as geographic range size, body mass, population density, trophic level, life history and their interactions are associated with extinction risk (8, 9). Recently, these functional traits have been identified as surrogates of ecosystem function, resilience, and environmental services (10-14), and the evaluation of functional diversity in a macro-ecological perspective has become a powerful tool for evaluating species and ecosystem dynamics and conservation potential (8, 9, 15). Originally developed for plants and recently applied to animals (11, 16-18), functional diversity analyses emphasize understanding the effects and responses of species and assemblages to ecosystem processes (16, 19). Because mammals play a critical role in ecosystems, declines of many mammal populations and loss of species (4, 5, 20-22) warrants urgent assessments of functional diversity and how it may vary across geographical scales (15, 23-25). In a first attempt to assess global mammal functional diversity, Safi et al. (13), evaluated the relationship and surrogacy of functional and phylogenetic diversity and species richness across a global grid of cells. Their demonstrated the importance of environmental conditions such as annual temperature and seasonality as determinants of the spatial mismatches between different diversity measures. Here we extend their work by analyzing patterns of mammal functional diversity at four biogeographic scales, which may have greater biological relevance. We also evaluated the relationship of functional diversity with primary macro-ecological determinants (*i.e.,*species richness and geographic area), identifying the frequency and distribution of hot spots and spatial mismatches at an ecoregional resolution. We used emergent functional groups, determined by Gower similarity (26), on the basis of the three traits (*i.e.,*mass, habitat type and trophic guild) that represent different dimensions of niche and resource use of each species (13) and therefore influences biodiversity and ecosystem functioning relationship (27). We also used the Petchey and Gaston functional diversity index (28), based on the functional richness definition (29), using the same three traits, following previous recommendations (30, 31). The biogeographical scales used include realms (8; also known as ecozones), biomes (14 major habitat types) and ecoregions (867), which seems a logical regionalization of the globe from the ecological perspective, and yet, with few support of macroecological processes acting at these scales. Few assessments of macro-ecological trends of functional diversity have been done to our knowledge, especially for mammals (13), therefore exploratory assessments can increase our knowledge of the spatial scale most relevant ecologically. Traditional conservation and macroecological studies have evaluated the influence of area on multiple diversity measures (32-37), have identified hot spots of high or unique diversity features (38-42), the spatial mismatch between diversity measures (13, 24, 43) and the value and meaningfulness of the ecological regionalization of the world (44-50). However, to our knowledge this topic and associated hypothesis have received limited attention, including those related to mammal functional diversity. Nevertheless, we expected similar predictions of these four topics when exploring patterns of functional diversity. Based on these previous approaches, our work is focused on how geographic extent exerts and effect on mammal functional diversity, the influence of multi-scales ecological regionalization on this measure, the identification of functional diversity hot spots and where spatial mismatch occur between species richness, area and functional diversity.

We specifically address the following questions: i) How does species richness and functional diversity vary across biogeographic scales?; ii) are there functional diversity hot spots and gradients of functional diversity globally and what is the conservation status of those hot spots?; iii) what are the macroecological relationships of mammal functional diversity with species richness and area at different biogeographic scales?; and iv) where does spatial mismatch occur between species richness, geographic area and functional diversity occur?

Our predictions include that both functional diversity and species richness vary spatially across ecoregions but exert similarities according to similar biomes; also that area has a significant effect on both measures and that there are considerable hot spots of both measures and significant mismatches spatially, where the two measures do not coincide.

Results and discussion

Species richness and functional diversity variation at different biogeographic scales

Species richness (SR) is related to functional diversity, so understanding the patterns of distribution of mammal richness at different global biogeographic scales was the first step to understand the variation of functional diversity across scales. Mammal species richness from realms to ecoregions, showed the classic latitudinal trends of species richness, with greater species richness at lower latitudes and continental landmasses (4, 51-53). For example, greatest species richness occurred in tropical and subtropical grasslands and savannas (Mean ± SD = 142 ± 85 species) whereas lowest species richness occurred in the tundra (25 ± 19 species; Figure S1B). Interestingly, species richness was remarkably constant across similar biomes (e.g., tropical and subtropical) in different Realms. For example, biomes within the Afrotropics and Australasia, and Oceania, the Neotropics, and Indomalayan (ML-X^2= 82711.72, $p<0.0001$; Figure S2). The mean (± SD) number of mammal species across all ecoregions was 93 ± 65. The global frequencies of the number of mammal species across the world's 867 ecoregions fit a Weibull distribution with more ecoregions with lower species richness (Figure S3). This suggests that independent of its location, the same biomes and ecoregions in different realms have roughly similar species richness (50).

We estimated the Functional Diversity (FD) for the world's ecoregions based on Petchey and Gaston FD index (28) and generated mammal emergent Functional Groups (FG) for each ecoregion (26). Global distribution of both functional diversity measures showed a latitudinal trend with higher values centered on the tropics (Figure 1). Both functional diversity and functional groups were heterogeneous, with regions of high functional diversity towards the tropics especially in the Andes-Amazon (Neotropics), Equatorial and East Africa (Afrotropics), and southeast Asia (Indomalaya). From those tropical regions, functional diversity tended to decrease towards the poles (Fig. 2). Functional diversity and number of functional groups also varied at the biome scale ($H = 1 74.53$, $p < 0.0001$ and $H = 176.31$, $p < 0.0001$, respectively). Tropical and subtropical grasslands, savannas, and scrublands had the greatest functional diversity and mangroves the highest number of functional groups. Mean (±SD) functional diversity values for all ecoregions were 3.42 ± 2.31 and mean number of functional groups (±SD) was 6.46 ± 2.38. Both measures were higher for the Afrotropic, Neotropic, and Indomalaya realms (H = 223.08, $p < 0.0001$ and H = 258.83, $p < 0.0001$, respectively). Our results are generally similar to studies comparing functional diversity of site-specific communities and global patterns with other taxa, such as spiders (54), birds (55), and mammals (13, 56). In relation to the patterns observed in our study, we hypothesize d that striking differences between temperate and tropical regions could be related to larger mammal geographic ranges in higher latitudes, which reflects a lower beta diversity (*i.e.,*species turnover) and species evolutionary history. We believe there are more morphologically cryptic species in temperate regions (multiple lineages within the same taxonomic species), and those species may underestimate our evaluation of functional diversity.

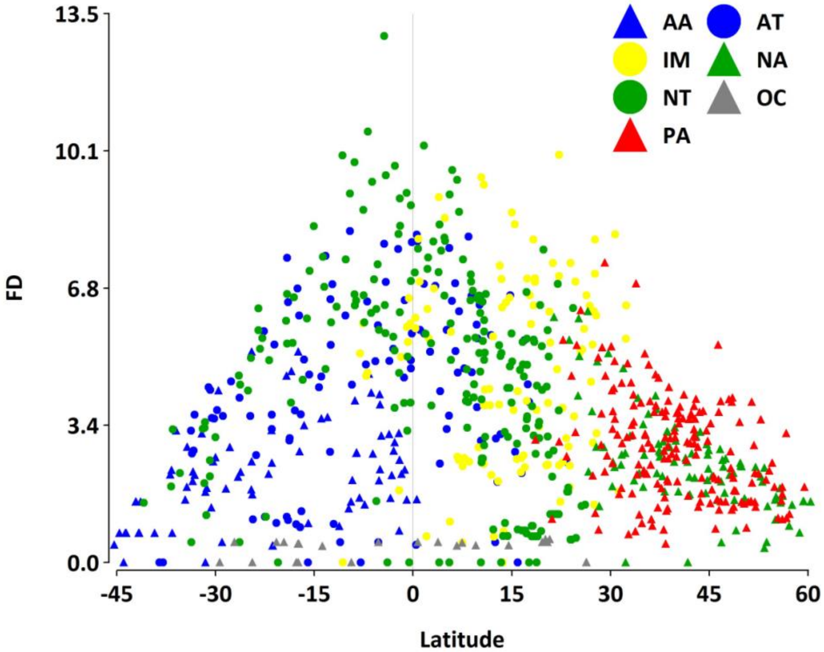

Fig. 1. Mammal functional diversity (FD) across the world's ecoregions by latitude and categorized by realm: AT = Afrotropic, IM = Indomalaya, NT = Neotropic, AA = Australasia, AN = Antarctic, NA = Neartic, OC = Oceania and PA = Palearctic**.**

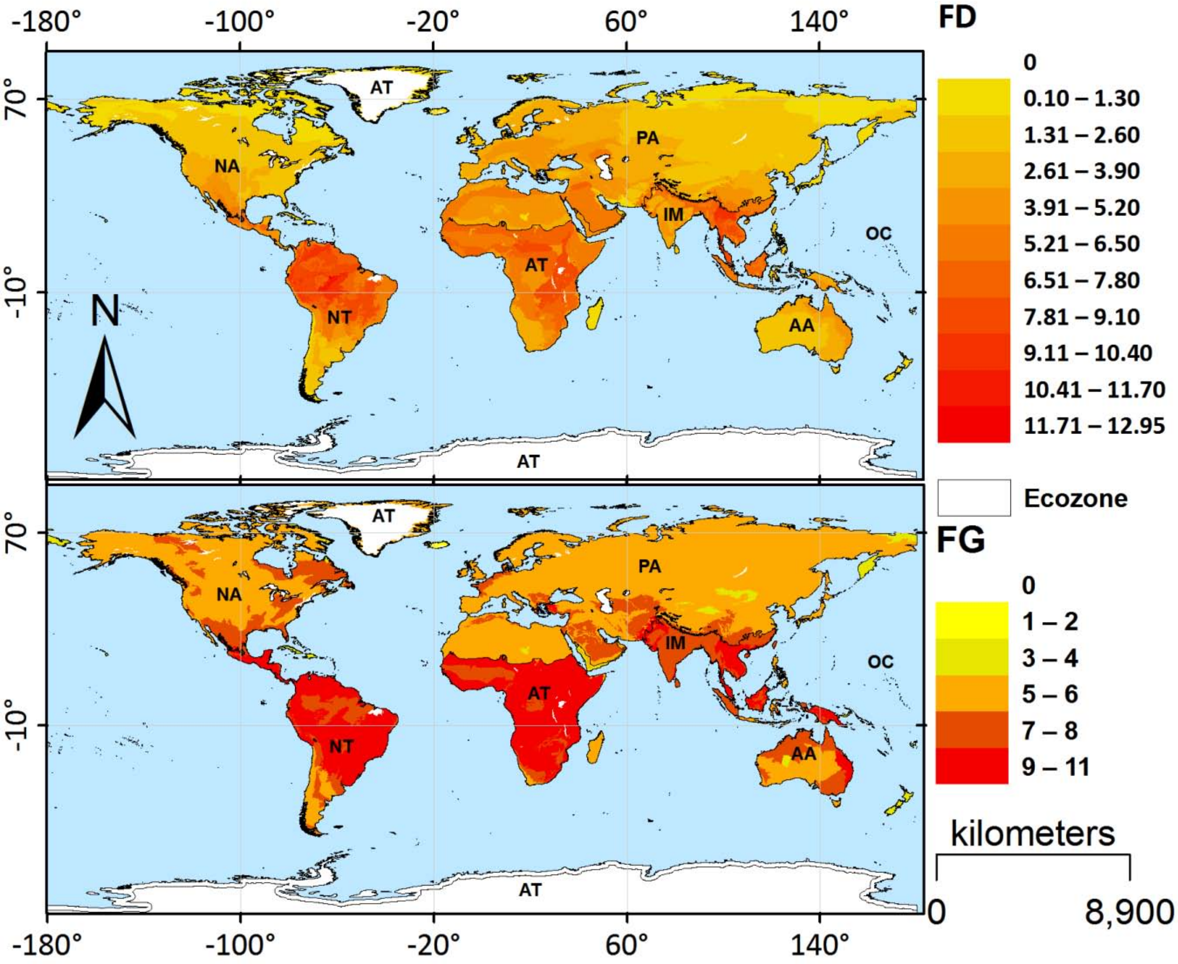

Fig. 2. Spatial representation of mammal functional diversity (FD) across the world's ecoregions by latitude and categorized by realm: AT: Afrotropic, IM: Indomalaya, NT: Neotropic, AA: Australasia, AN: Antarctic, NA: Neartic, OC: Oceania and PA: Palearctic.

Cluster analysis separated and grouped tropical from temperate realms and biomes (Fig. 3), suggesting both measures of functional diversity behaves similarly at finer resolutions. These results may have implications for conservation since most functionality studies occur at local scales and large areas often lack information about functional processes (10). While many aspects of functional diversity still need to be addressed, our results of biome-based similarities can be used to support defining conservation measures at different spatial scales. Hypothetically, we might expect similar functional diversity characteristics when shifting among scales, such as from biomes to landscapes. The need for 'reference' assemblages becomes important when the conservation priorities include the reconstruction of functionally complete assemblages (57). Our results also suggest that ecoregions are suitable for establishing global patterns based not only on structural and environmental features (46, 50), but also when assessing species' roles and the relationship between biodiversity and ecosystem function. This however opens a new series of questions regarding the mechanisms operating on abiotic filtering of species assemblages (58, 59) or potential convergent trait evolution (60).

Hot spots and gradients of functional diversity at biogeographic scales

As a first approach to evaluate conservation goals based on functional diversity across ecoregions, we assessed where higher functional diversity occurred by selecting those areas where high or low functional diversity values clustered spatially. This spatial clustering analysis allowed us to identify spatial gradients of functional diversity and where dramatic changes in this measure occurred globally. We found a general clustering of high functional diversity values in all tropical realms and clusters of low values mostly in boreal areas of the Nearctic and Palearctic realms (Fig. 4). Noticeable shifts occurred at southern South America and Northern Mexico, Equatorial Africa and Southeast Asia. Of the high ecoregion clusters, 50.2% occur in the Neotropical realm, followed by 24.2% in the Afrotropics, 22.8% in the Indomalaya and only 1.4% for the Palearctic and Nearctic realms. For biomes, 50.2% occur in the T&S moist broadleaf forests; followed by T&S grasslands, savannas, and shrublands (13.0%) and T&S dry broadleaf forests (9.8%). Of the total hotspots, 49% are considered as Critical/Endangered and 28.8% as Vulnerable.

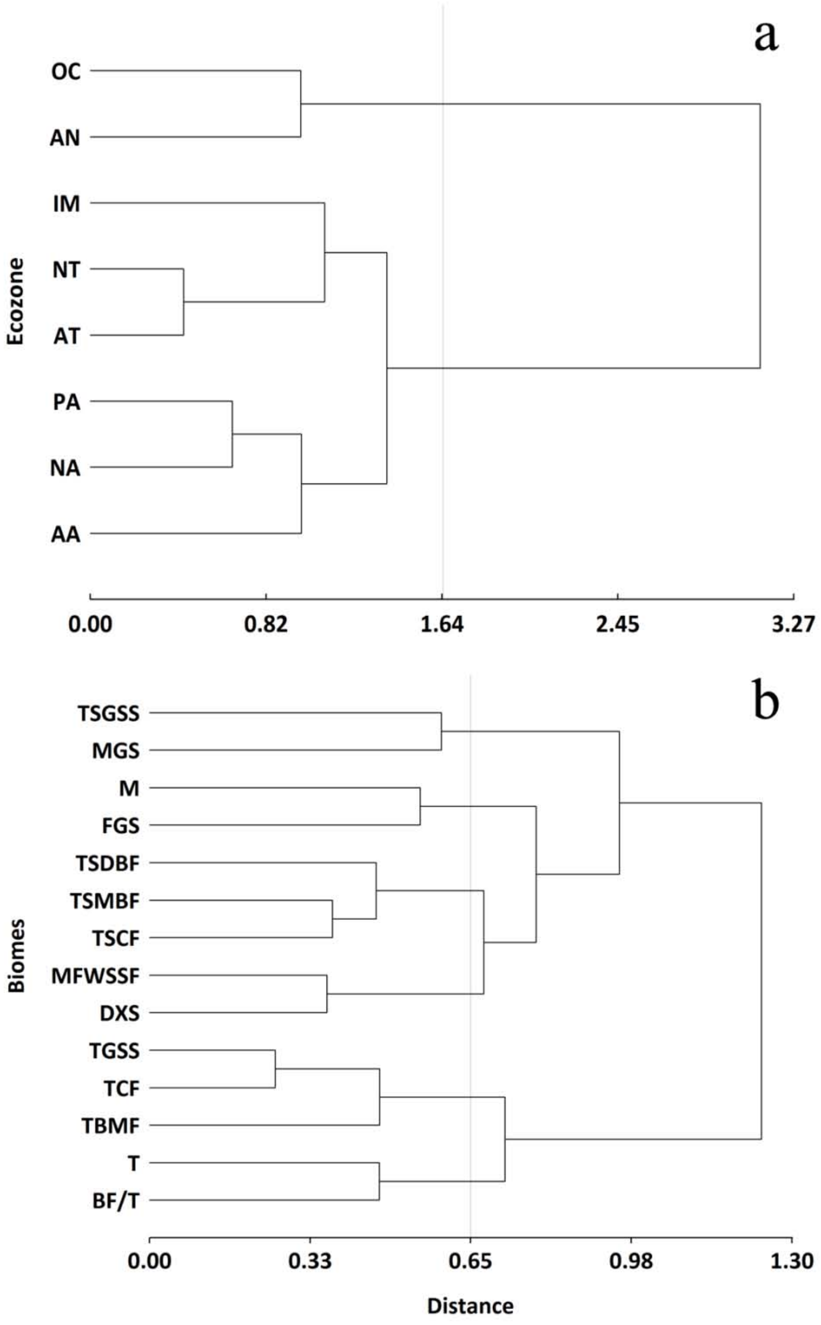

Fig. 3. Cluster analyses for a) realms and b) biomes according to mammal species richness (S), Functional Diversity (FD) and number of Functional Groups (FG). Mahalanobis distance with weighted average linkage was used to account for colineality between variables. Realms abb.: AT: Afrotropic, IM: Indomalaya, NT: Neotropic, AA: Australasia, AN: Antarctic, NA: Neartic, OC: Oceania and PA: Palearctic; Biomes: B F/T: Boreal Forest/Taiga, DX S: Deserts and xeric shrublands, FGS: Flooded grasslands and savannas, M: Mangroves, MFWS: Mediterranean forests, woodlands and scrub, MGS: Montane grasslands and shrublands, TBMF: Temperate Broadleaf and mixed forests, TCF: Temperate Coniferous forests, TGSS: Temperate grasslands, savannas, and shrublands, TSCF: Tropical and subtropical coniferous forests, TSDBF: Tropical and subtropical dry broadleaf forests, TSGSS: Tropical and subtropical grasslands, savannas, and shrublands, TSMBF: Tropical and subtropical moist broadleaf forests and T: Tundra.

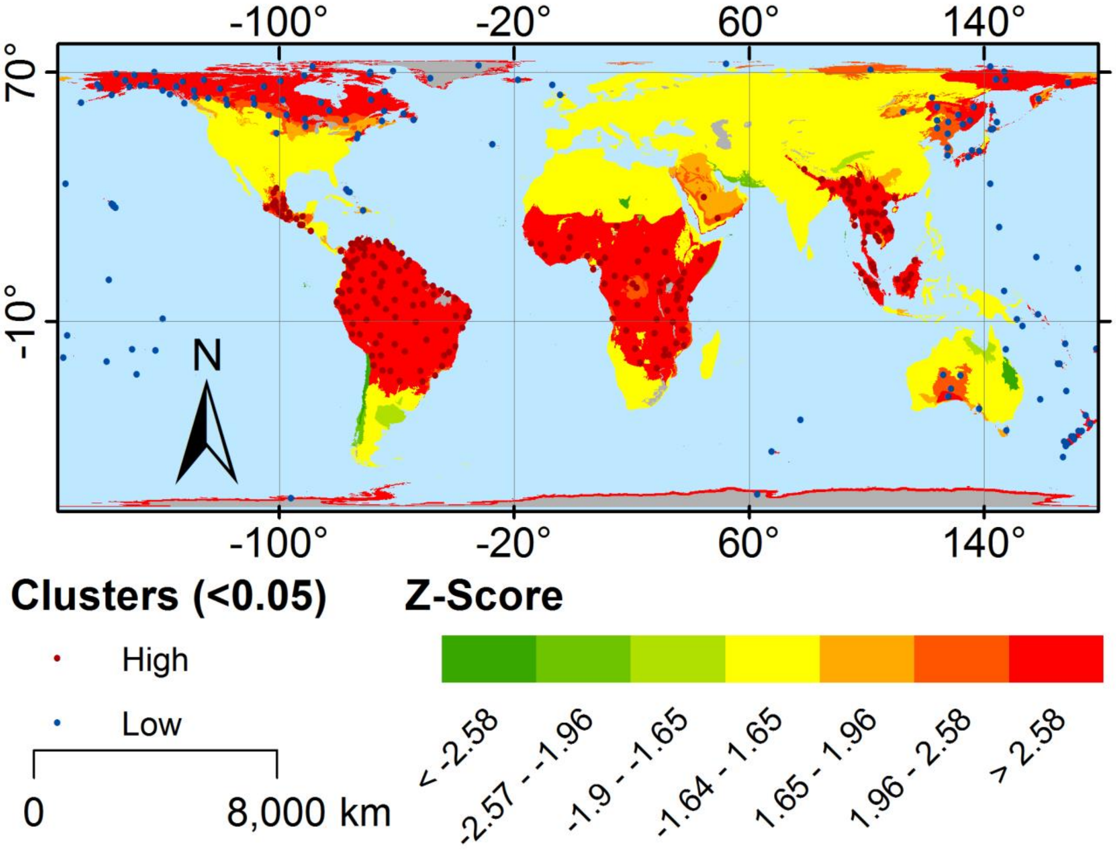

Fig. 4. Hot spots of mammal functional diversity across the world´s ecoregions. Z-scores accounts for Standard Deviations of the Getis-Ord Gi test and red and blue dots indicate significant (<0.05) hot and cold spots, respectively, according to FD values. Note the gradients on functional diversity where significant high and low values occur.

The clustering of functional diversity values for most tropical ecoregions supports previous assessments of latitudinal gradients of species diversity (53, 61). Considering the functional diversity measures used incorporated species richness, we expected they would covary with species richness (31). Nevertheless, this first approach to ecoregion functional diversity gradients can potentially inform where changes in functional diversity occur, adding to our understanding of ecosystem functional gradients as related to ecosystem-species relationship gradients (62, 63). We believe this approach is not necessarily an exclusive approach for defining priority areas but instead, functional diversity hotspots should be defined on the basis of those areas where this diversity measure has been more affected by intervention and disturbance (64). We expected that functional diversity would vary across ecoregions and biomes (65); therefore conservation priorities should be based more on the likelihood of change or functional diversity loss than the values per se (27, 66, 67).

Influence of species richness over functional diversity at biogeographic scales

Functional diversity and the number of functional groups were related to species richness, and this relationship was related to the biogeographical scale and biome. We used a generalized linear squares model to test such relationships and accounted for heterogeneity and spatial autocorrelation by using centroid coordinates as a smoothing factor. The best model for functional diversity included the species richness, realm, and their interactions with scale (SR*biome and SR*realm; Table S1-S2). The realm and the realm-species richness interaction influenced functional diversity and our model tested for non-spatial autocorrelation of the residuals (Moran's I Index = 0.01). Tropical realms generally have higher species richness and functional diversity than temperate realms; however, within each type of realm, likely intercepts differ according to biome (Fig.5a). This is likely a consequence of realms encompassing more than one biome, therefore having higher habitat heterogeneity. Nevertheless, the different intercepts indicate there an effect of biogeographic scales, and the ecological characteristics of these realms will likely define functional diversity regardless of species composition.

Functional groups also showed a strong relationship with species richness and biogeographical scale. The high correlation between functional groups and functional diversity index indicated that this index could be used as a surrogate of functional groups.

The best model that explained functional groups included species richness, realm, and their interaction (richness*biome/richness*realm; Table S1); all variables except biome were correlated with the number of functional groups (Table S2). The relationship between functional groups for tropical and temperate realms and biomes followed a different pattern. Tropical ecoregions generally had both higher functional groups and species richness, and the relationship between functional groups and species richness was always positive. Despite differences in the intercept values for biomes across ecoregions, species richness positively affected the number of functional groups.

The measure of functional complementarity or divergence among species trait-space can be considered an indirect measure of species function overlap (28). When considering our results, there was apparent high complementarity when using few traits for certain realms. Thus, further development of 'ideal' functional traits is necessary to better estimate functional diversity for mammals. This will be difficult since the required empirical data is limited or unavailable due to difficulties in obtaining quantitative measures of functional traits (13). However, it remains clear that global variation exists for functional diversity and this variation can be explained by scale.

As expected, variation in functional diversity and functional groups was explained largely by species richness (28, 31). However, the influence of biogeographic scales requires addition considerations for spatial scaling of this diversity measure (10) and may indicate assembly coincidence among similar habitats and biogeographic realms. For example, potential habitat and environmental filtering or trait convergence can be operating at biogeographical scales shaping evolutionary history in turn linked to ecosystem structure and function (13, 58-60, 68, 69). Varying intercepts for this diversity measure highlights how species vary in trait space and how functions among similar ecosystems are coincident, operating independent of species taxonomic composition (70).

Petchey and Gaston (28) identified problems using the number of functional groups as a measure of functional diversity and proposed the FD index as an alternative. Our work defining FD at ecoregional and biome scales were consistent with their assumptions and show that functional diversity is probably the best metric at present to represent functional variety in the world's ecoregions. For the following analyses we only considered functional diversity.

Effect of the area on Functional Diversity at biogeographic scales

Area, defined as geographic extent (32), was a major factor in explaining mammal functional diversity. We observed that ecoregion area and its interaction with realm and biome were strongly correlated to functional diversity globally (Table S1-S2) with non-spatial autocorrelation of the residuals (Moran's I Index = 0.03). As with species richness, functional diversity increased with area. The implications for this relationship will differ based on the scale of observation. Functional diversity tends to increase in most realms, as functional diversity is likely locally-driven (71). In large realms with high variation in biomes and species richness, area affects functional diversity. Excepting Oceania, most realms showed significant increases but intercepts different among realms. The Afrotropic and Neotropic realms had highest variation, likely reflecting the effect of increasing species richness with area due to smaller species´ distributions with both realms near the equator (Fig.5b).

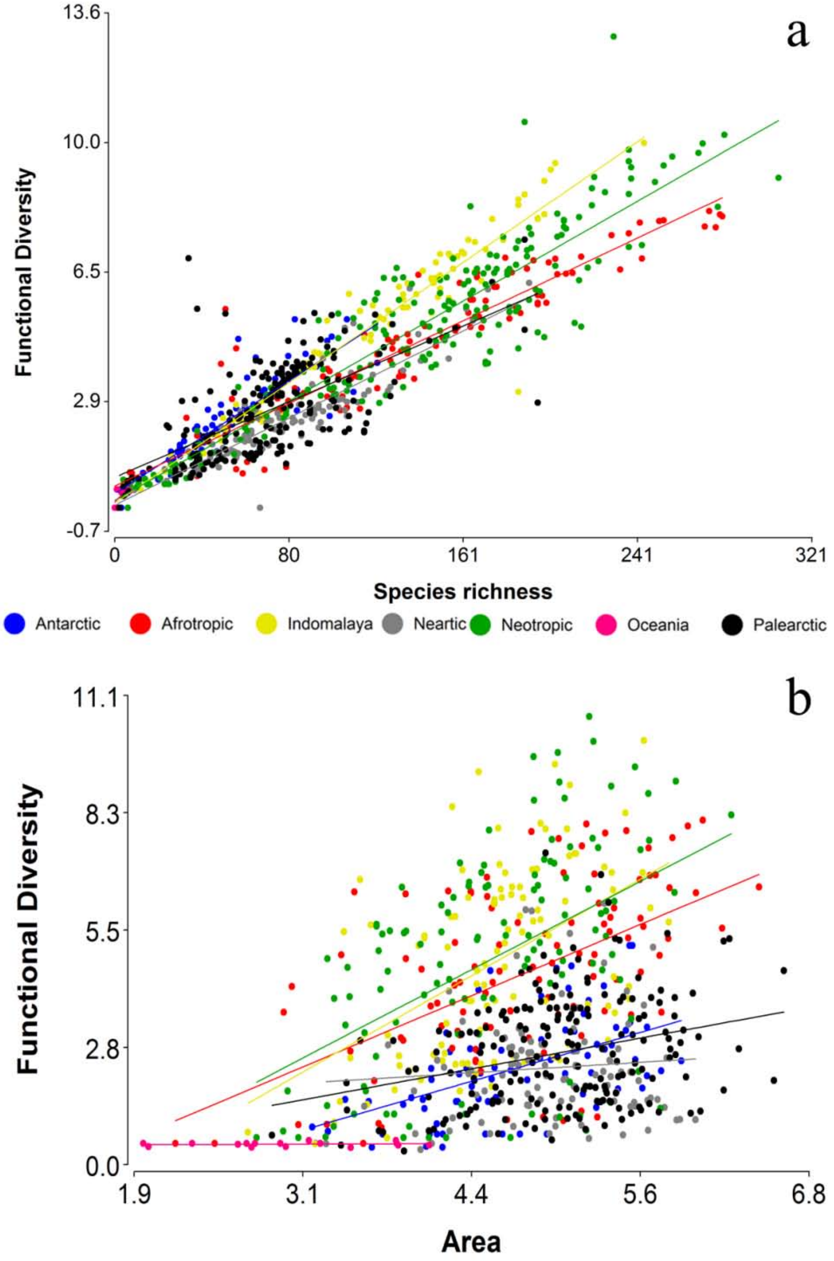

Fig. 5. Relationship between mammal functional diversity (a) and functional groups (b) with mammal species richness and ecoregion geographic extent (area) across the world´s ecoregions classified according to biogeographic realms.

The relationship between diversity and area has been well reviewed in ecological literature (72, 73); in contrast, the area-functional diversity relationship has not. Our results suggest that some general principles observed in the species diversity-area relationship also apply to functional diversity. For example, the size and diversity relationship depends on geographic location (74) and trophic characteristics (33), which suggest it is mediated by site and scale-dependent mechanisms (73) as our results indicated for FD. Thus, variation of traits will consequently affect functional diversity because it largely depends on species traits (*i.e.*, complementarity/singularity of species in trait-space) and different traits respond differently to area effects (32). When functional diversity is used in conservation planning, the effect of area should be considered because functional diversity is influenced by spatial scale. Knowing the magnitude and direction of this relationship across biomes represents a considerable advance in knowledge of the characteristics and trends of the functional diversity of mammals.

Spatial mismatch between species richness and functional diversity

Since functional diversity was strongly influenced by species richness, it is expected that one could be a good surrogate for the other, and that conservation planning and priority selection could use either for determining where to allocate resources for conservation action. However, our identification of spatial mismatches of these two measures could be used to determine those areas where other variables, such as evolutionary history, could be exerting a significant influence (13). We evaluated spatial mismatch between species richness and functional diversity in geographic space by estimating high and low spatial clusters of the residuals from our model. Analyzing patterns of residual clustering allowed us to identify where underlying spatial processes occurred; if clusters of under- or over-prediction occurs, it would mean one or more variables are missing from the model that likely operate at different geographic scales with a non-stationarity pattern from the overall (*i.e.*,global) models (75). We found spatial mismatch between species richness and functional diversity for 96 ecoregions in the Afrotropic, Australasia, Indomalaya, Oceania and Palearctic realms (Fig.6). Overall, ~23% of mismatched ecoregions were in the T&S broadleaf moist forests, ~22% in the deserts and xeric shrublands and ~16% in the Mediterranean forests and woodlands biomes. Of these at least 56% are considered as Critically/Endangered (Fig.6). Interestingly, all the mismatch for ecoregions in the Afrotropic and Palearctic realms tends to the under-prediction, thus some variables other than species richness (e.g., competition, and biogeographic or local environmental variables) explain functional diversity, while all those in the Indomalaya, Australasia and Oceania realms seem to be over-predicted (Fig.6a-b; likely because large patterns and environmental filtering (59, 60)). Nevertheless, as some missing variables are likely influencing functional diversity, species richness may not be a good surrogate for functional diversity in those areas. For the relationship between area and functional diversity we found spatial mismatch in 140 ecoregions in Afrotropic, Australasia, Indomalaya, Neartic, Oceania and Paleartic realms, and in 13 biomes with the largest number in the T&S moist broadleaf forests (Fig.6b). Of the total ecoregions, 55% are considered Critically/Endangered and 25% Vulnerable.

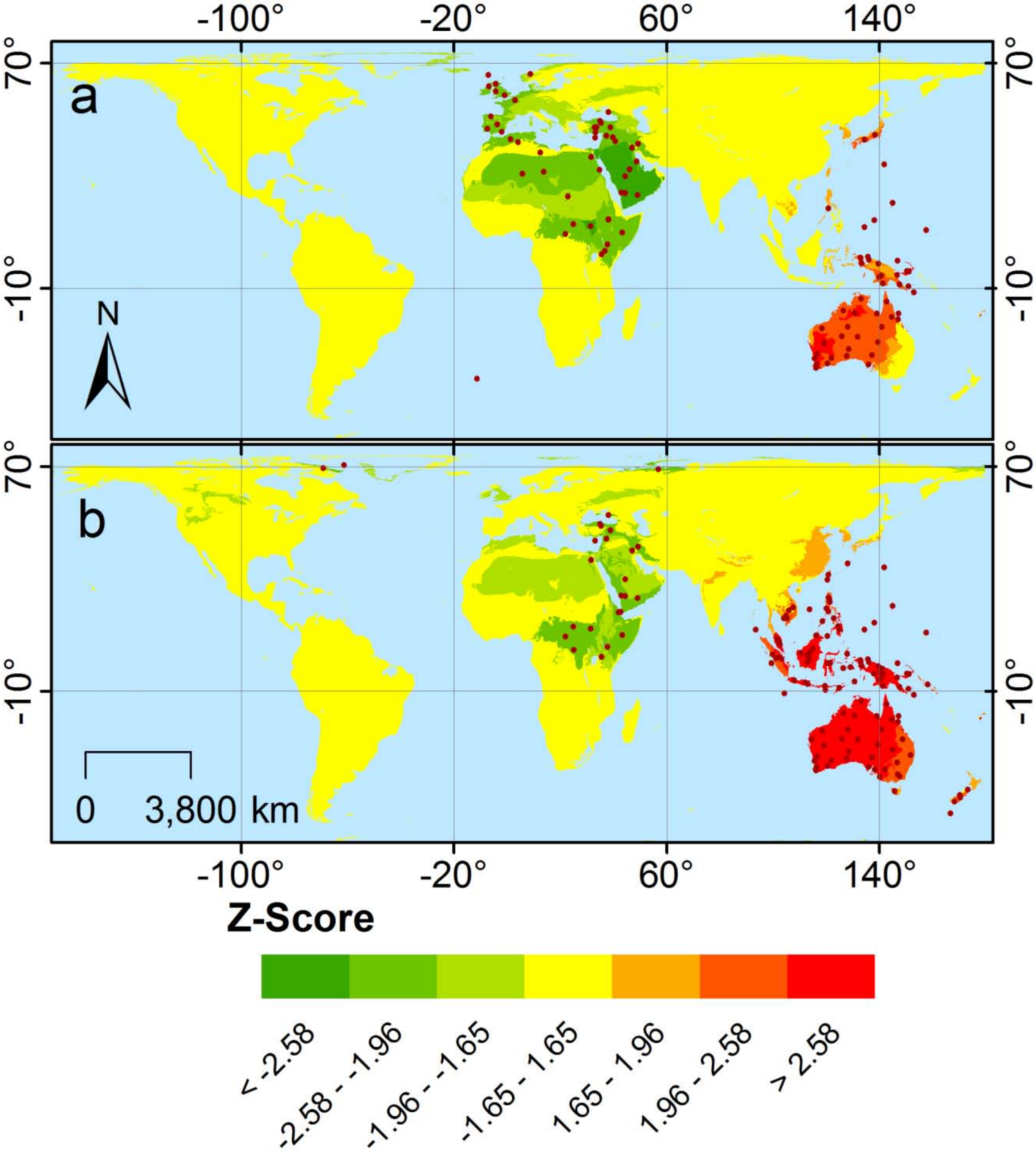

Fig. 6. Spatial mismatch between mammal species richness and mammal functional diversity (a) and ecoregion geographic extent (area) and mammal functional diversity across the world´s ecoregions. Z-scores account for standard deviations of the Getis-Ord Gi test and red dots indicate where significant clusters occur (<0.05). Lower and higher z-scores indicate under- and over-predictions of the model, respectively.

Spatial mismatch indicates where the overall relationship models fail to explain the full variation of the response variable (24). Despite congruence between functional diversity explained by species richness and geographic areas for most ecoregions, we identified mismatches for over 10 % of all ecoregions considering species richness and almost 15% for geographic extent. This indicates that even if species richness could serve as a surrogate for functional diversity (13, 24), it would not explain the underlying processes that would explain the full variation in functional diversity. Assessing how functional varies at multiple biogeographic scales as well as how the influence of species richness and area varies at these scales, could help inform decision-making for conservation. Quantifying FD gradients and spatial mismatches could serve as baselines to understand the effects of disturbance and where functional diversity loss is occurring across multiple spatial extents.

General considerations

Despite biogeographical differences, functional assemblages have similar compositions and can potentially reveal patterns of mammal assemblage (68, 76). Our results revealed complementarity and coincidence across scales, where functional diversity patterns emerge at the global-ecoregional gradient. The generally strong association of functional diversity measures across scales confirms the importance of initially considering multiple ecological scales (77) in functional diversity analyses (10). Understanding these relationships may facilitate predictability of functional diversity composition among ecoregions and potentially larger scales.

Previous studies have described patterns of species richness, especially the high values observed in the tropics (51, 78, 79) with numerous niches and associated mechanisms (13, 52, 79, 80). While species richness and functional diversity in most ecoregions appears positively correlated, these do not necessarily correspond directly with the availability of niches. Since ecosystem stability depends largely on species functions (11), extinction risk represents a direct threat to ecosystem stability and resilience (81). Previous studies have explored the influence of species loss on functional diversity (7, 27, 67) by using different approaches to identify species functional redundancy. Trait-different species are expected to contribute more to functional diversity because species are more functionally complementary within a more species-rich community (*i.e.,*higher functional diversity). In general, the more specialized or rare species have a greater risk of extinction than generalists (82, 83). Understanding global variation in functional diversity and determinants of this variation, together with the understanding the effects of species loss influence on this measure, would better inform conservation priority setting and decision-making. Environmental filtering and trait-convergence seem to play a critical role on species assemblages and therefore on functional diversity, as indicated by correspondence of this measure across similar habitat types. This has important implications for macro-ecological understanding of functional processes, and a trait-based ecological approach (60, 84) seems warranted to understand underlying ecological processes shaping ecosystem functioning and the related conservation implications.

Safi et al. (13) provided insights into functional diversity behavior on a global basis. While our analyses complemented their approach, we also incorporated multiple biogeographic scales. Our approach also differed from other analyses of global mammal diversity in that we used ecologically relevant units in contrast with political boundaries (85) or arbitrary geographical units (e.g. usually plots or hexagons) (4, 6, 13, 23) to explore large geographical and macro-ecological patterns (23). We contend our scales are more sensitive to functional diversity analyses (16), and thereby more applicable to conservation practice (85). Since functional diversity affects ecosystem processes at local scales (11), and probably at the scale of similar habitat types (i.e., biomes) (10). Ecological regions have been quite useful for understanding global scale patterns of ecological functioning and for conservation science (46, 47, 50), therefore, we suggest that FD patterns should be also explored at defined biogeographical scales for ecological and conservation purposes.

We demonstrate the importance of ecological scale on functional diversity and suggest this measure be incorporated in future mammal macro-ecological analyses and for the identification of conservation priorities.

Methods

We analyzed the distribution of mammal functional diversity and number of functional groups across the world's ecoregions. This involved: 1) identifying the areal extent of occurrence for all mammal species at global scale (86); 2) grouping 3,554 species according to trophic guild, habits and body mass; and 3) identifying their distribution on the basis of global ecoregions. We used previously published works (5, 6, 8) and updated databases of mammal traits for three main characters: body mass, diet (herbivore, omnivore and carnivore) and habit (aquatic, fossorial, arboreal, terrestrial, and volant). We consider these traits appropriate for representing different dimensions of resource and habitat use (13). These traits have been identified as drivers of biodiversity and ecosystem function (27), and have proved useful in previous studies for exploring functional diversity in mammals (8, 13, 87, 88) and are available for most species (8, 57, 88). We used the distribution polygons for the world's mammals based on the IUCN Global Mammals Assessment (4, 86). For biogeographical realms, we used the database from WWF (50). The WWF ecoregional approach spatially partitions the planet at three levels or scales: i) ecozones, which divide the globe in eight large biogeographic realms (*i.e.,*Antarctic, Australasia, Afrotropic, Indomalaya, Nearctic, Neotropic, Oceania and Palearctic); ii) 14 biomes or major habitat types; and iii) ecoregions which are the locally specific ecological regions for the world. We performed statistical analyses using Infostat (89) and R software (90), and all spatial analyzes in ArcGIS 10.2 (91). All reported significant statistical tests were considered at 95% (*i.e.,*$p<0.05$).

After consolidating the traits database, we linked the mammal data to its distribution (*i.e.,*extent of occurrence) and overlapped data layers to enumerate and identify all species associated with each ecoregion. Each ecoregion was then associated to its realm, biome, conservation status, and species composition and richness. We used a cluster analysis with Mahalanobis distance and weighted average linkage to account for collineality between species richness, functional diversity and number of functional groups among realms and biomes.

We based our analyses on the Functional Richness definition, which is "… the amount of functional trait space filled by species in the community" (29), herefore, we generated a Functional Diversity (FD) index for each ecoregion using the metric proposed by Petchey & Gaston (67). We selected this metric since it does not depend on abundance data and performs adequately with multiple traits (31), and selected the method used by following previous recommendations on distance selection and other considerations (30). FD is defined as the sum of the dendrogram branch distances necessary to connect all species in the functional space and does not account for abundance (12, 13). We estimated a distance matrix and functional dendrogram based on the Gower distance (unweighted pair group with arithmetic averages) and summed the branches necessary to connect all the species within the ecoregion (13, 30, 31). FD index considers high complementarity when the index is high and thereby indicating species are distant in trait-space, and low complementarity occurs when the index is low, indicating species are more similar. We ruled out the potential unreliability of our index by assessing the closeness of the initial dissimilarity matrix to the ultrametric distance metric between pairs of objects (92). Details on the index and tests can be found elsewhere (13, 28, 92). Following the method proposed by Casanoves et al. and Pla et al. (12, 26), we also estimated the number of Functional Groups (FG) for each ecoregion using the similarity of Gower through a Principal Coordinates Analysis because we had mixed traits (qualitative and quantitative).

We identified functional diversity hot spots and gradients by analyzing spatial clusters of high and low values. We analyzed the functional diversity values for each ecoregion and assessed clusters using the Getis-Ord Gi test by estimating Z-values (*i.e.*,standard deviations) and its associated probability for each ecoregion (93). This analysis identifies where clusters of high or low values are more pronounced than one from a random distribution by comparing the FD values distribution with a theoretical complete spatial randomness distribution as the null hypothesis (93). Mapping ecoregion centroids with their respective FD values allowed us to identify high and low clusters and if they were different. Our conceptualization of spatial relationship was defined by selecting a fixed bandwidth distance ensuring each ecoregion had at least eight ecoregions for spatial comparison; this distance was estimated from ecoregion centroids and was defined as 5,277 km. We then mapped the z-values and selected those that were differed from random, indicating underlying spatial processes influencing FD values and clusters. Continued areas of significant hotspots and corresponding limits with non-significant, or random distributed, ecoregions FD values indicated ruptures or significant changes on FD values, therefore allowing identification of FD gradients.

We performed analyses to test our hypothesis that Functional Diversity, number of Functional Groups and species richness were spatially related. We performed fixed effects generalized linear models in the NLME R package (94), to assess the relationship between Functional Diversity and number of Functional Groups with species richness, ecoregion geographic area, realms, and biomes. The model accounted for variance heterogeneity by fixing the variances for each factor included in the model. We used the Bayesian Information Criterion (BIC) to select the best model from the different variance structures after testing the influence of each factor. Following procedures noted by Schabenberger and Pierce (95), we incorporated the X and Y (*i.e.,*latitude, longitude) coordinates of the ecoregion centroid as smoothing factors to determine spatial correlation. We then again selected the best models based on BIC and built the final model using the selected variance and spatial correlation structures. We tested if spatial autocorrelation occurred for our models by using the Global Moran's I test of the model residuals.

To identify spatial mismatch between species richness and area respecting functional diversity we analyzed significant clusters of the residuals to test if over- or under-prediction areas were spatially clustered, indicating underlying spatial processes or one or more variables missing from our model. We used the residuals of the species richness and the area selected models and performed a Getis-Ord Gi test to identify where high and low clusters or spatial match occurred for species richness and area in response to variation of functional diversity using the same spatial relationship conceptualization as for identifying hot spots.

Acknowledgements

This paper constitutes a partial fulfillment of the Graduate Doctoral Degree Program in Biomedical Sciences (Programa de Doctorado en Ciencias Biomédicas) of the National Autonomous University of México (UNAM) of the first author. J.F. González-Maya acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT), and UNAM (scholarship 255983). This study was supported partially by the Programa de apoyo a proyectos de investigación e innovación tecnológica Project No. IN211811 from UNAM. Partial support was also provided by The Sierra to Sea Institute and The Mikelberg Family Foundation. We would like to thank E. Martínez-Meyer, L. Viquez-R, A. Arias-Alzate, R. Medellín, J. Belant, H. Zarza and J. Schipper for insightful comments and permanent support throughout the research and the early versions of the manuscript. M. Bejarano provided substantial support to the statistical analyses and the manuscript.

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Supporting Information

Here we present the model selection and statistical results for the analyses presented in the text, and supporting figures, all cited in the text.

Table S 1. Generalized Linear Square model (GLS) selection for FD related to species richness, biome, ecozone and interactions. Model and BIC in bold cases was the selected model for each variable. Variance Structure (VS): 1=~1|Ecozone, 2=~1|Biome, 3=~1|Ecozone*Biome. Spatial Correlation Structure (SCS): 1= corSpher(form= ~x + y), 2=corLin(form= ~x + y), 3= corRatio(form=~ x + y), 4=corGaus(form= ~x + y), 5= corExp(form= ~x + y).

Model name	Terms	Variance structure (VS)	Spatial Correlation Structure (SCS)	BIC
Species Richness and Functional Diversity FD				
Model 0	FD~S*Ecozone+ S*Biome	-	-	2514.139
Model 1	FD~S*Ecozone+ S*Biome	1	-	2378.834
Model 2	FD~S*Ecozone+ S*Biome	2	-	2423.41
Model 3	FD~S*Ecozone+ S*Biome	3	-	2391.846
Model 4	FD~S*Ecozone+ S*Biome	1	1	2439.53
Model 5	FD~S*Ecozone+ S*Biome	1	2	2442.488
Model 6	FD~S*Ecozone+ S*Biome	1	3	2299.708
Model 7	FD~S*Ecozone+ S*Biome	1	4	2374.439
Model 8	FD~S*Ecozone+ S*Biome	1	5	2136.094
Model 9	FD~S*Ecozone+ S*Biome / Method ML	1	5	**1866.217**
Species Richness and Number of Functional Group FG				
Model0	GF~S*Ecozone+ S*Biome	-	-	3369.93
Model1	GF~S*Ecozone+ S*Biome	1	-	3375.4
Model2	GF~S*Ecozone+ S*Biome	2	-	3411.42
Model3	GF~S*Ecozone+ S*Biome	3	-	3638.53
Model4	GF~S*Ecozone+ S*Biome	-	1	3346.34
Model5	GF~S*Ecozone+ S*Biome	-	2	3357.33
Model6	GF~S*Ecozone+ S*Biome	-	3	3340.16
Model7	GF~S*Ecozone+ S*Biome	-	4	3370.3
Model8	GF~S*Ecozone+ S*Biome	-	5	**3278.78**
Area and Functional Diversity FD				
Model 0	FD~Area*Ecozone+ Area*Biome	-	-	4149.256
Model 1	FD~Area*Ecozone+ Area*Biome	1	-	3880.271
Model 2	FD~Area*Ecozone+ Area*Biome	2	-	4001.996
Model 3	FD~Area*Ecozone+ Area*Biome	3	-	4083.056
Model 4	FD~Area*Ecozone+Area*Biome	1	1	3350.675
Model 5	FD~Area*Ecozone+Area*Biome	1	2	3350.675
Model 6	FD~Area*Ecozone+Area*Biome	1	3	3600.917
Model 7	FD~Area*Ecozone+Area*Biome	1	4	3780.554
Model 8	FD~Area*Ecozone+Area*Biome	1	5	**3315.073**

*ML: Maximum Likelihood

S= Species Richness

Table S 2. ANOVA results for significance of the relationships of the Generalized Linear Square model (GLS) for FD and FG related to species richness, biome, ecozone and interactions and FD related to Ecoregion Area.

Variable	DF	F-value	p-value
Species richness and Functional Diversity FD			
(Intercept)	1	0.11	0.7405
Species richness (S)	1	19.46	<0.0001
Ecozone	6	3.76	0.0011
Biome	13	1.64	0.0688
S:Ecozone	6	15.09	<0.0001
S:Biome	13	2.23	0.0073
Model	820		
Species richness and Functional Groups FG			
(Intercept)	1	4.72	0.0302
Species richness (S)	1	19.52	<0.0001
Ecozone	6	14.34	<0.0001
Biome	13	1.54	0.0975
S:Ecozone	6	10.47	<0.0001
S:Biome	13	2.84	0.0005
Model	820		
Area and Functional Diversity FD			
(Intercept)	1	0.91	0.345
Area	1	4.10	0.0432
Ecozone	6	23.62	<0.0001
Biome	13	3.64	<0.0001
Area:Ecozone	6	2.52	0.0202
Area:Biome	13	3.63	<0.0001
Model	820		

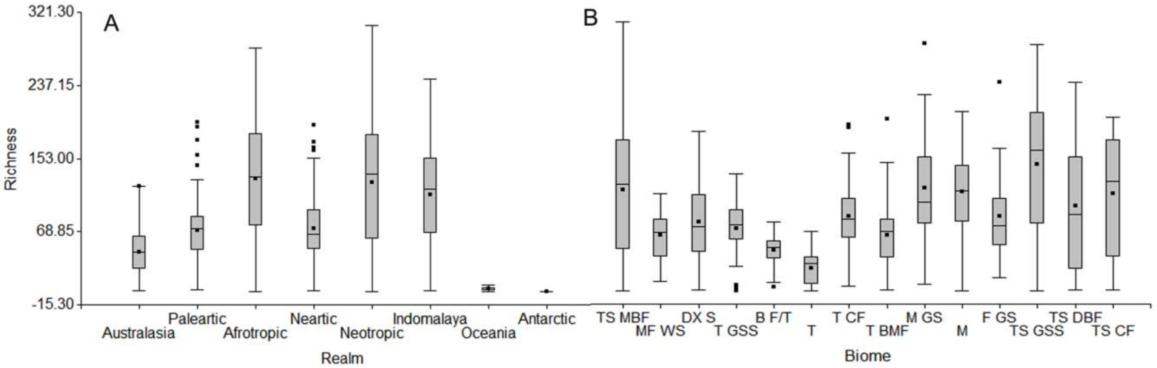

Fig. S 1. Box-plot of species richness in the world's ecoregions in (A) ecozones and (B) biomes. Ecozones abb.: AT: Afrotropic, IM: Indomalaya, NT: Neotropic, AA: Australasia, AN: Antarctic, NA: Neartic, OC: Oceania and PA: Palearctic. Biomes abb.: B F/T: Boreal Forest/Taiga, DX S: Deserts and xeric shrublands, FGS: Flooded grasslands and savannas, M: Mangroves, MFWS: Mediterranean forests, woodlands and scrub, MGS: Montane grasslands and shrublands, TBMF: Temperate Broadleaf and mixed forests, TCF: Temperate Coniferous forests, TGSS: Temperate grasslands, savannas, and shrublands, TSCF: Tropical and subtropical coniferous forests, TSDBF: Tropical and subtropical dry broadleaf forests, TSGSS: Tropical and subtropical grasslands, savannas, and shrublands, TSMBF: Tropical and subtropical moist broadleaf forests and T: Tundra.

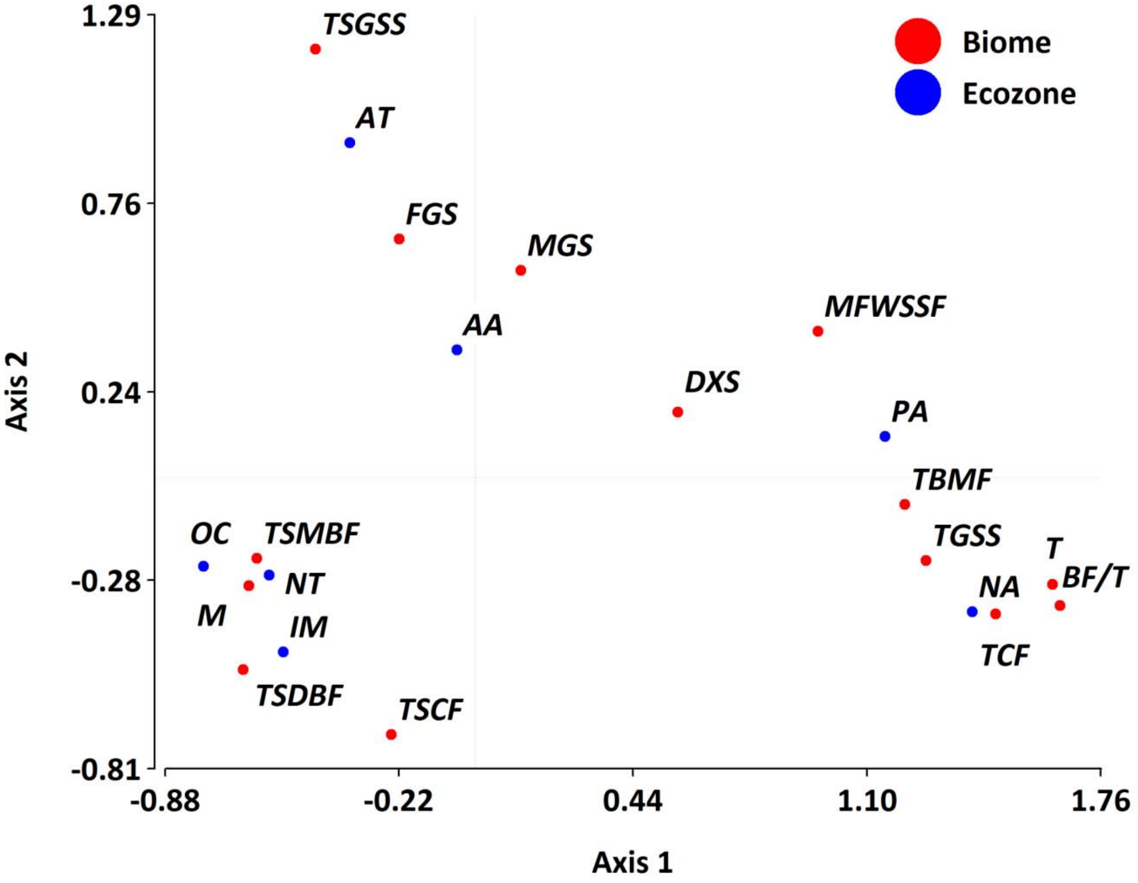

Fig. S 2. Correspondence analysis associating ecozones and biomes according to species richness. Ecozones abb.: AT: Afrotropic, IM: Indomalaya, NT: Neotropic, AA: Australasia, AN: Antarctic, NA: Neartic, OC: Oceania and PA: Palearctic. Biomes abb.: B F/T: Boreal Forest/Taiga, DX S: Deserts and xeric shrublands, FGS: Flooded grasslands and savannas, M: Mangroves, MFWS: Mediterranean forests, woodlands and scrub, MGS: Montane grasslands and shrublands, TBMF: Temperate Broadleaf and mixed forests, TCF: Temperate Coniferous forests, TGSS: Temperate grasslands, savannas, and shrublands, TSCF: Tropical and subtropical coniferous forests, TSDBF: Tropical and subtropical dry broadleaf forests, TSGSS: Tropical and subtropical grasslands, savannas, and shrublands, TSMBF: Tropical and subtropical moist broadleaf forests and T: Tundra.

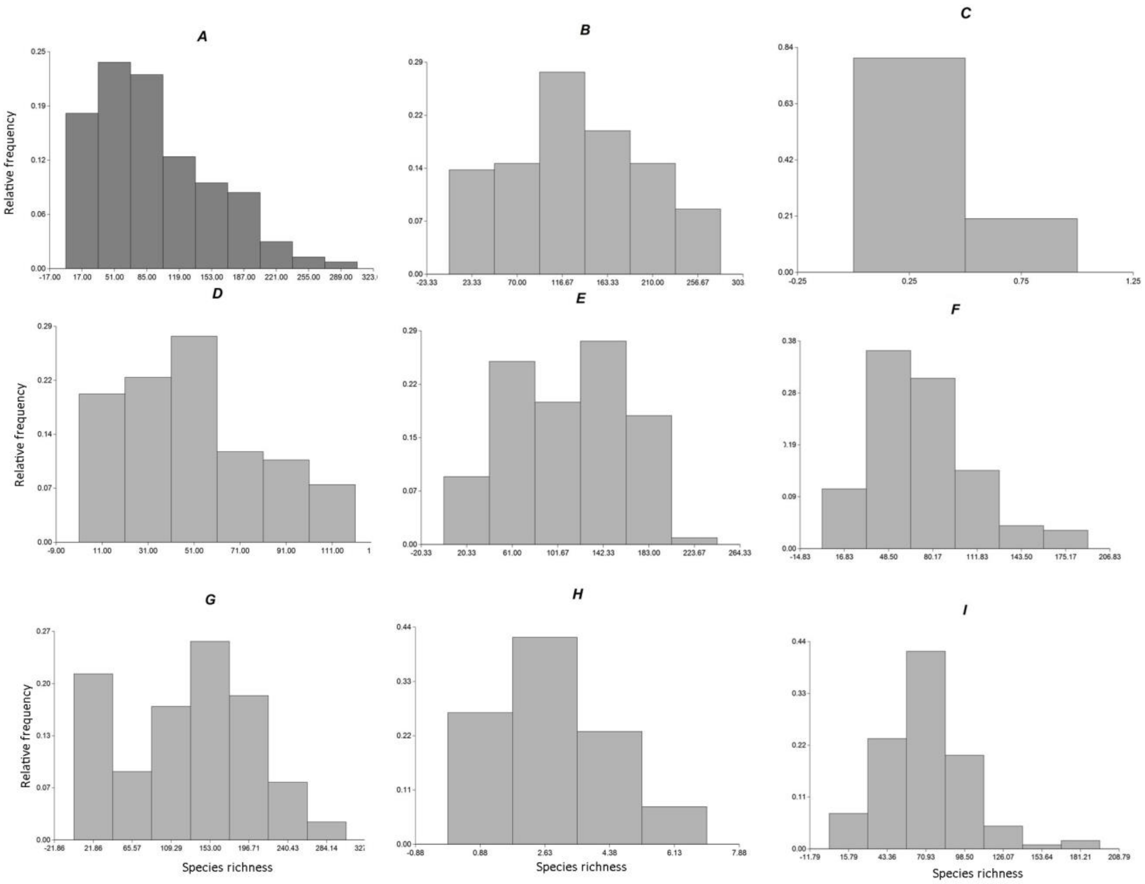

Fig. S 3. Species richness histogram on each ecoregions by (A) Total, and in biomes (B) Afrotropic, (C) Antarctic, (D) Australasia, (E) Indo-Malay, (F) Nearctic, (G) Neotropic, (H) Oceania y (I) Palearctic.

5.2. Mammals at risk and the potential meltdown of the world´s ecoregions

Mammals at risk and the potential meltdown of the world´s ecoregions

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Abstract: Ecosystem function and capacity for resilience depends largely on the species inhabiting each ecosystem and their ecological roles. Functional diversity is a statistical measure of the diversity of functions within ecosystems. We assessed the global influence of mammal species at risk, identified by the IUCN Red List of Threatened Species, on global mammal functional diversity at global to ecoregion scales. Overall models at the global scale showed a significant effect on functional diversity of mammal species at risk, and this influence appears greatest at the regional scale. At least 65% of functional diversity is determined by endangered species in selected ecoregions, primarily in Asia, Europe, eastern coastal areas of North America, Mesoamerica and South America. Since functional diversity at the ecoregion scale is disproportionally influenced by species at risk of extinction in the short-term, ecosystems supporting such species are more vulnerable to ecological meltdown through loss of its functional and resilience capacity.

One Sentence Summary: Species at risk exert a disproportionate influence on ecological functioning, and while this influence varies across ecoregions globally, near-term species extinctions may result in ecosystem meltdown.

Ecosystem functioning and resilience is determined in large part by the functions and roles species play in those ecosystems (1). Like other recently employed techniques, functional traits diversity can be used to evaluate the relative importance of plant or animal group diversity in the functioning of an entire ecosystem (2, 3). Despite recent advances in our understanding of functional diversity and its role in ecosystem processes (1, 4-6), the potential impact of species extinction on functional diversity has not been explored (7). A more comprehensive understanding of this question can provide improved prioritization and conservation planning (8-10). As the roles of species in functional diversity can be complementary or redundant (11), the extinction or colonization of a given species can have varying effects on the functional diversity of an ecosystem (12-15).

Mammals play a major role in shaping and maintaining ecosystems, functioning as architects, pollinators and consumers (16-18). Currently, at least 25% of mammal species worldwide are facing extinction (19), and this trend is even more prevalent at population levels (20). Therefore, a comprehensive understanding of the effect of mammal population and species loss on functional diversity is critical to address the larger extinction crisis (21, 22) and subsequent degrading of the world's ecosystems (23, 24). We assess mammal functional diversity across the world´s ecoregions and estimate the effects of threatened mammal species loss on global and regional variation of functional diversity. Understanding the magnitude of this influence, and its geographical variation, can provide insights to where ecosystem meltdown can occur when functional assemblages are at risk of extinction.

We estimated mammal functional diversity of the world's ecoregions using three primary life-traits: body mass, habits, and guild of 3,554 mammal species (25, 26); these traits represent a broad array of resource and habitat use and have been useful in similar previous analyses (25, 27). Based on the Global Mammal Assessment distribution ranges (19) and the worlds' ecoregions, biomes and realms defined by the World Wildlife Fund (28), we estimated a functional diversity index, based on the functional richness definition (29) using the Petchey and Gaston FD index (3) for each ecoregion. We then determined for each ecoregion the number of species in each risk category of the IUCN Red List of Threatened Species ((30); Fig.S1).

Since functional diversity is expected to be closely related to species richness, the variability explained by only threatened species is complemented by those not under threat. Because we expected global variation in the degree of influence of functional diversity exerted by threatened species and subsequent variation at finer scales, we initially used ordinary least squares (OLS) models with all possible combinations of variables (i.e., number of Data Deficient - DD, Vulnerable - VU, Endangered- EN and Critically Endangered - CR species) as a global model. We then selected the best performing models based on Akaike Information Criteria weights (*w*; (31); Table S1) and assessed the variability explained by the regressor variables based on the corrected R^2 value. We used the Koenker statistic to assess the nonstationarity characteristics of the models and to establish if the influence of species at risk on functional diversity was consistent across geographic scales (32).

To explore spatial variability of this effect influence, we employed a geographically weighted regression (GWR) with all possible variable combinations and selected the best performing model based on w and variability explained based on the corrected R^2 values ((32, 33); Table S1). We then compared the *w* and R^2 for both OLS and GWR models and estimated the R^2 values weighted for both biomes and realms to ascertain if there was a stronger influence relative to major habitat types (i.e., biomes) and biogeographic realms (i.e., ecozones). Once a model was selected, we projected the local R^2 on each ecoregion to identify those in which species at risk had the highest influence on functional diversity. Ecoregions with greater R^2 values would suggest that functional diversity is more influenced by the number of species in each risk category, while lower R^2 values would indicate less influence with non-threatened species (*i.e.,*Least Concern and Near Threatened species) having a greater influence on functional diversity.

Globally, Data Deficient and Vulnerable species contributed to 59% of the influence on functional diversity (Table 1). However, this trend was nonstationary and suggests that the relationship between species at risk and functional diversity varies geographically (Koenker (BP) Statistic [f] = 106.89 $p< 0.001$) (Figure S2). When we selected the best performing geographically weighted model for this global variation we noted that Data Deficient, Vulnerable, Endangered and Critically Endangered species accounted for 73% of the variation in functional diversity (Table 1). However, coefficients for each variable, such as the direct influence of each variable and the local R^2, which represents functional diversity variation by the selected variables, varied across the world's ecosystems. Ecoregions in eastern Asia, Europe, Mesoamerica, northern South America, and the eastern coast of North America were areas where threatened species exerted more influence on functional diversity in contrast to ecoregions in Alaska and southern Africa (Fig 1A). Threatened species of the Neotropical, Palearctic, Indomalaya and Oceania ecozones had a substantially greater influence on functional diversity (>0.63) than Threatened species in the Afrotropic ecozone, where the influence index of 0.36 (Fig.1B) is one of the lowest identified.

At the biome scale, the overall influence was greatest for tropical and subtropical broadleaf moist forests and tundra and least for temperate coniferous forests and tropical and subtropical grasslands, savannas, and shrublands (Fig.1C). The greatest effect on ecoregion functional diversity was by the number of Vulnerable species (mean coefficient (M.Coef.) ± SD = 0.184 ± 0.07; Fig. 2C), followed by Endangered (M.Coef. ± SD = 0.111 ± 0.168; Fig. 2B), Data Deficient (M.Coef. ± SD = 0.101± 0.069; Fig. 2D) and Critically Endangered species (M.Coef. ± SD = -0.023 ± 0.169; Fig. 2A). Geographically, functional diversity increased with an increasing number of Vulnerable species, with strongest relationships noted in Europe, southwestern South America and eastern Africa. In contrast, the influence of Endangered species was positive with North American and negative for South American, African and European functional diversity values. There was a strong positive relationship between Data Deficient species and functional diversity of species in North America, South America, Africa and Europe, and a negative relationship in ecoregions of Southeast Asia and Australia.

Table 1. Summary statistics of the ordinary least squares (OLS) and geographically weighted regression (GWR) models selected, including the corrected Akaike Information Criteria (AICc) and R^2 values for both models and the variable significance value (p), variance inflation factor (VIF), Koenker nonstationarity statistic, and probability (p_2) for the OLS model.

OLS

Parameter	Coefficient	Standard Error	p	VIF	AIC	R^2	Koenker (BP) Statistic [f]	p_2
Intercept	1.856	0.066	<0.001	--	3105.96	0.599	106.89	<0.001
DD	0.142	0.009	<0.002	1.808				
VU	0.171	0.011	<0.003	1.808				

GWR

Parameter	Mean Coeff.	Standard Deviation	AIC	R^2
DD	0.101	0.069	2769.85	0.735
EN	0.184	0.072		
VU	0.111	0.168		
CR	-0.023	0.169		

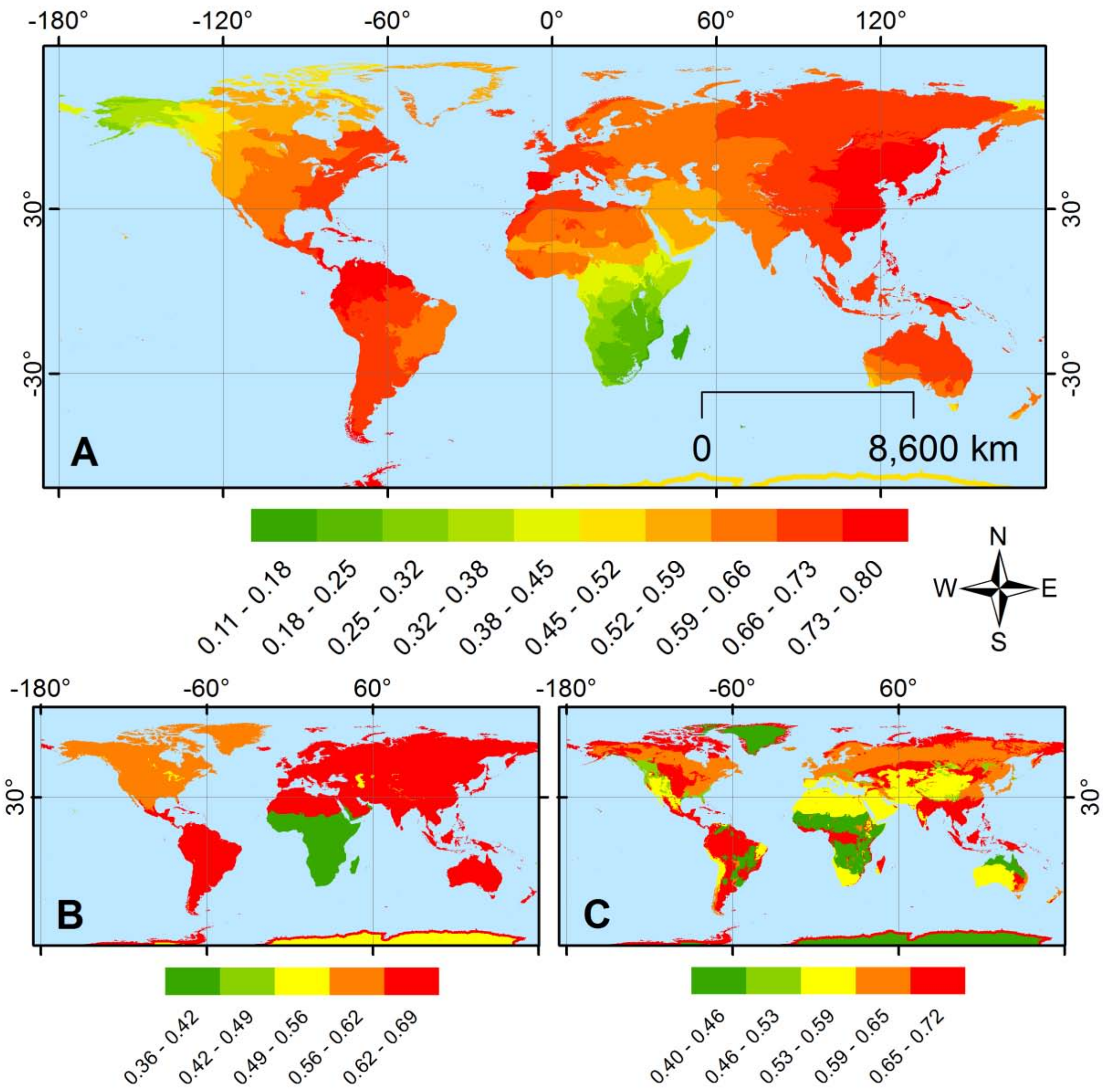

Fig. 1. Maps depicting the variation of functional diversity explained by the number of threatened species (Local R^2) on the world´s ecoregions (A) and weighted by realm (B) and biome (C) scales. Local R^2 values derived from a geographically weighted regression model. Note the high R^2 values for northern South America, Europe and Asia (A), the overall higher influence in the Neotropic, Paleartic and Indomalaya realms (B), and the tropical and subtropical broadleaf moist forests and tundra (C).

Our findings further refine our understanding of indicators of extinction risk, ecosystem functioning and the potential impacts of the extinction crisis (20, 34-37). Recent advances in ecosystem functioning theory (10, 37) and understanding of animal functional diversity (15, 27, 38) have facilitated our ability to more accurately anticipate the potential impact of species loss on ecosystem functionality. By using the well-recognized IUCN guidelines on species threat assessment (30) we documented the relative influence of the species in each risk category on functional dynamics. Understanding this relationship is critical for predicting ecosystem changes resulting from species and population loss. The IUCN model classifies species risk on an ordinal structure based on extinction likelihood where the Critically Endangered category encompasses those species with the highest likelihood of extinction. Considering the relatively short timeframe of the potential extinction of some threatened species and the strong linkage between ecosystem functioning and functional diversity (39), species loss will most likely affect ecosystem dynamics and resilience. Since species at higher risk significantly contributing to functional diversity, their extinction would be expected to adversely affect ecosystem processes. The Data Deficient category includes those species for which there is insufficient information to be categorized in one of the highest risk categories (i.e., VU, EN or CR; (30), and may have a latent high risk of extinction. The influence of Data Deficient species on our model suggests that ecosystem functioning largely depends on species for which basic data on demographics and functional roles are lacking.

Beyond a presentation of a rather pessimist perspective on the extinction crisis and the likelihood of a geographically differential meltdown of ecosystems, we believe our results contribute to a better understanding of the potential impact to the environment resulting from species loss. Our previous work on the impact of species and population losses, especially for mammals (19-22), helped define global conservation priorities. The results we presented here further reinforce these priorities and provide a new perspective on what may be lost following species extinction. A well-functioning ecosystem is a requisite for resilience against global pressures such as climate change and other threats (40-43) and the provision of ecosystem services necessary to sustain human populations and biodiversity life on earth (34, 36, 38, 44, 45). The results of our work and similar endeavors have the potential to identify strategies on how to best address these global-level threats resulting from species extinction.

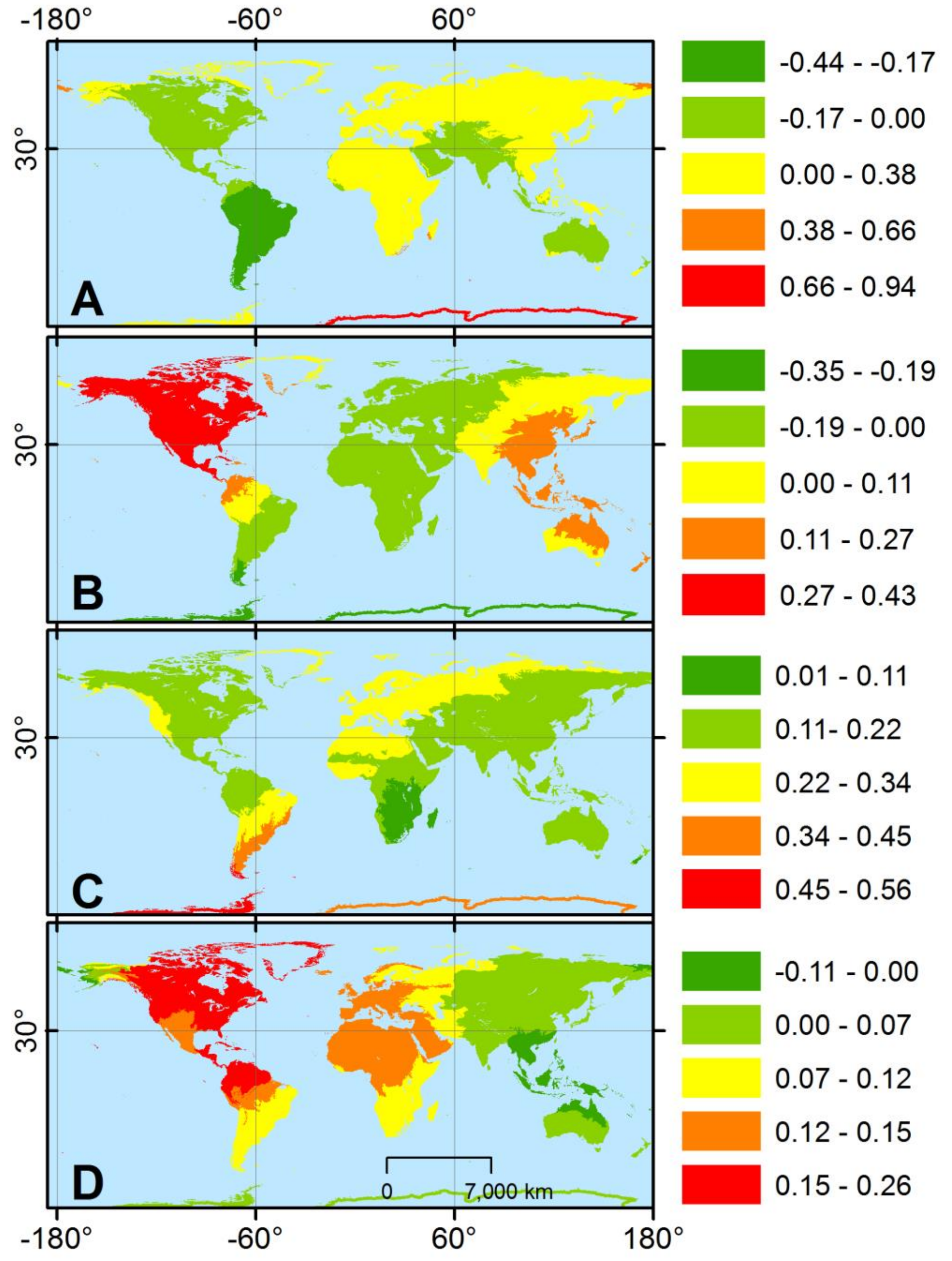

Fig. 2. Local influence coefficients of risk categories in the world´s ecoregions by Critically Endangered (A), Endangered (B), Vulnerable (C) and Data Deficient (D) species estimated from a geographically weighted regression model. Note the differential weighted influence relative to geographic location.

Acknowledgments: This paper constitutes a partial fulfillment of the Graduate Doctoral Degree Program in Biomedical Sciences (Programa de Doctorado en Ciencias Biomédicas) of the National Autonomous University of México (UNAM) of the first author. J.F. González-Maya acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT) and UNAM (scholarship 255983). This study was supported in part by the Programa de apoyo a proyectos de investigación e innovación tecnológica Project No. IN211811 of UNAM. Partial support was also provided by ProCAT Colombia. The authors would like to thank E. Martínez-Meyer, L. Viquez-R, A. Arias-Alzate, R. Medellín, J. Belant, H. Zarza and J. Schipper for insightful comments and support throughout the research and writing of this manuscript. R. Bjorkland significantly improved language and manuscript style.

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Supplementary materials:

Materials and Methods

Figures S1-S2

Tables S1

References (19, 25-32, 38, 46-52)

Materials and methods

We assessed global distribution of mammals in the worlds´ ecoregions by overlapping mammal distribution polygons derived from the Global Mammal Assessment (19, 30) over the world ecological regionalization according to WWF´s ecoregions at all scales (28). WWF ecoregions classify the world in three scales: i) ecozones, which divide the globe in eight biogeographic realms (Antarctic, Australasia, Afrotropic, Indomalaya, Nearctic, Neotropic, Oceania and Palearctic); ii) 14 biomes or major habitat types; and iii) 868 ecoregions which are the locally specific ecological regionalizations for the world. We then classified each species on a threat category according to the IUCN Red List of Threatened Species (30) in six categories: Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR); according to this ordinal classification, those species classified as VU, EN, CR and DD are those most threatened by extinction.

We collected information regarding ecological and life traits for all mammals based on global trait databases (25, 26) and our own updates, classifying 3554 mammal species according to body size (i.e., mass), trophic guild (*i.e.,*omnivore, carnivore and herbivore) and habits (*i.e.,*aquatic, fossorial, terrestrial, arboreal and volant). We selected these traits as they are good proxies of species resource use and niche dimensions (27, 38), thus potentially influencing diversity and ecosystem function relationship (38), and are readily available for most mammal species (25). We developed a database with species traits and IUCN category for each ecoregion, then estimated the number of threatened species and a functional diversity index. Our functional diversity index was estimated using Petchey and Gaston's functional traits diversity index (3) (FDI) based on the functional richness definition by Mason et al (29): "the amount of niche space filled by species in the community". We selected this metric as it can be used with multiple traits, does not depend on abundance data and has a significant interaction with species richness (46). Therefore, we could better estimate the amount of variation in FDI explained by threatened species with remaining variation explained by species not at risk, therefore accounting for most of the FDI variation. We estimated FDI using the sum of the branch distances in a dendrogram necessary to connect all species in functional space (27, 47). For estimating this, we estimated a distance matrix and a functional dendrogram using the Gower distance (unweighted pair group with arithmetic averages) and summed the branches necessary to connect all species within each cell. Comparatively, low FDI values can indicate low complementarity (*i.e.,*species are distant in trait-space), and vice versa (*i.e.,*high complementarity, species are more similar). We generated a global map of functional diversity across the world´s ecoregions and the number of threatened species.

In order to explore the influence of species at risk on our FDI, we used an ordinary least squares (OLS) modelling approach (48, 49) for exploring overall variation of FDI according to the number of species at each risk category on each ecoregion and divided in realms and biomes. We generated models with all possible combinations of species at risk, without interaction terms, and selected those models with the lowest Akaike Information Criterion corrected for small samples (AICc; (50)) and AIC weights for competing models (31). We assessed the proportional variation of FDI according to the number of species on each category based on the R^2. Final selected model was tested for spatial autocorrelation using Moran´s I test over the residuals, heteroskedaticity and non-stationarity using the Koenker´s statistic, multicolineality by checking the Variance Inflation Factor of each variable(*i.e.*,>7.5 means two variables are informing the same to the model), and normality with the Jarque Bera test (32, 51). Since we identified non-stationarity of the model, thus geographic variation on the influence of species at risk on FDI, we plotted OLS standard residuals to see if missing variables could be identified at multiple locations (*i.e.*,high or low residuals on standard deviations scale), then performed geographically weighted regression (GWR) models with all the variables, and then selected again the best performing models according to the lowest AIC. Geographically weighted regression models identify spatial variation and clusters of high and low predictability or mismatch (52). Geographically weighted regression estimates separate equations for each variable and incorporates dependent and independent variables within a bandwidth (51) defined for our study base on a kernel-based adaptive selection with corrected AIC as an adaptive function of spatial context, selecting the best smoothing factor. With the selected GWR model we plotted the local estimated R^2 and each variables coefficient for each ecoregion, assessing how much variation on FDI was explained by species at risk and to understand in which ecoregions each variable exerts higher influence. Also, we weighted R^2 values by biomes and realms, and projected those spatially to identify which had greater influence on the different risk categories.

Supplementary information

We assessed the influence of mammal species at risk over mammal functional diversity across the worlds ecoregions classified by biomes and realms (Figure S1). For each ecoregion we obtained the number of species on each IUCN risk category: DD, VU, EN and CR, and estimated a functional diversity index (Figure S1). We modeled this relationship at overall scale and with a geographic weighted approach. We found five competing, lowest AIC, models for overall ordinary least squares models. We selected the best performing model according to AIC weights for these competing models (Table S1). The best OLS model tested for non-stationarity (Koenker (BP) Statistic [f] = 106.89, p< 0.001) and normality (Jarque Bera= 433.52, p=<0.001). Once an OLS model was selected, we evaluated FDI variation explained by the selected categories, and plotted the model standard residuals in order to identify region where regressor variables were missing (Figure S1). Since many ecoregions showed high and low residual values, and Moran´s I tested for clustering of the residuals (Moran´s I Index = 0.33, p=<0.01), thus there was less than 1% likelihood that the clustered pattern could be the result of random chance, we generated geographic weighted regression models with all possible combinations, and again selected for the best performing model using AIC weights of competing models (Table S1).

Table S1. Best competing ordinary least squares (OLS) and geographically weighted regression (GWR) models and Akaike Information Criterion (AICw) weights for explaining mammal functional diversity variation according to the number of threatened species in the world´s ecoregions. Models identified by * indicates the selected model.

Model	Δ AIC	Parameters	Likelihood	AICw	R^2	AIC
OLS1*	0	DD-VU	1.0000	0.5344	0.59	3105
OLS2	2	DD-EN-VU	0.3679	0.1966	0.59	3107
OLS3	2	DD-VU-CR	0.3679	0.1966	0.59	3107
OLS4	4	DD-EN-VU-CR	0.1353	0.0723	0.59	3109
OLS5	104	DD-EN	2.6E-23	1.4E-23	0.54	3209
GWR1*	0	DD-EN-VU-CR	1.0000	0.9820	0.73	2769
GWR2	8	DD-EN-VU	0.0183	0.0180	0.73	2777
GWR3	66	DD-VU-CR	4.7E-15	4.6E-15	0.71	2835
GWR4	75	DD-VU	5.2E-17	5.1E-17	0.70	2844
GWR5	110	EN-VU-CR	1.3E-24	1.3E-24	0.71	2879

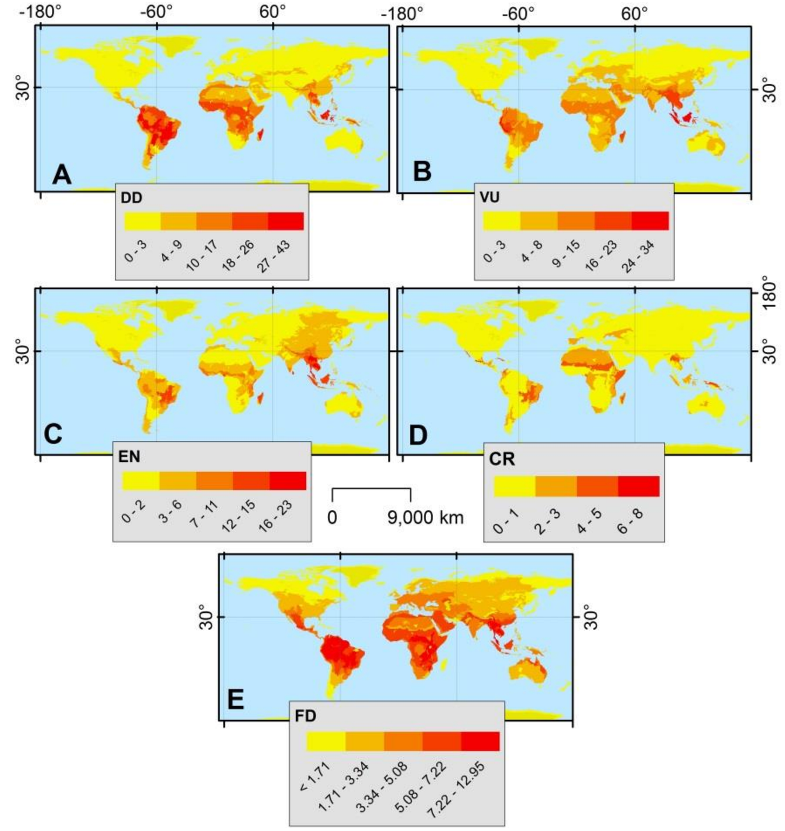

Figure S1. Map depicting distribution of mammal species at risk (A-D) and mammal functional diversity (E) on these ecoregions. Maps in order for Data Deficient (DD; A), Vulnerable (VU; B), Endangered (EN; C) and Critically Endangered (CR; D) species and Functional Diversity (FD; E).

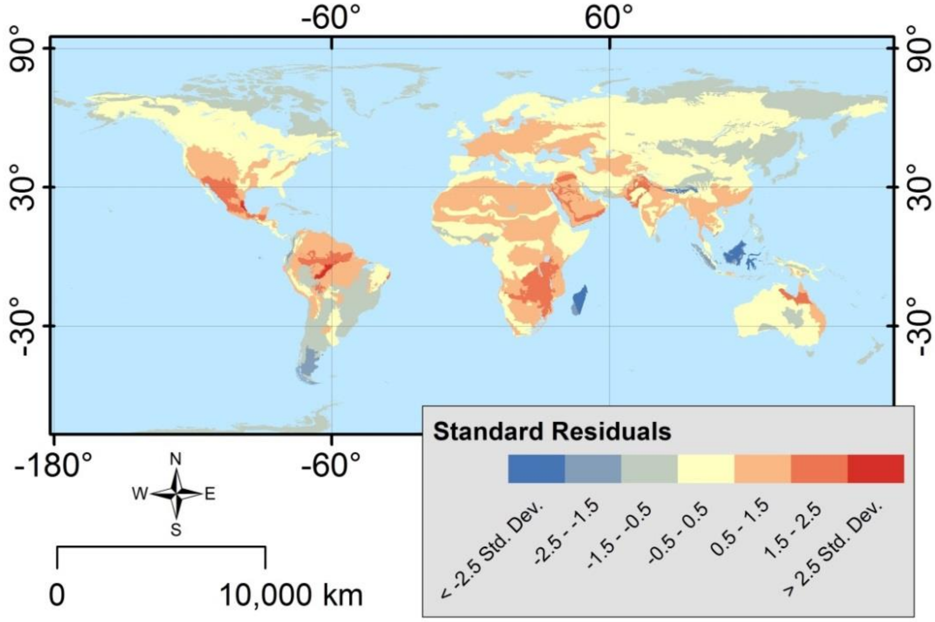

Figure S2. Map depicting the distribution of standard residuals from ordinary least squares model assessing the variation of mammal functional diversity influenced by mammals at different risk categories in the world´s ecoregions. High or low residual values on different ecoregions indicate missing variables for the model.

6. Capítulo 2. Diversidad funcional a escalas regionales: determinantes y variación funcional a escala del Neotrópico

6.1. Spatial determinants of mammal functional diversity in the Neotropical Realm: influence of land-use and extinction risk

Spatial determinants of mammal functional diversity in the Neotropical Realm: influence of land-use and extinction risk

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Abstract

Functional diversity represents a measure of diversity that incorporates the role of species in an ecosystem, and therefore its dynamics and resilience. Assessing its determinants and spatial variation represents an important step forward in our understanding of functional ecosystem dynamics and it is also necessary to achieve a comprehensive conservation planning. In this paper we assessed mammal functional diversity for the 218 ecoregions within the Neotropical realm. We evaluated the overall influence and spatial variation of species richness, ecoregion extent, intervention and species at risk on functional diversity. We used both ordinary least squares and geographically weighted regression modeling approaches. We found that intervened areas and threatened and non-threatened species are the most influential overall determinants of functional diversity. However, we also detected that these variables do not operate equally across scales. Our local analyses indicated both that variation explained and local coefficients vary spatially depending on the ecoregion and major habitat type. As estimates of functional diversity are based on current distribution of all mammals, negative influence of intervened areas and positive influence of non-threatened species may reflect a potential degradation of functional processes for some ecosystems. Most generally, the negative influence of intervention together with the influence of threatened species indicates that some areas are currently more susceptible to functional diversity loss. Our results help to pinpoint key areas requiring urgent conservation action to reduce natural landcover loss and areas where threatened species play influential roles on ecosystem functioning.

Key words: Functional diversity; geographically weighted regression, Neotropical realm, Biomes, Ecoregions, IUCN Red List of Threatened Species, extinction risk.

Introduction

Biological diversity has historically been measured via multiple approaches, ranging from basic counts of species richness to more sophisticated measures of evolutionary and functional diversity (Calba et al. 2014; Monnet et al. 2014). As more refined and complex measures arise, more aspects of community and ecosystem dynamics are assessed, allowing more precise inferences about ecosystems functioning, resilience and services (Monnet et al. 2014; Spasojevic et al. 2014), and in turn, better conservation planning (Díaz et al. 2013). The Neotropics is one of the most diverse and yet complex regions in the world (Brown & Svenning 2014; Schipper et al. 2008), but also one of the most threatened regions due to anthropogenic factors (Le Saout et al. 2013). As human intervention increases in Neotropical ecoregions, more precise, effective and efficient conservation measures are needed, and at better resolution, in order to reduce biodiversity loss and thus preserve ecosystem services (Boitani et al. 2011; Ceballos et al. 2005). Understanding underlying determinants of ecosystem function and diversity may allow designing better conservation actions (Armsworth et al. 2007; Biswas & Mallik 2011).

Considering that almost not baseline information exist for most taxonomic groups in the Neotropics (Lees et al. 2012), and not until recently complete groups were assessed in terms of their conservation status and distribution information (Boitani et al. 2011; Hoffmann et al. 2011; Hoffmann et al. 2010; Rondinini et al. 2011), assessing changes and variation, or original conditions, in terms of ecological processes and extinction occurring at large scales its a difficult task (Lees et al. 2012). Some previous analyses assessed the magnitude of changes in terms of land-cover for the Neotropics (Etter & van Wyngaarden 2000; Sánchez-Cuervo et al. 2012), but to our knowledge no studies have related these changes to ecosystem functionality or functional diversity as for other regions (Barragán et al. 2011; Biswas & Mallik 2010; Biswas & Mallik 2011). Furthermore, so far, mammal diversity has been mostly studied from the macroecological perspective at global scales (Ceballos & Ehrlich 2002; Ceballos et al. 2005; Schipper et al. 2008), with very few analyses assessing mammal diversity at regional/national scales (Ceballos 2007; Farias & Svensson 2014).

Here we provide a regional-scale analysis of mammal taxonomic and functional diversity as a basis for developing adequate conservation planning. Our specific goal was to assess the determinants of functional diversity in the Neotropical ecoregions and its implications for conservation. We specifically address the following questions: i) how is species richness and mammal functional diversity distributed across the Neotropical realm and how is distributed according to similar major habitat types?, ii) what is the influence of land-cover, ecoregion area and species extinction risk on mammal functional diversity?, (iii) what is the spatial variation of these relationships?, and (iv) what are critical ecoregions for conservation action based on mammal functional diversity?

Methods

We assessed mammal species richness and functional diversity for all 218 Neotropical ecoregions and 11 biomes (TableS1) according to WWF ecological regionalization of the world (Olson et al. 2001), excepting St.Peter-St.Paul Rocks. We overlapped the maps of all ecoregions and mammal distributions, derived from current distribution polygons of all mammals derived from the IUCN Red List (Schipper et al. 2008), identifying all species present in each ecoregion. These maps were selected as they represent a unique source comprising systematic information for most mammals and corrected by region and expertise (Schipper et al. 2008). We estimated species richness as the total number of mammal species present on each ecoregion. To evaluate functional diversity we first compiled life-traits for all mammals present in all ecoregions (1593 spp.), including trophic guild (i.e., carnivore, omnivore, herbivore), habit mode (i.e., volant, arboreal, terrestrial, fossorial, and aquatic) and body size (i.e., body mass), derived from PanTHERIA (Jones et al. 2009) and other databases (Davidson et al. 2009); these traits were selected since they adequately resume niche selection and species use of space and resources (Flynn et al. 2009; Safi et al. 2011) and thus driving biodiversity and ecosystem function relationship (Flynn et al. 2009). Furthermore, these traits are available for most species (Davidson et al. 2009) and have been informative previously for exploring risk and functional diversity in mammals (Flynn et al. 2009; Safi et al. 2011).

Mammal diversity measures

Once a species list for each ecoregion was obtained, we estimated species richness and a functional diversity (FD) index based on these traits. The FD index was calculated based on Petchey and Gaston (2002), which is defined as the sum of the dendrogram branch distances necessary to connect all species in the functional space (Casanoves et al. 2011; Safi et al. 2011). We used this metric of FD since it can be used and has shown good performance with multiple traits interacts with species richness but performs especially well for species rich communities –such as the Neotropics, and does not depend on abundance data (Mason et al. 2012). Also, our metric is appropriate for nominal data types (Gower 1971). We estimated a distance matrix and functional dendrogram based on the Gower distance (unweighted pair group with arithmetic averages) and summed the branches necessary to connect all the species present in the ecoregion. The FD index considers that complementarity is high when the index is comparatively high, thereby indicating species are distant in trait-space, and low complementarity occurs when the index is comparatively low, indicating species are more similar (Petchey & Gaston 2002b; Safi et al. 2011).

We assessed variation and similarities of species richness and FD across ecoregions and according to corresponding biomes. To do so, we used ecoregions classification according to major habitat types (Olson et al. 2001), classifying each in eleven biomes: Tropical and subtropical (T&S) moist broadleaf forests (TSMBF), T&S dry broadleaf forests (TSDBF), T&S coniferous forests (TSCF), T&S grasslands, savannas, and shrublands (TSGSS), Mangroves (M), Flooded grasslands and savannas (FGS), Temperate broadleaf and mixed forests (TBMF), Mediterranean forests, woodlands, and scrub-sclerophyll forests (MFWSSF), Montane grasslands and shrublands (MGS), Temperate grasslands, savannas, and shrublands (TGSS), and Deserts and xeric shrublands (DXS; Fig.1A). Then, we assessed normality using a Shapiro-Wilk test, and subsequently performed a Kruskal-Wallis non-parametric test to determine differences on species richness and functional diversity values, and post-hoc tests for identifying the biomes with higher FD and richness values (Conover 1999). In order to evaluate similarities between biomes according to species richness and FD, we performed a cluster analysis with square Euclidean distances and different linking methods, selecting those with the highest cophenetic correlation (Kaufman & Rousseeuw 1990).

Determinants of mammal functional diversity

In order to assess the influence of ecological, macroecological and anthropogenic factors and species at risk on FD, and its spatial variation, we used Ordinary Least Square models (OLS). We considered six main variables accounting for gradients and different dimensions of ecological, intervention and risk identified by previous studies (Biswas & Mallik 2011; Calba et al. 2014; Petchey & Gaston 2002a; Safi et al. 2011). The variables included: 1) mammal species richness, defined as the total number of species present in each ecoregion since it is expected this is the most important driver of FD (Petchey & Gaston 2002b); 2) the area of the ecoregion, defined as its geographic extent (Olson et al. 2001), considering it has been previously identified as a driver of FD and trait-richness (Franzén et al. 2012); 3-4) intervention, defined as the area of natural and artificial land-covers derived from the GlobCover database (ESA & UCLovain 2009), based on previous analyses indicating the influence of disturbance on FD (Barragán et al. 2011; Biswas & Mallik 2010; Biswas & Mallik 2011), and; 5-6) the number of species classified as threatened and non-threatened present in the ecoregion, derived from the IUCN Red List of Threatened Species (IUCN 2012), classifying those species assessed as Least Concern and Near Threatened as non-threatened and those assessed as Data Deficient, Vulnerable, Endangered and Critically Endangered as threatened, and based on the assumption than species at risk will likely disappear earlier therefore affecting FD (Petchey & Gaston 2002a).

We performed models with all possible variable combinations (i.e., 68 combinations) and no interaction terms, and selected those with the lower Akaike Information Criterion value (AIC) corrected for small samples and AIC weights (AICw; (Wagenmakers & Farrell 2004)). We assessed model performance based on both the AICc and the adjusted R^2 (adjR^2), and selected the best fitting model with significant predictive variables. In order to assess correlation of determinant variables, we assessed Variance Inflation Factors (VIF) for each variable and assessed large VIFs (>7) according to the model as potentially correlated with other variables (O'brien 2007). In case a variable showed a large number of models with high VIF, we performed a Spearman correlation test to see which variables were highly correlated, potentially informing similarly the model. For assessing the significance of the variables, we estimated Koenke studentized Breusch-Pagan statistic (K(BP)) and its probability, in order to assess the reliability of standard errors when heteroskedaticity is present; in case the K(BP) was significant, we used the Robust Probability instead of the raw probability estimation. Jarque-Bera statistic and Moran´s I were used for testing for residuals normality and clustering, respectively; in case residuals were clustered; we generated a spatial weights matrix and included the weights in the model. The K(BP) statistic also assess the non-stationarity of the model, meaning that explanatory variables do not behave the same everywhere (overall OLS model), therefore that the influence of determinants is not constant in geographic space (Brunsdon et al. 1998).

Spatial variation of determinants influence on Functional diversity

After identifying non-stationarity, we performed a Geographic Weighted Regression (GWR) with the selected variables, where we assessed if the local models performed better than the overall OLS model by comparing Pseudo R^2 values (McFadden 1973), and assessed the local explanatory magnitudes (adjR^2) and coefficients for each variable over each ecoregion, assessing where stronger influence relationships occur for all variables (adjR^2) and where certain variables are more important or negatively/positively influence FD (local coefficients; (Brunsdon et al. 2010; Fotheringham et al. 2002). GWR evaluates the influence of variables for each ecoregion generating a model for each using a defined number of adjacent ecoregions (i.e., neighbors); for selecting the number of neighbors we used an adaptive corrected AIC method with cross-validation, considering that ecoregions are distributed continuously across the Neotropical realm, and aiming to minimize AIC values (Brunsdon et al. 2010). We used the condition number as a diagnostic of local multicollinearity, therefore indicating a locally unstable model; as a rule-of-thumb, condition numbers larger than 30 are likely unreliable. To test for the generalized FD explained by selected variables derived from local relationships according to biomes, we included all biomes as prediction localities when defining the model in order to compute coefficients and weighted R^2 for each biome. Also we used condition numbers generated as an indication of unstable models and multicolineality.

Ecoregions of high conservation priority

To select the ecoregions of high conservation priority we used two approaches; first we compared the FD-observed values against the predicted by our model. Higher differences between these values indicated higher chance of FD change if one or all the parameters are modified, thus indicating those ecoregions more sensible to intervention and threatened species change, considering that predicted values assume that the slopes and means for all variables are the same. We then divided the proportions change into three categories accordingly (*i.e.*,low, medium and high). As a second priority definition, we identified those that are more influenced by threatened species, according to estimated coefficients, and divided the coefficient values in three classes (*i.e.*,low, medium and high priority). We mapped both methods and spatially identified those ecoregions as priority for conservation action.

All geographic and statistical analyses were performed in ArcGIS 10.2 (Environmental Systems Research Institute 2013) and R environment (R Team Development Core 2008).

Results

Mammal species richness and functional diversity distribution

Mammal FD and species richness across all Neotropical ecoregions showed a gradient distribution from the lowest values in the southern cone towards higher values in the central and northern regions of South America, Mesoamerica and decreasing towards central Mexico and the Caribbean (Fig.1B). Both measures showed a non-parametric distribution (Shapiro-Wilks; $W=0.96$, $p<0.0001$ and $W=0.95$, $p<0.0001$, respectively) with a dominance of lower values in most ecoregions. There were significant variation in FD (Kruskal-Wallis; $H=44.71$, $p<0.0001$) and species richness ($H=48.80$, $p<0.0001$) among major habitat types (i.e., biomes). Four biomes (T&S Dry Broadleaf Forests, Grasslands, Shrublands and Savannas and Moist Broadleaf Forests, and Montane Grasslands and Shrublands) had the highest mean (±SD) species richness (116 ± 73, 148 ± 89, 160 ± 72 and 169 ± 61, respectively) and mean (SD) functional diversity values (4.14 ± 2.44, 5.09 ± 3.11, 5.77 ± 2.855, 6.02 ± 2.17, respectively). Both measures tended to increase with decreasing latitude (Fig.1B), with greater FD values towards the Amazon basin (Fig.1C).

Two main clusters with one subdivision were identified among biomes according to measures (Squared Euclidean Distance, average linkage; Cophenetic correlation= 0.668). One group included Temperate grasslands, savannas, and shrublands, Temperate broadleaf and mixed forests and Mediterranean forests, woodlands, and scrub or sclerophyll forests, all temperate biomes; the second cluster was divided in two groups, one consisting on T&S grasslands, savannas, and shrublands, moist broadleaf forests, and Montane grasslands and shrublands; and a second group including T&S dry broadleaf forests, coniferous forests, Mangrove, Flooded grasslands and savannas, and Deserts and xeric shrublands (Fig.1D). Variation in both measures responded significantly to the major habitat type (i.e., biomes).

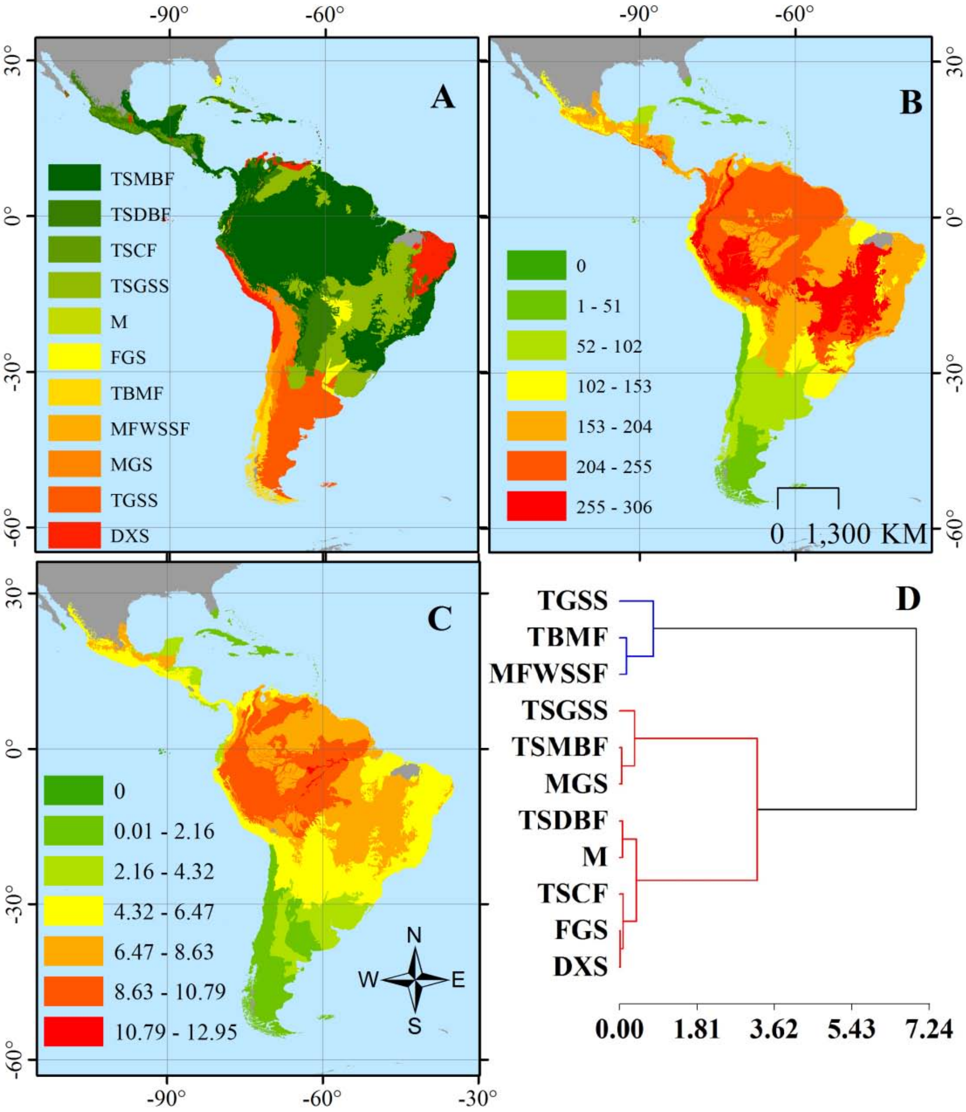

Figure 1. Ecoregions of the Neotropical realm indicating (A) major habitat types (biomes) distribution, (B) species richness and (C) functional diversity. (D) Cluster analyses for ecoregions classified according to major habitat type (*i.e.,*biome) based on species richness and functional diversity values. Euclidian squared distance and average linking was the best linking method according to cophenetic correlation (0.668).

Mammal functional diversity determinants

Mammal FD showed a significant influence of three variables across the entire Neotropical realm, while ecoregion area had not a significant effect on this measure. The best selected model indicated a positive relationship between both threatened and non-threatened species, more species increases FD, and a negative relationship with the intervened area of the ecoregion, indicating that when the area of degraded land-covers increases, FD tends to decrease (Table 1). The first variable excluded from the model, despite it was used in all possible combinations, was species richness, as expected from previous studies and the FD index used, since it showed a significant correlation with other determinant variables (*i.e.,*threatened and non-threatened species), potentially hiding the effect of the other determinants (Spearman correlation=0.92, p<0.001). Our model indicated a significant variation explained by the predictor variables (R^2=0.872), and residuals tested for normality (JB=84.6, p=0.08) and non-clustering (Moran´s I=0.03, Z-score=0.36). The model also showed non-stationarity, indicating that the relationships found do not remain constant across space and scale (K(BP)=19.69, p<0.001), therefore, robust probabilities were used for all variables (Table 1).

Spatial variation of the relationship between selected variables and functional diversity

The geographically weighted regression (GWR) indicated a differential relationship according to the spatial location of each ecoregion. The weighted model (Pseudo R^2=0.98) performed better than the overall OLS model (Pseudo R^2=0.89), and the variation explained by influencing variables also increased significantly (adjR^2=0.9248). The variability explained for each ecoregion "neighborhood" varied significantly across the Neotropical realm, varying R^2 values between 0.53 and 0.99 (mean±SD=0.84±0.09); Northern South America, and the South Cone showed the strongest relationship between FD and species threatened and non-threatened and intervention, while the lowest values were located in the southern Amazon basin (Fig.2A).

Table 1. Best performing selected model including the selected determinant variables influencing mammal functional diversity in the ecoregions of the Neotropical realm. AIC: Akaike Information Criterion, adjR^2: adjusted R^2, AICw: AIC weights, VIF: Variance Inflation Factor.

Model	Parameters	Coef.	VIF	Robust p	AIC	adjR^2
1	Intercept	0.244	-	<0.001	606.15	0.872
	Intervened	-2.46E-07	1.17	<0.001		
	Threatened	0.022	3.80	0.026		
	Non-threatened	0.029	3.56	<0.001		

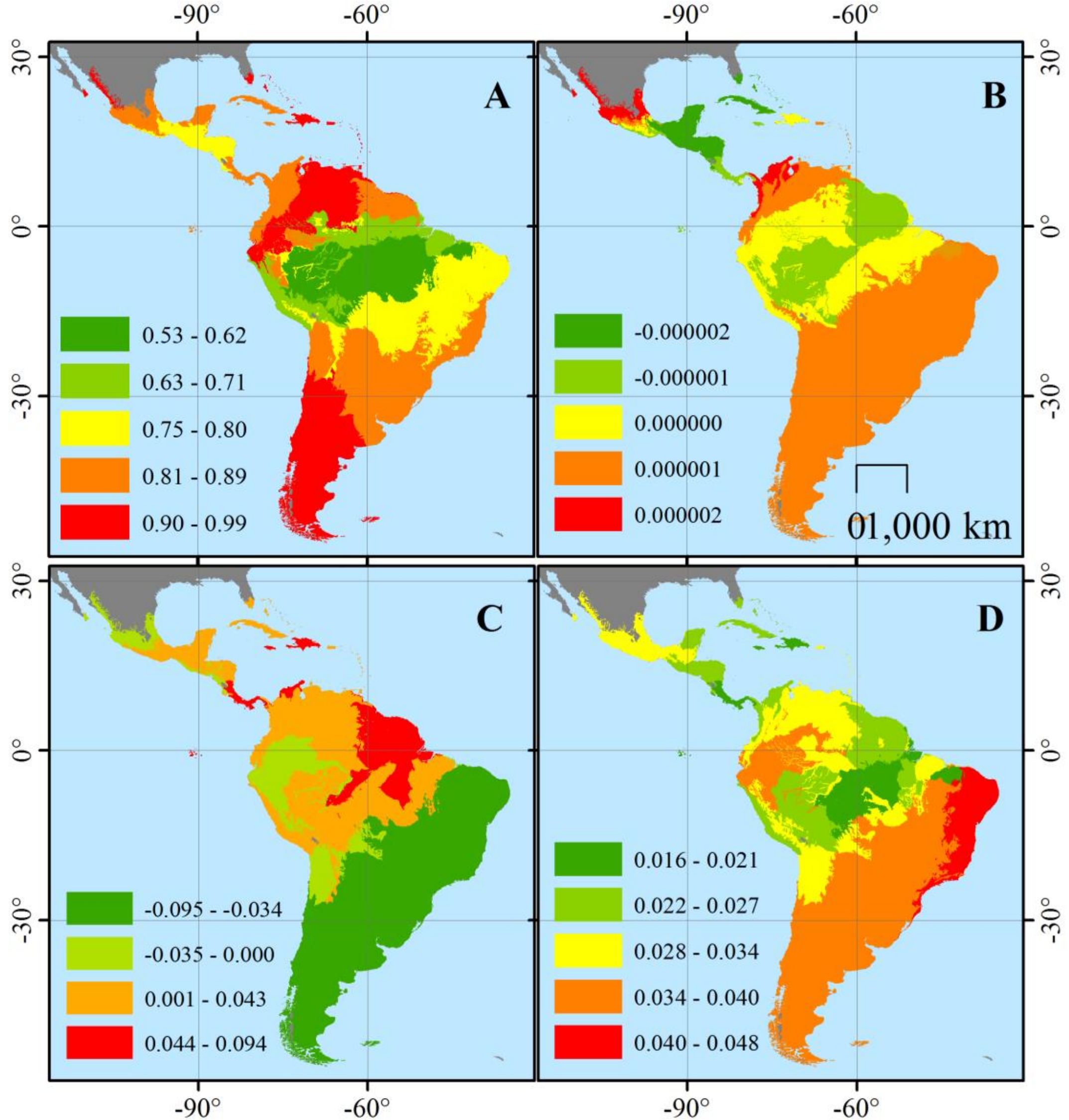

Figure 2. Local values of variation explained by selected variables – R^2 (A) and coefficients for intervened land use (B), threatened (C) and non-threatened species (D) influencing mammal functional diversity for each ecoregion of the Neotropical realm based on a geographically weighted regression. Higher R^2 values indicate higher functional diversity variation explained by the selected variables; higher coefficient value indicate higher positive influence of each variable while negative values indicate negative influence on functional diversity values.

Condition numbers indicated no multicollinearity among the local models for each ecoregion (Mean±SD=12.28±4.56). In terms of the influence of each variable across each ecoregion, we found that intervention negatively influenced functional diversity more notably in the Amazon Basin and Northern Mesoamerica (Fig.2B) with overall, low intervention coefficients (mean coefficient±SD=-4.86E-07±9.64E-07). Threatened species positively influenced most significantly in the Guyanas and negatively influenced in South America's Atlantic coast (mean coefficient±SD=0.006±0.042; Fig.2C). Finally, non-threatened species had higher influence in the Caatinga and Northern Brazil and lowest influence for the Southern Amazon basin (mean coefficient±SD=0.03±0.007; Fig.2D). Overall variation explained weighted and projected by biomes was high (R^2 mean±SD= 0.93±0.03), where the highest influence was determined for Temperate grasslands, savannas, and shrublands and the lowest for Flooded grasslands and savannas; no multicollinearity was found for local biome models (Table2). T & S Broadleaf Moist Forests, Dry Broadleaf Forests, and Montane Grasslands and Mangroves were the biomes more significantly affected both by human intervention and species risk, while the ecoregions located in Northern South America, Mexico and Southern Argentina and Chile were the ones suffering the strongest influence of only intervention on functional diversity. Condition numbers of weighted models for each biome showed stability and no effects of multicolineality (Mean±SD= 8.18±2.56).

Table 2. Local explanatory magnitude (R^2) and Intervened, Threatened and Non-threatened species coefficients influence over mammal functional diversity weighted and projected for each major habitat types (biome) in the Neotropical realm. TSBMF: Tropical and subtropical moist broadleaf forests, TSDBF: Tropical and subtropical dry broadleaf forests, TSCF: Tropical and subtropical coniferous forests, M: Mangroves, TBMF: Temperate broadleaf and mixed forests, TSGSS: Tropical and subtropical grasslands, savannas, and shrublands, TGSS: Temperate grasslands, savannas, and shrublands, FGS: Flooded grasslands and savannas, MGS: Montane grasslands and shrublands, MFWSSF: Mediterranean forests, woodlands, and scrub or sclerophyll forests and DXS: Deserts and xeric shrublands.

Biome	**Condition numbers**	**Local R^2**	**Coefficients**		
			Intervened	**Threatened**	**Non-threatened**
TSBMF	10.32	0.91	-1.4E-08	-0.04	0.04
TSDBF	10.49	0.93	-1.2E-08	-0.02	0.04
TSCF	6.26	0.94	1.9E-06	0.01	0.03
TBMF	4.82	0.99	-4.8E-07	0.04	0.03
TSGSS	10.95	0.89	5.1E-08	-0.11	0.05
TGSS	5.24	0.99	-4.5E-07	0.04	0.03
FGS	10.28	0.89	2.2E-08	-0.09	0.05
MGS	10.01	0.94	2.0E-08	-0.04	0.04
MFWSSF	9.76	0.90	4.9E-08	-0.09	0.05
DXS	9.57	0.92	5.0E-08	-0.07	0.05
M	10.22	0.93	-2.0E-09	-0.02	0.04

Priority ecoregions for conservation action

We identified 57 ecoregions as more susceptible to change according to proportional change between predicted and observed FD values as estimated by our model (TableS1). These ecoregions are scattered along the realm with some geographic clusters; ecoregions throughout the Pacific and south of Mexico and the central region of Guatemala, some ecoregions in the Caribbean islands, the Andean and Caribbean region of Colombia, the coast of Ecuador, some ecoregions in Amazon, the Caatinga, Serra da Costa and Japurá-Solimoes-Negro region in Brazil, the Coast and Puna of Peru and Puna in Bolivia and the Monte and Espinal in Argentina (Fig.3A). For ecoregions more susceptible to FD loss by the loss of threatened species, 49 high priority ecoregions were identified were these species more significantly influences FD (TableS1); most of the ecoregions are located in the Caribbean, the continuum between southern Nicaragua throughout Costa Rica and Panama into the Caribbean, Choco and Magdalena valley in Colombia, and the Guyana shield in South America (Fig. 3B). The biomes with higher estimated influence of threatened species were the T&S Coniferous, Temperate Broadleaf forests and Tropical

Grasslands (Table2) while intervention is more significantly reducing functional diversity for T&S Moist and Dry forests, temperate forests, Tropical Grasslands and Mangroves (Table2).

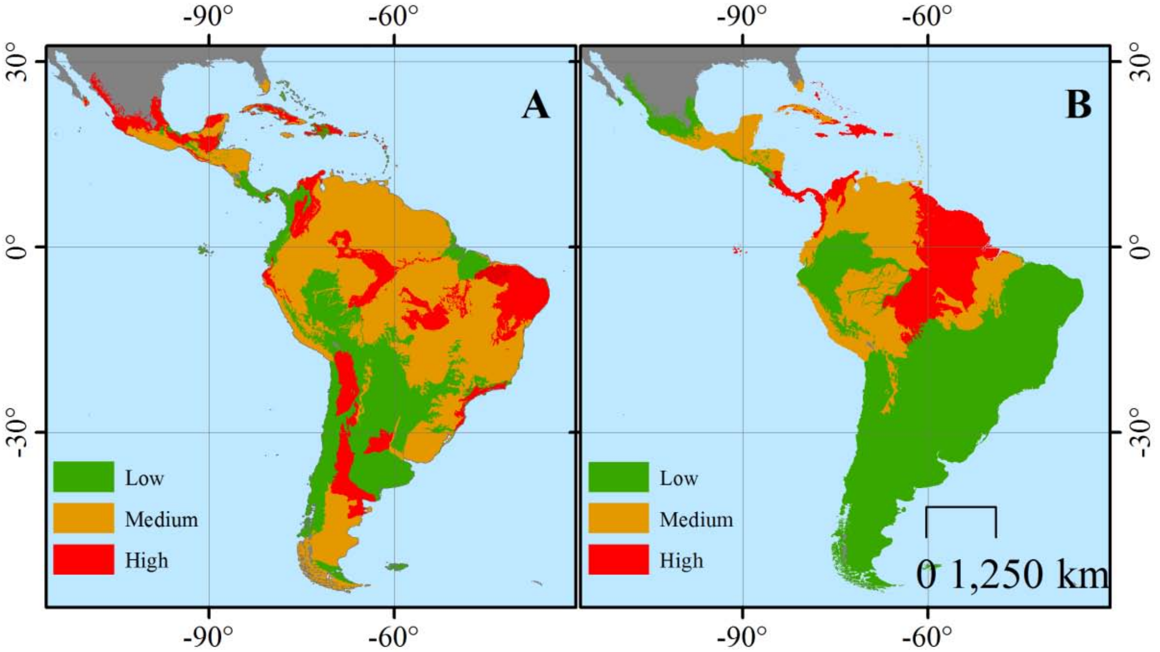

Figure 3. Priority ecoregions for mammal functional diversity change according to observed/predicted proportion according to modelled estimates (A) and priority ecoregions were mammal functional diversity is more significantly influenced by threatened species therefore more susceptible to species loss (B) for the Neotropical realm.

Discussion

Mammal functional diversity (FD) across the Neotropical realm showed considerable variation across most ecoregions, but was very similar across major habitat types (Figure 1D), and was significantly influenced both by human impact and species at risk. Differences in FD among major habitat types probably reflect natural differences due to habitat and environmental constraints, which affects both ecosystems and animal assemblages through environmental filtering (Messier et al. 2010; Swenson et al. 2012). Furthermore, similarities among habitats of the same kind (e.g., T&S forests) highlight how this filtering is potentially defining ecosystem structure in terms of functional types or species roles.

Our results highlight the importance of anthropogenic intervention, both at the ecosystem and species levels (i.e., disturbance and species at risk), regarding ecosystem resilience and dynamics (Peterson et al. 1998; Sundstrom et al. 2012). Also indicated geographic variation of the influence of the explanatory variables, indicating the large variation along small space gradients characteristic of the Neotropics (Stein et al. 2014), but also, in terms of anthropogenic factors: how certain ecoregions are under more severe threat of losing functionality than others. The results of the model are robust (i.e., high variation explained) in terms of explaining the variation of FD as defined by species richness (i.e., species threatened and non-threatened) and current human intervention. Overall model variation explained by selected variables, and geographically weighted maximum variation explained for certain ecoregions, indicates that some regions are heavily affected by human intervention; however, for ecoregions with low levels of intervention only ~50% of this variation was explained.

Previous studies of global variation on FD -in mammals and other groups- have shown similar patterns than those obtained here (Cardoso et al. 2011; Freudenberger et al. 2012; Safi et al. 2011), and most studies have identified anthropogenic intervention (in terms of land-cover transformation) as a major driver for FD loss (Barragán et al. 2011; Biswas & Mallik 2010; Flynn et al. 2009; Newbold et al. 2014). However, very few studies have assessed the influence of species at risk and the potential functional loss due to species extinctions (Flynn et al. 2009; Fonseca & Ganade 2001; Petchey & Gaston 2002a). Our results support the premise that human intervention and species at risk can significantly alter ecosystem function (Flynn et al. 2009; Petchey & Gaston 2002a), but also, highlight how threatened species, that according to IUCN standards are mostly those restricted, vulnerable or rare, contribute significantly (i.e., complementarity) to unique ecosystem functions (Mouillot et al. 2013; Schmera et al. 2009). Furthermore, the impact of ecosystem functionality loss has deeper implications in terms of ecosystem resilience and vulnerability (Armsworth et al. 2007; Díaz & Cabido 2001; Díaz et al. 2013); therefore, species loss not only means a reduction in the number of species in a system, but also serious impacts at the community and ecosystem levels (Ceballos & Ehrlich 2002).

Species richness have previously shown high correlation with FD (Mason et al. 2005), especially when using our metric (Petchey & Gaston 2002b), therefore it was expected these variables were highly related. Nevertheless, in order to determine the influence of threatened and non-threatened species, likely a substitute for species richness, allowed us to distinguish the effect of these two categories in order to better explain FD, resulting in more precise inferences on the negative impact of species loss. The strong influence of intervention and species at risk on FD in certain ecoregions and biomes helps to identify specifically where priorities should be focused in order to reduce species and ecosystem functionality loss (Biswas & Mallik 2010; Ceballos & Ehrlich 2002; Díaz et al. 2013; Flynn et al. 2009; Petchey & Gaston 2002a). Biomes and ecoregions at higher risk, as identified by our model, demand prior attention since impacts of functional loss affect beyond biological diversity, it reduces ecosystem resilience and ecosystem services (Armsworth et al. 2007; Díaz & Cabido 2001; Díaz et al. 2013). Our identification of priority ecoregions, both by likelihood of change and influence of species at risk, indicate how certain areas require more urgent conservation actions at species, populations and ecosystem levels so FD, and thus ecosystem functioning, can be maintained. Most of the ecoregions encompassing most of the Neotropical human population are those requiring reduction of deforestation and intervention in general. Ecoregions in the likely most diverse areas of the Neotropics are those requiring species-level protection since threatened species considerably influence FD and hence ecosystem function.

The coarse resolution distribution maps for certain species, and limitations from index calculations, functional grouping and diversity estimations being relatively new for mammals, and animals in general (Blaum et al. 2011), may give rise to some constraints of our approach. However, most of the discussion is in terms of which life and ecological traits are more relevant for functional roles of species in ecosystems. In addition, our approach still highlights that even when few traits are used, human intervention is a severe threat to FD, and it is likely that future analyses at finer resolutions will show the same trend, since it is expected that lower redundancy will be observed among species (Fonseca & Ganade 2001; Mouchet et al. 2010). Because we analyzed current mammal distribution ranges, positive influence of intervention can be related to already degraded assemblages or already-affected FD, suggesting that common species play more significant key roles in ecosystems than rare species; this trend coincides in those ecoregions where non-threatened species have the highest influence.

This is among the first studies assessing the influence of human impacts over mammal FD, especially for one of the largest and most diverse areas globally, to our knowledge. Further explorations into mammal FD at finer and more detailed resolutions and definitions and precise approaches to represent human intervention would provide confirmation and increase the precision of the trends found in our results. Our definition of FD, as linked to the concept of functional richness, is the functional trait space occupied by species within a community (Mason et al. 2005), influencing productivity and in turn functionality and resilience at ecosystem and community scale. Therefore, despite our coarse assessment of FD, influence of determinant variables will definitely have significant conservation implications.

Definition of conservation priorities at regional scales have proved an efficient tool to effectively tackle biodiversity loss, and region-wide assessments and actions may bring threat reduction and better conservation planning (Farias & Svensson 2014; Fitzpatrick et al. 2007; Gauthier et al. 2010). Our results help refine conservation planning analyses by providing new insights and tools on different biodiversity measures, especially by linking both species risk and human intervention with ecosystem vulnerability and resilience (Díaz et al. 2013). Previous priority-selection schemes have identified priority areas based on species richness, threat or singularities (Le Saout et al. 2013), our approach do not undermine these initiatives by proposing new priorities, instead call for attention to those regions suffering functionality loss due to intervention and species loss, likely improving conservation actions not only for selecting conservation areas but as a tool for conservation planning and decision making by selecting adequate policies (Visconti et al. 2011). Also, this study can help enhance our understanding on how natural and induced spatial variability can be incorporated in conservation planning to improve our conservation practices aiming to reduce biodiversity loss, which is the current paramount environmental problem worldwide.

Acknowledgements

This paper is a partial fulfillment of the Graduate Doctoral Degree Program in Biomedical Sciences (Programa de Doctorado en Ciencias Biomédicas) of the National Autonomous University of México (UNAM) of the first author. J.F. G.-M. acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT), and UNAM (scholarship 255983). Partial support was provided by The Sierra to Sea Institute and The Mikelberg Family Foundation. Thanks to J. Schipper and J. Belant for continued support throughout the research.

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Supporting information – Appendix S1

Table S1. Neotropical ecoregions classified by biome (*i.e.,*major habitat type) and classified according to priority based on likelihood of change and influence of threatened species over mammal functional diversity.

Biome	Ecoregion	Change likelihood			Influence of Threatened species		
		Low	Medium	High	Low	Medium	High
T&S moist broadleaf forests	Alta Paraná Atlantic forests	X			X		
	Araucaria moist forests		X		X		
	Atlantic Coast restingas	X			X		
	Bahia coastal forests		X		X		
	Bahia interior forests		X		X		
	Bolivian Yungas	X				X	
	Caatinga Enclaves moist forests			X	X		
	Caqueta moist forests		X		X		
	Catatumbo moist forests		X			X	
	Cauca Valley montane forests			X		X	
	Cayos Miskitos-San Andrés & Providencia moist forests	X					X
	Central American Atlantic moist forests		X			X	
	Central American montane forests	X				X	
	Chiapas montane forests	X				X	
	Chimalapas montane forests			X		X	
	Chocó-Darién moist forests	X					X
	Cocos Island moist forests	X					X
	Cordillera La Costa montane forests		X			X	
	Cordillera Oriental montane forests			X		X	
	Costa Rican seasonal moist forests	X					X
	Cuban moist forests		X				X
	Eastern Cordillera real montane forests		X		X		
	Eastern Panamanian montane forests	X					X
	Fernando de Noronha-Atol das Rocas moist forests	X			X		
	Guayanan Highlands moist forests		X			X	
	Guianan Freshwater swamp forests		X				X
	Guianan moist forests		X				X
	Gurupa varzeá			X			X
	Hispaniolan moist forests			X			X
	Iquitos varzeá		X		X		
	Isthmian-Atlantic moist forests	X					X
	Isthmian-Pacific moist forests	X					X
	Jamaican moist forests		X				X
	Japurá-Solimoes-Negro moist forests			X		X	
	Juruá-Purus moist forests		X			X	
	Leeward Islands moist forests			X		X	
	Madeira-Tapajós moist forests		X				X
	Magdalena Valley montane forests			X		X	
	Magdalena-Urabá moist forests	X					X
	Marajó Varzeá forests	X					X
	Maranhao Babaçu forests			X	X		
	Mato Grosso seasonal forests			X		X	
	Monte Alegre varzeá			X			X
	Napo moist forests		X		X		

Continue Table S1.

T&S moist broadleaf forests	Negro-Branco moist forests		X			X	
	Northeastern Brazil restingas		X		X		
	Northwestern Andean montane forests	X				X	
	Oaxacan montane forests		X			X	
	Orinoco Delta swamp forests		X				X
	Pantanos de Centla		X			X	
	Pernambuco coastal forests			X	X		
	Pernambuco interior forests			X	X		
	Peruvian Yungas		X		X		
	Petén-Veracruz moist forests			X		X	
	Puerto Rican moist forests		X				X
	Purus varzeá		X		X		
	Purus-Madeira moist forests			X			X
	Rio Negro campinarana		X			X	
	Santa Marta montane forests			X			X
	Serra do Mar coastal forests			X	X		
	Sierra Madre de Chiapas moist forest			X	X		
	Sierra de los Tuxtlas	X				X	
	Solimoes-Japurá moist forest		X		X		
	South Florida rocklands		X			X	
	Southern Andean Yungas		X		X		
	Southwest Amazon moist forests	X				X	
	Talamancan montane forests	X					X
	Tapajós-Xingu moist forests		X				X
	Tepuis		X			X	
	Tocantins/Pindare moist forests	X				X	
	Trindade-Martin Vaz Islands tropical forests	X			X		
	Trinidad and Tobago moist forests		X			X	
	Uatuma-Trombetas moist forests		X				X
	Ucayali moist forests		X		X		
	Venezuelan Andes montane forests		X			X	
	Veracruz moist forests			X	X		
	Veracruz montane forests			X	X		
	Western Ecuador moist forests	X				X	
	Windward Islands moist forests	X				X	
	Xingu-Tocantins-Araguaia moist forests		X			X	
	Yucatán moist forests		X			X	
T&S dry broadleaf forests	Apure-Villavicencio dry forests		X			X	
	Atlantic dry forests		X		X		
	Bahamian dry forests	X					X
	Bajío dry forests			X	X		
	Balsas dry forests		X		X		
	Bolivian montane dry forests	X			X		
	Cauca Valley dry forests			X		X	
	Cayman Islands dry forests			X		X	
	Central American dry forests		X		X		
	Chaco	X			X		
	Chiapas Depression dry forests	X				X	
	Chiquitano dry forests	X			X		
	Cuban dry forests			X		X	
	Ecuadorian dry forests	X				X	
	Hispaniolan dry forests	X					X
	Islas Revillagigedo dry forests	X			X		
	Jalisco dry forests			X	X		
	Jamaican dry forests		X				X
	Lara-Falcón dry forests		X			X	
	Leeward Islands dry forests			X		X	
	Magdalena Valley dry forests			X		X	
	Maracaibo dry forests		X			X	
	Marañón dry forests		X		X		
	Panamanian dry forests			X			X
	Patia Valley dry forests		X			X	
	Puerto Rican dry forests			X			X
	Sierra de la Laguna dry forests			X	X		

Continue Table S1.

T&S dry broadleaf forests	Sinaloan dry forests			X	X		
	Sin· Valley dry forests			X			X
	Southern Pacific dry forests		X			X	
	Trinidad and Tobago dry forests		X			X	
	Tumbes-Piura dry forests			X	X		
	Veracruz dry forests	X				X	
	Windward Islands dry forests	X				X	
	Yucatán dry forests			X		X	
T&S coniferous forests	Bahamian pine forests		X				X
	Belizian pine forests	X				X	
	Central American pine-oak forests		X			X	
	Cuban pine forests		X			X	
	Hispaniolan pine forests	X					X
	Miskito pine forests		X			X	
	Sierra Madre de Oaxaca pine-oak forests		X			X	
	Sierra Madre del Sur pine-oak forests		X			X	
	Sierra de la Laguna pine-oak forests			X	X		
	Trans-Mexican Volcanic Belt pine-oak forests			X	X		
Temp. broadleaf and mixed forests	Juan Fernandez Islands temperate forests			X	X		
	Magellanic subpolar forests		X		X		
	San Felix-San Ambrosio Islands temperate forests		X		X		
	Valdivian temperate forests	X			X		
T&S grasslands, savannas, and shrublands	Arid Chaco	X			X		
	Beni savanna		X			X	
	Campos Rupestres montane savanna		X		X		
	Cerrado		X		X		
	Córdoba montane savanna	X			X		
	Guyanan savanna		X				X
	Humid Chaco	X			X		
	Llanos		X			X	
	Uruguayan savanna		X		X		
	clipperton Island Scrub and Grassland	X			X		
Temp. grasslands, savannas, and shrublands	Argentine Espinal			X	X		
	Argentine Monte			X	X		
	Humid Pampas	X			X		
	Patagonian grasslands	X			X		
	Patagonian steppe		X		X		
	Semi-arid Pampas	X			X		
Flooded grasslands and savannas	Central Mexican wetlands			X	X		
	Cuban wetlands	X				X	
	Enriquillo wetlands	X					X
	Everglades		X			X	
	Guayaquil flooded grasslands			X	X		
	Orinoco wetlands		X			X	
	Pantanal		X		X		
	Paraná flooded savanna		X		X		
	Southern Cone Mesopotamian savanna	X			X		
Montane grasslands and shrublands	Central Andean dry puna			X	X		
	Central Andean puna	X				X	
	Central Andean wet puna	X				X	
	Cordillera Central paramo			X	X		
	Cordillera de Merida paramo		X			X	
	Northern Andean paramo		X			X	
	Santa Marta paramo			X			X
	Southern Andean steppe	X			X		
	Zacatonal			X	X		
Mediterranean forests, woodlands, and scrub or sclerophyll forests	Chilean matorral	X			X		
Deserts and xeric shrublands	Araya and Paria xeric scrub		X			X	
	Aruba-Curacao-Bonaire cactus scrub			X		X	
	Atacama desert	X			X		

Continue Table S1.

Deserts and xeric shrublands	Caatinga			X	X		
	Cuban cactus scrub		X				X
	Galapagos Islands xeric scrub	X					X
	Guajira-Barranquilla xeric scrub			X			X
	La Costa xeric shrublands		X			X	
	Leeward Islands xeric scrub			X		X	
	Malpelo Island xeric scrub	X					X
	Motagua Valley thornscrub		X			X	
	Paraguana xeric scrub		X			X	
	San Lucan xeric scrub		X		X		
	Sechura desert		X			X	
	Tehuacan Valley matorral	X				X	
	Windward Islands xeric scrub		X			X	
Mangrove	Alvarado mangroves	X				X	
	Amapa mangroves		X				X
	Bahamian mangroves	X					X
	Bahia mangroves	X			X		
	Belizean Coast mangroves	X				X	
	Belizean Reef mangroves	X				X	
	Bocas del Toro-San Bastimentos Island-San Blas mangroves		X				X
	Coastal Venezuelan mangroves		X			X	
	Esmeraldes/Chocó mangroves	X				X	
	Greater Antilles mangroves			X			X
	Guianan mangroves		X				X
	Gulf of Fonseca mangroves			X	X		
	Gulf of Guayaquil-Tumbes mangroves		X		X		
	Gulf of Panama mangroves		X				X
	Ilha Grande mangroves	X			X		
	Lesser Antilles mangroves		X			X	
	Magdalena-Santa Marta mangroves		X				X
	Manabi mangroves		X			X	
	Maranhao mangroves		X		X		
	Marismas Nacionales-San Blas mangroves			X	X		
	Mayan Corridor mangroves		X			X	
	Mexican South Pacific Coast mangroves	X			X		
	Moist Pacific Coast mangroves		X				X
	Mosquita-Nicaraguan Caribbean Coast mangroves		X			X	
	Northern Dry Pacific Coast mangroves			X		X	
	Northern Honduras mangroves	X				X	
	Para mangroves	X					X
	Petenes mangroves		X			X	
	Piura mangroves		X		X		
	Rio Lagartos mangroves		X			X	
	Rio Negro-Rio San Sun mangroves	X					X
	Rio Piranhas mangroves			X	X		
	Rio Sao Francisco mangroves			X	X		
	Southern Dry Pacific Coast mangroves	X			X		
	Tehuantepec-El Manchon mangroves			X	X		
	Trinidad mangroves	X				X	
	Usumacinta mangroves	X				X	
Total		68	93	57	82	87	49

6.2. Connecting two continents: species richness, functional traits and extinction risk in the Panamanian Isthmus-Choco continuum

Connecting two continents: species richness, functional traits and extinction risk in the panamanian isthmus-choco continuum

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Abstract

Macroecological analyses provide a powerful tool for evaluating the animal communities and the conservation status of an ecoregion. Using this approach in smaller scales allows reaching solid results in how the species richness, functional traits and extinction risk are changing throughout a specific region. The connectivity area between the Costa Rican Seasonal forest and the Chocó Darien Moist Forest represents the bridge between the Mesoamerican region and the Andean tropical region. This area has historical importance based on the role played in the great mammal exchange, currently containing over 327 species of mammals and possessing well preserved forest patches as well as highly deforested areas. Species composition follows a clear pattern within a geographic logic, but extinction risk and functional traits do not follow the same pattern. Here we provide exploratory and preliminary analyses of the ecological continuum between Costa Rica and Colombia, based on a macro-ecological perspective, in order to provide insights on current biogeographical and threat patterns as a basis for ecological understanding and conservation planning.

Key words: Chocó, Costa Rica, Darién, extinction risk, mammal diversity, Panamá Isthmus, species turnover

Introduction

Understanding the mechanisms of geographical variation in species richness across an specific taxa represents a major challenge for ecology and conservation strategies (McGill 2003, Jetz et al. 2009, Soberon and Ceballos 2011). Macroecological analyses have acquired a great deal of importance over the last two decades, mainly due to that large scale analyses allow a different perspective to evaluate the animal communities and the conservation status of an ecoregion. This is important in designing new management strategies for the regions transcending the political borders of the countries. The techniques have been generally applied in assessing how the communities are structured in large scales and have proven to be very successful in describing general patterns, but the same approach has not been use to understand the processes that are linked to the patterns in the structuring of communities at smaller scales (Beck et al. 2012).

Smaller scale analysis with a macroecological approach will allow reaching consistent results (Rondinini et al. 2011), especially when determining how the species richness, functional traits and extinction risk are changing throughout a specific area. The region between the Costa Rican Seasonal forest and the Chocó Darien Moist Forest represents the connecting bridge between the Mesoamerican region and the Andean tropical region. Besides the historical importance that this same region played in the great mammal Interchange , currently the regions harbors over 327 species of mammals and possess well preserved forest patches as well as highly deforested areas along the landscape (Sánchez-Azofeifa et al. 2001).

Over the years, the research has focused in the comparisons made between ecoregions analyzing how the species composition changes from one site to another. Although this classical approach is useful, due to species introduction and local extinctions, there is a great deal of redundancy in the communities across a large region. Here is when it becomes important to evaluate the functional traits and groups of an animal community in order to obtain more plausible comparisons between the sites (Vitousek et al. 1997, McGill et al. 2006, Messier et al. 2010). Thereby to understand these functional traits, we need more research and understanding of the deficiencies in the current data gaps, the missing data on species, distribution and phylogenetic relatedness since this aspects make more difficult to assess the global and regional biodiversity patterns and underlying processes. This exploratory analysis is based on current knowledge (including biogeographical patterns and threats) and the idea is to relate all this information with the current challenges in the management and conservation planning of the ecological realms. Here we provide an exploratory and preliminary analysis of the ecological continuum between Costa Rica and Colombia, based on a macroecological perspective, in order to provide insights on current biogeographical and threats patterns as a basis for ecological understanding and conservation planning.

Materials and methods

Study area

Our study focused on the mammal fauna present on five ecoregions defined by the World Wildlife Fund (WWF; Olson et al. 2001), covering from Costa Rica towards northwestern between Panama and Colombia (Figure 1). The ecoregions analyzed were the Chocó-Darién moist forests (C-D MF), Costa Rican seasonal moist forests (CR SMF), the Isthmian-Atlantic moist forests (I-A MF), the Isthmian-Pacific moist forests (I-P MF) and the Talamancan montane forests (T MF). This continuum represents the connection between the two subcontinents, North and South America. We selected these ecoregions based on ecological and ecosystem affinities (in terms of biomes), including the area where more shared ecological affinities could be expected. Of the five ecoregions, the largest one corresponds to Chocó-Darién moist forests, whilst the smallest is the Costa Rican seasonal moist forests, been this ecoregion and the Isthmian-Pacific moist forests the most threatened according to WWF classification (Table 1; Olson et al. 2001, Olson & Dinerstein 2002). So, even that the ecoregions shared a common geological past and stand close of each other, the conservation needs and the threats differ greatly from one to another.

Table1. Ecoregions analyzed and their characteristics (WWF 2009)

Ecoregion name	Area (km^2)	Global Status	Biome
C-D MF	73.556,27	Relatively Stable/Intact	Tropical and subtropical moist broadleaf forests
CR SMF	10.699,08	Critical/Endangered	
I-A MF	58.761,68	Vulnerable	
I-P MF	29.177,08	Critical/Endangered	
T MF	16.287,19	Relatively Stable/Intact	

Methods

Based on the five ecoregions studied, we analyzed the composition of mammal assemblages based in three variables: species composition, life traits and extinction risk. We extracted the geographic information for the five ecoregions from the WWF Ecoregions Database (WWF 2009), and used the distribution polygons for all mammals from the IUCN Red List of Threatened Species (IUCN 2012). We extracted those species present on each ecoregion by a spatial overlapping using ArcGIS (ESRI (Environmental Systems Research Institute) 2009). After obtaining the species composition, we classified each species according to the following traits: Mass (five categories: Small, Small-Medium, Medium, Medium-Large and Large), Guild Realm (three categories: Herbivore, Carnivore and Omnivore) and Habits (five categories: Terrestrial, Aquatic, Fossorial, Arboreal and

Volant) based on previous databases (Davidson et al. 2009, Jones et al. 2009) and our updates. Also, each species was classified according to its conservation status following the IUCN Red List of Threatened Species categorization, available at IUCN (2012).

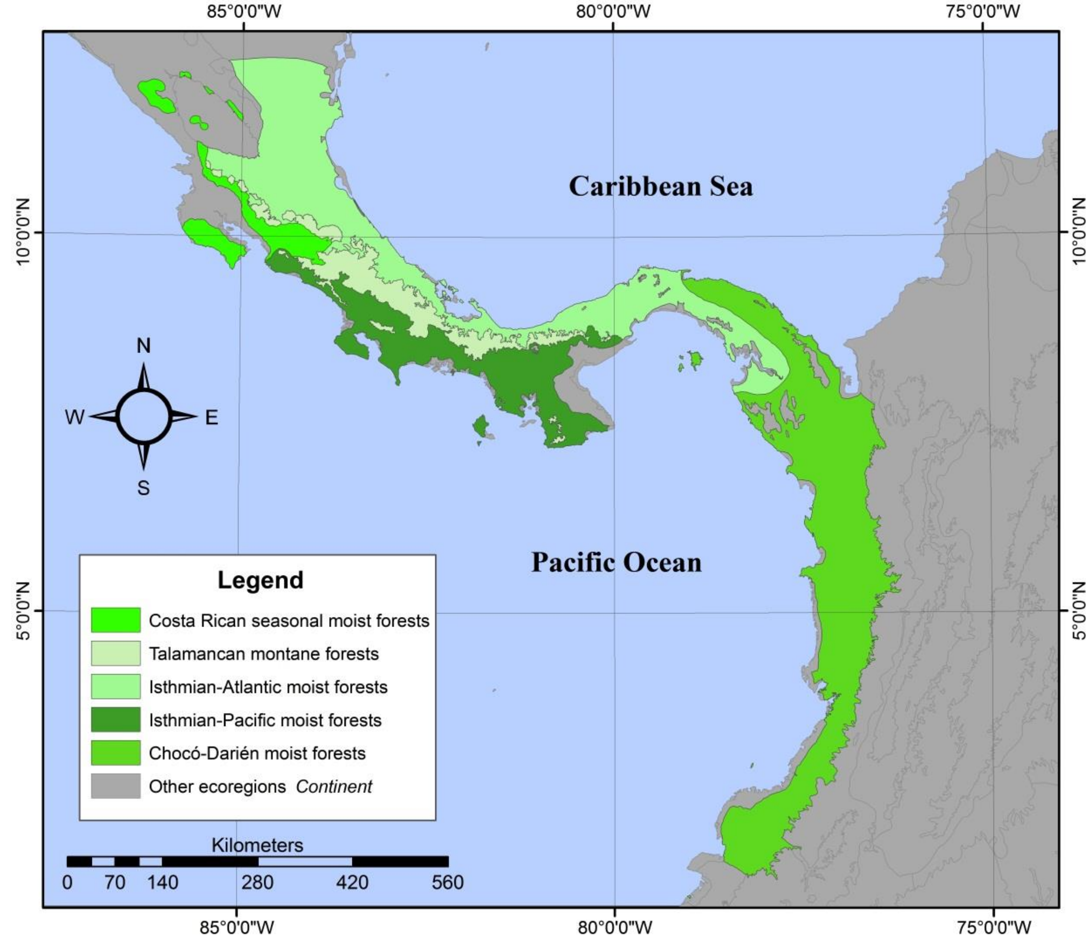

Figure1. Ecoregions used for macroecological analyses in the Costa Rica-Panama-Colombia isthmus.

We explored the species composition on each ecoregion and compared the compositions across the five of them using cluster analyses (Jaccard mean average distance for species richness and traits and Euclidian Average linkage for threat categories). Also, a Simple Linear Regression was used to relate the area of each ecoregion and the species richness. Contingency tables were used to explore the relationship between the number of traits and number of species on each threat category and the ecoregions. All the statistical analyses were performed in Infostat (Di Rienzo et al. 2011).

Results

A total of 327 species of mammals were obtained for the five ecoregions. The Chocó-Darién moist forests was the ecoregion with the highest richness, followed by the Isthmian-Atlantic moist forests, while the Costa Rican seasonal moist forests showed the lowest species richness (Table2, Figure 1). In this sense the area of the ecoregion significantly explained the number of species present in each area (Lineal Regression: R^2=0,8036, p=0,0394).

Table2. Total richness and number of species per mammal order in the five ecoregions of the isthmus.

Order	C-D MF	CR SMF	I-A MF	I-P MF	T MF
Artiodactyla	6	4	4	4	4
Carnivora	22	20	20	18	18
Chiroptera	135	104	100	93	93
Cingulata	2	2	2	2	2
Didelphimorphia	14	8	8	7	7
Insectivora	1	4	4	3	3
Lagomorpha	1	3	3	2	2
Pilosa	5	5	5	5	5
Primates	11	4	3	3	3
Paucituberculata	2	0	0	0	0
Pterissodactyla	1	1	1	1	1
Rodentia	57	45	40	34	34
Total	**257**	**200**	**190**	**172**	**172**

The relationship and similarity between the ecoregions according to the number of species on each area showed a significant relationship between the Talamancan Montane Forests and the Isthmian Pacific Moist Forests, decreasing the association respectively with the rest of ecoregions, while the Chocó-Darién Moist Forests were the most distinctive (Figure 2).

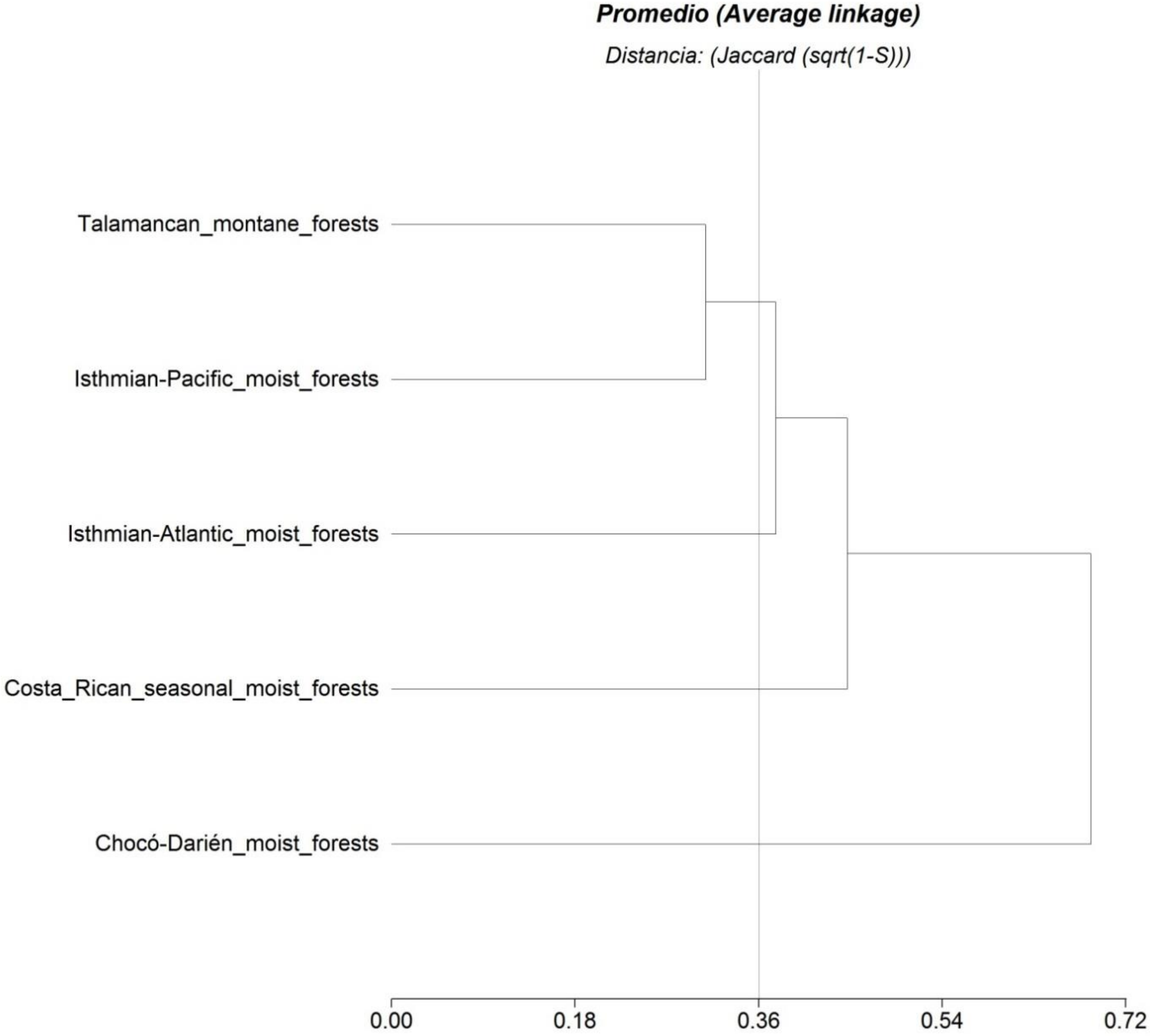

Figure 2. Cluster analyses based on Jaccard average distance for each ecoregion according to species richness.

In terms of functional traits, for all ecoregions the most abundant traits (number of species) were Carnivores, Volant and Small, showing a significant decreasing pattern according to species richness (Figure 3). No significant relationship was found between the number of species of each trait and the ecoregion (p>0,99).

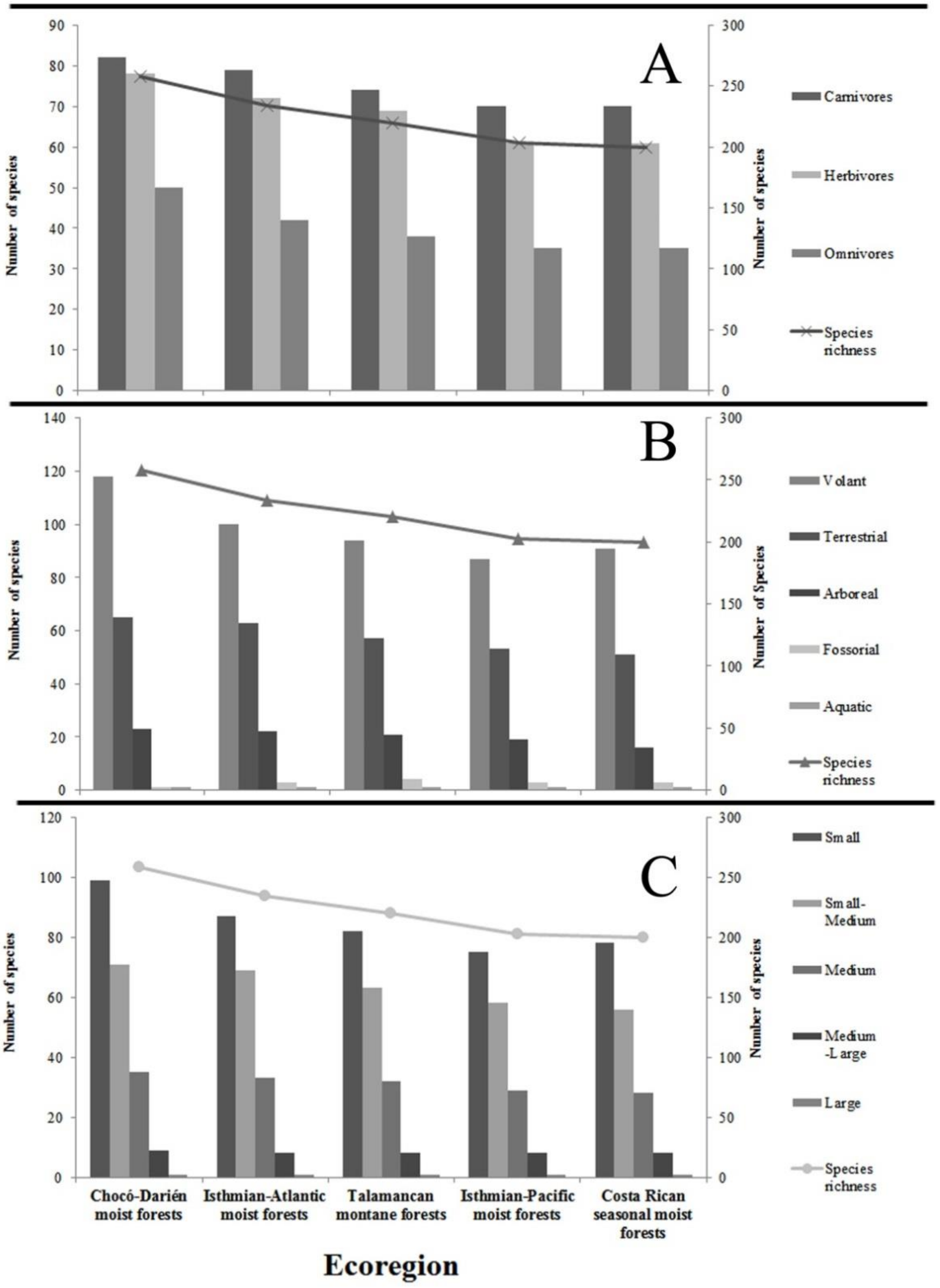

Figure 3. Number of species on each trait in the five ecoregions. (A) Trophic Realm, (B) Habit and (C) Body size.

The relationship between the richness of each trait relating all the ecoregions showed significant relationships between the Isthmian-Pacific moist forests with Costa

Rican Seasonal moist forests and the Talamancan montane forests with the Isthmian-Atlantic moist forests, while the Chocó-Darién moist forests was significant different from the rest (Figure 4).

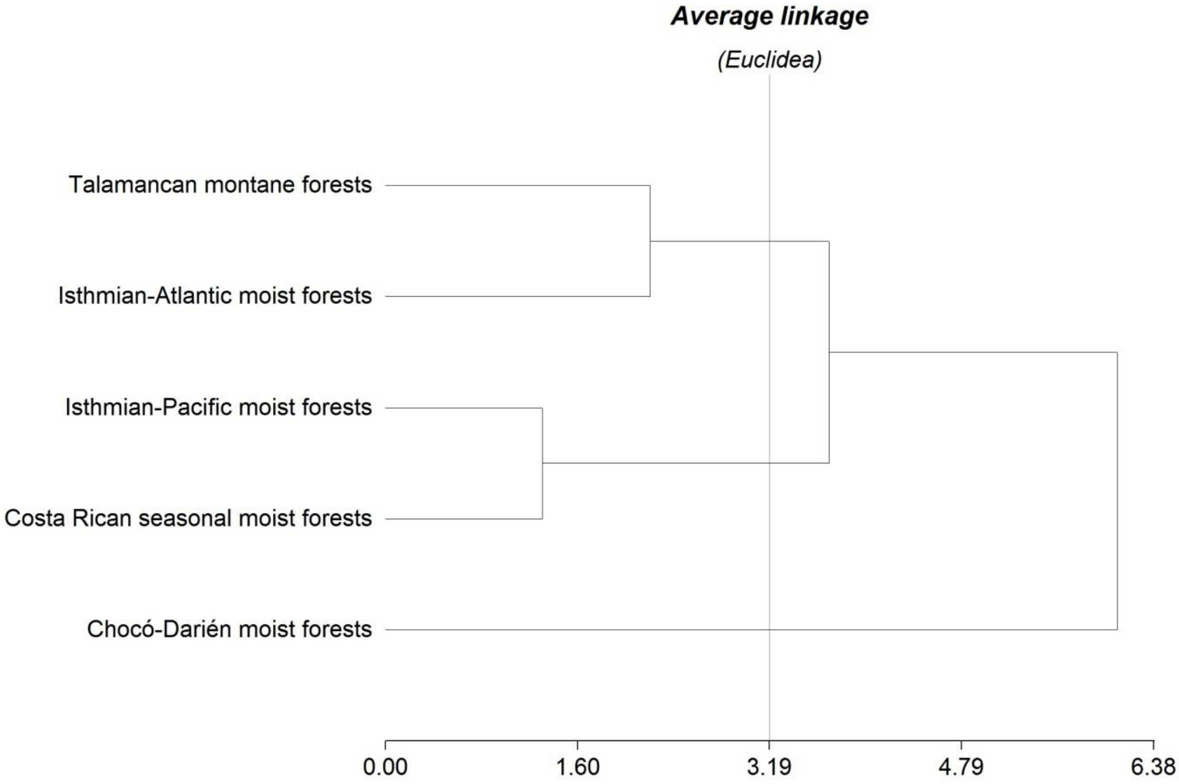

Figure 4. Cluster analyses based on Euclidean average distance for each ecoregion according to traits richness.

In terms of threats and conservation status, the vast majority of species on each ecoregion belonged to the Least Concern category (LC), followed by Data Deficient (DD) and Near Threatened (NT) (Figure 5). No significant relationship was found between the IUCN category and ecoregions (Contingency Table: $p < 0,3713$). Although, the association between ecoregions based on the number of species on each category showed a significant relationship between the Isthmian-Pacific moist forests and Costa Rican Seasonal moist forests followed by the Talamancan Montane Forests (Figure 6).

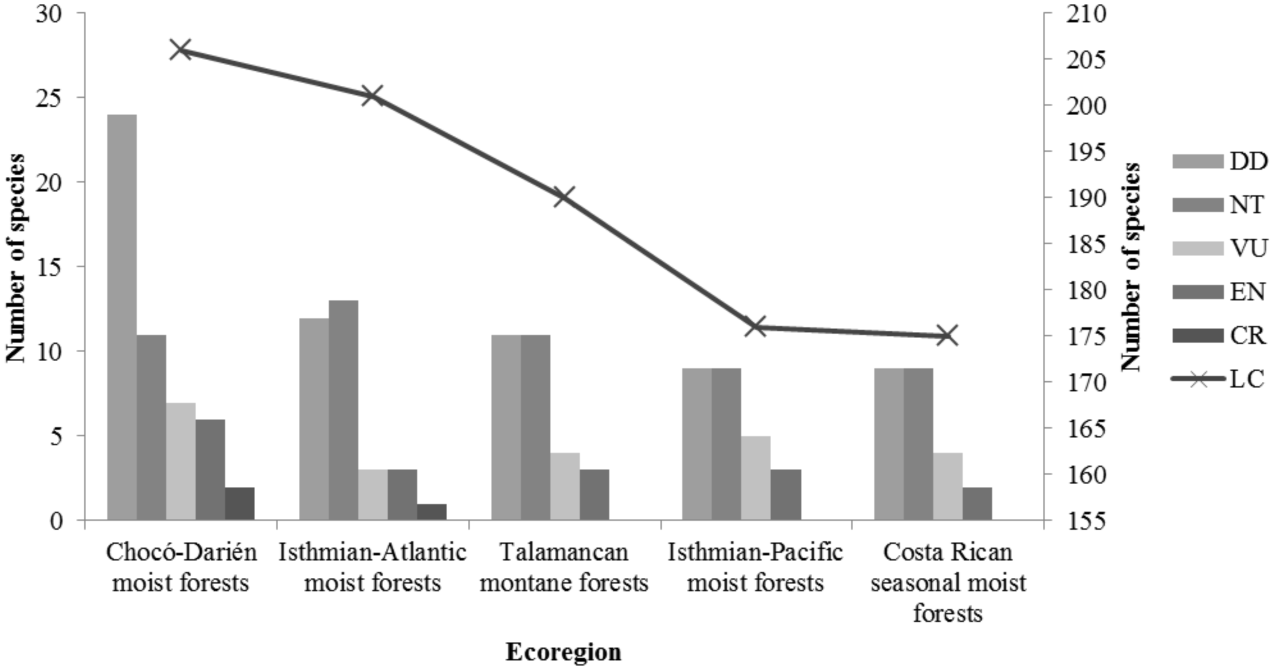

Figure 5. Number of species on each IUCN Red List of Threatened species category per ecoregion

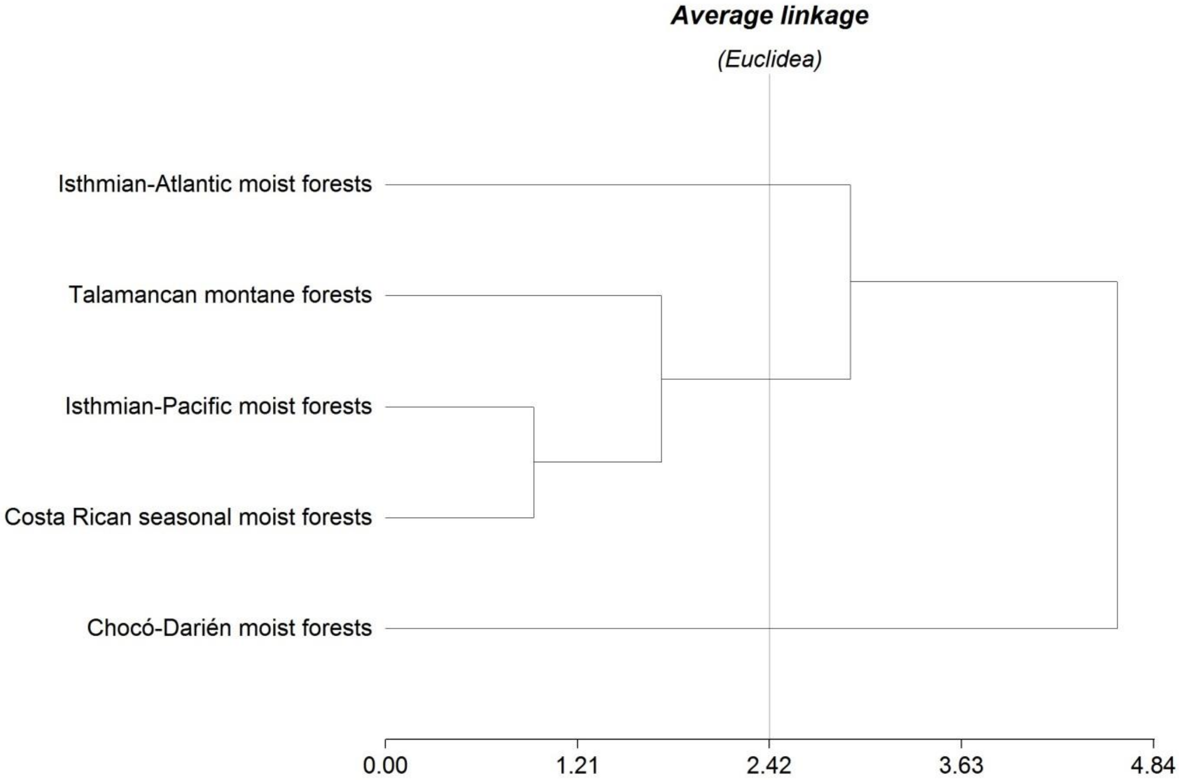

Figure 6. Cluster analyses based on Euclidean average distance for each ecoregion according to species richness on each Red List category.

Discussion

Mammal richness in the isthmus varies significantly among ecoregions, however, with no significant differences among the different orders. While the C-D MF is the ecoregion with the highest richness and T MF has the lowest, there is not a consistent gradient neither North-South nor South-North direction. Despite the geographic position of all the ecoregions and the closeness among them, differences in the number of species can be found in terms of species composition between the regions. One possible explanation is related with elevation and environmental factors. Rahbek (1995) demonstrated that diversity decreases with elevation, although for mammals there is consistent evidence that the highest richness is nested in mid-elevation (McCain 2005, Belmaker and Jetz 2011), and the mammal assemblages in high elevations are composed of complementary species (i.e. species that are less similar in their functional traits; Safi et al. 2011).

Our results indicate that the T MF ecoregion, located right in between of I-A MF and I-P MF, showed the highest similarity, significantly differencing those on the extremes (C-D MF and CR SMF), showing an interrupted pattern towards the middle. This represents an interesting trend showing a turning point in the ecoregions with a significant difference towards the “connection” between both sub-continents, with C-D MF representing the South American component and CR SMF the Central American counterpart. The T MF and the I-P MF showed the highest correlation in terms of Species Richness; this may be explained by the fact that this particular region is more or less well preserved and the continuity of this is maintained by conservation areas such as the La Amistad binational park between Costa Rica and Panamá (United Nations Environmental Programme/World Conservation Monitoring Centre 2011).

However, it is interesting how this pattern do not follow the same trend in terms of species traits and threat status. Whilst according to species richness T MF, I-A MF and I-P MF are highly similar and differentiated from the two extremes and in terms of species traits the patter follows a South-North trend, decreasing the number of species, especially for carnivores, volant and small mammals. In this case, the clusters are formed differently, with a highest association between T Mf and I-A MF, even higher for CR SMF and I-P MF and both clusters totally differentiated from the C-D MF. This trend indicates a rupture on the functional patterns of the mammal assemblages from South America, relating all the Central American ecoregions and showing a threshold exactly located in the Panamanian isthmus. This rupture may be explained by environmental factors such as rainfall and more importantly latitude with some groups being more diverse south of the Panamanian isthmus threshold. Lyons & Willig (2002) showed the species richness decreased with latitude for bats and marsupials. Although our study is covered in a much smaller scale the same pattern is expected, and this may be an explanation for the rupture on functional patters shown in our analyses. Furthermore, it is possible that this tendency can be also related with the level of disturbance for some of the ecoregions, influencing how some species and functional traits are significantly reduce, changing the composition of the assemblage.

In terms of conservation status, the same South-North pattern arises, but with the interesting trend of equal Data Deficient and Near Threatened species for all Central American ecoregions, but in the C-D MF, representing a huge gap of knowledge, mostly described by the number of Data Deficient species. The number of Least Concern species also decreases from South to North, probably related with the conservation status of the ecoregion itself. The cluster analyses for threat categories also organizes the Central American ecoregions together and separate them from C-D MF, but showed a different pattern, also clustering T Mf with I-A MF, but organizing CR SMF and I-P MF more highly associated. Land use changes and other human activities represent a major threat for all the tropical ecosystems, for example the effects on biodiversity of the pineapple and oil palm plantations in Costa Rica and Panama are not fully understood, but the global tendency shows that the oil plantations are a major driver of deforestation worldwide even though that much sod of the studies have been conducted in southeast Asia (Koh and Wilcove 2007, Carlson et al. 2012).

The interesting patterns found for the three variables analyzed herein, highly relates with a potential turning point on the mammal fauna from the two subcontinents, highlighting the differences and importance of the region in terms of small-scales variation. Even when the species richness varies among ecoregions because the assemblage structure might vary with the size of ecoregions, in smaller areas like I-P MF and CR SMF the extinctions probabilities increase because this ecoregions are more vulnerable to environmental disturbances, while in larger areas like C-D MF and A-I MF the structure of the assemblages potentially is more stable (Cardillo 2011). It seems that traits are better proxies of the differences, which implies interesting patterns in terms of species assemblages and ecosystem functioning. Macroecological analysis have shown that the functional diversity tends to be more stable across a particular ecoregion than among ecoregions or vast areas (Safi et al. 2011), so it is necessary to understand the variability between and within biogeographical units.

The analysis of conservation status is also very interesting as it indicates how despite geographic proximity some ecoregions have significant higher knowledge, but also, how geographic restrictions together with human activities, conducts to completely different threat patterns. The future of tropical dry and moist rainforest is threaten by five major anthropogenic forces: hunting, wood extraction, land use changes, atmospheric and climate changes (Miles et al. 2006, Wright 2010). The continuum showed differences not only in terms of species richness and traits, but also in terms of data gaps, risk and conservation status in general. For most Central American ecoregions herein analyzed, the general conservation status is deficient, with the exception of C-D MF and T MF, both that represent the two extremes in terms of species richness and trait composition. It seems clear that the analysis of species composition can lead to better understanding of ecological realms, accounting for differences even when small scales are analyzed. However, this specific region also shows an incredible variability, highlighting how species richness and uniqueness is so heterogeneous in tropical ecoregions.

With the environmental threats hanging over our heads like the Damocles sword, immediate actions must be taken to ensure the preservation of the tropical forests. Regional actions must integrate the local stakeholders and make them real conservation actors, in order to ensure the long-term participation in conservation programs (Harvey et al. 2008). This idea is not nearly new, Janzen (1986) urged the scientific community to establish this relationship, but yet here we stand more than 25 years later still stating the importance of this connection but without any real strategies.

Conclusions

Current knowledge suggests that the distribution of biodiversity should be a priority for political and biological processes since is directly related to human well – being (ecosystem services). With this work, we showed how a freely available set of variables (Richnness, Functional traits and Extinction risk) can provide interesting regional-scale results, giving new tools to the decision makers to conservation planning. Additionally, we have shown successfully that standard techniques taken form macroecological approaches can be applied to minor scales yielding consistent results. The information extracted from this kind of analyses has a major role in terms of conservation planning and species distribution understanding.

Our analysis of the conservation status shows that throughout the region the knowledge gaps are common. Given the constant ecological threats affecting the region, studies filling this information gaps must be a high priority for researchers and authorities in the area. It seems some of the ecoregion are subject to different levels of human disturbance, and this can be reflected not only on the status of the ecoregion itself, but in terms of the risk for the species present on each. Since some of this ecoregions are potentially more affected or vulnerable to threats, we highly recommend assessing and addressing the urgent threats to this ecoregions, especially those in Mesoamerica, in order to reduce mammal conservation risks and ensure the long term persistence of the assemblages, both in terms of species and functional diversity.

Acknowledgements

We would like to thank The Sierra to Sea Institute for the support in realizing this paper. Also, thanks to Instituto de Ecología-UNAM and CONACyt-México, for support and scholarships for JFGM and LRVR. Andrés Arias-Alzate provided insightful comments for the manuscript. Thanks to Alex Mauricio Jiménez for his support in the submission of the manuscript and reviewers for their comments.

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7. Capítulo 3. Distribución, conservación y determinantes de la diversidad taxonómica y funcional a escala nacional: estudios de caso en Colombia y Costa Rica

7.1. Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica

Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica

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Abstract

Costa Rica has one of the greatest percentages (26%) of protected land in the world. The National Protected Areas System (NPAS) of Costa Rica was established in 1976 and currently includes >190 protected areas within seven different protection categories. The effectiveness of the NPAS to represent species, populations, and areas with high species richness has not been properly evaluated. Such evaluations are fundamental to understand what is necessary to strengthen the NPAS and better protect biodiversity. We present a novel assessment of NPAS effectiveness in protecting mammal species. We compiled the geographical ranges of all terrestrial Costa Rican mammals then determined species lists for all protected areas and the estimated proportion of each species' geographic range protected. We also classified mammal species according to their conservation status using the IUCN Red List of Threatened Species. We found almost complete representation of mammal species (98.5%) in protected areas, but low relative coverage (28.3% on average) of their geographic ranges in Costa Rica and 25% of the species were classified as underprotected according to a priori representation targets. Interestingly, many species-rich areas are not protected, and at least 43% of cells covering the entire country are not included in protected areas. Though protected areas in Costa Rica represent species richness well, strategic planning for future protected areas to improve species complementarity and range protection is necessary. Our results can help to define sites where new protected areas can have a greater impact on mammal conservation, both in terms of species richness and range protection.

Key Words**:** SINAC; IUCN; Biodiversity, Protected Areas; Threatened species; WCPA; Mammals

Introduction

Protected areas are the primary biodiversity conservation strategy used across geographic scales to avert biodiversity loss [1, 2]. Though global biodiversity conservation goals for protected areas have been set to reduce possible negative effects of anthropogenic activities [3], many aspects of protected areas, such as representativeness of species and ecosystems, have not been fully examined [2, 4]. Though the global biodiversity crisis is typically measured at the species level, the effects of species loss occur first at the population level [5]. Because of the need for understanding conservation strategies at finer scales, the role of protected areas has gained greater relevance and their importance requires further assessment [6]. As more and better information is available regarding species distributions and population trends, assessments of protected area effectiveness can be conducted at increasingly finer resolutions [7]. Additionally, as new data becomes available, the use of global range data derived from systematic efforts can further help improve conservation effectiveness assessments.

Costa Rica's protected areas system is considered among the most successful in Latin America [8]. Established in 1976, Costa Rica's National Protected Areas System (NPAS) has evolved from a few areas of small geographic extent to a large and well-managed system [8, 9]. However, the full extent of protected areas effectiveness in representing species and other aspects of biodiversity conservation in Costa Rica have not been addressed. Further, the Convention for Biological Diversity goals [10] and earlier assessments have identified substantive under-representation of numerous ecosystems within this protected area network [11]. Given the need for assessing effectiveness at various biodiversity levels, and that most countries lack comprehensive information for many taxonomic groups, surrogate and/or particular taxonomic groups and their conservation status have been used as indicators of protected area effectiveness [12, 13]. Mammals play key roles in ecosystems, are considered charismatic and require relatively large areas to survive; therefore their conservation is warranted [4, 5, 14]. Furthermore, there is often more data available on mammals than for other taxonomic groups [15, 16]; therefore, we consider mammals an appropriate group for assessing representativeness of protected areas. We present the first comprehensive assessment of Costa Rican protected areas effectiveness and representativeness using the most recent geographic information for protected areas and the most updated available range information for mammals. Our objectives were to: 1) evaluate the extent and representativeness of protected areas for protecting terrestrial mammal species and their geographic ranges in Costa Rica, 2) determine priority areas for mammal conservation, and 3) assess the singularities and conservation gaps for mammal species within the NPAS.

Materials and Methods

Study area

Costa Rica is located in Mesoamerica between 8° and 12° N and 82° and 86° W, bordering with Nicaragua and Panama to the north and south, respectively. It has 51,100 km^2 of continental territory. Considered one of the most biologically diverse countries in the world [17], Costa Rica has strong environmental policies and a long-standing NPAS system [18], with more than 190 protected areas covering about 26% of the national territory [19, 20]. Due to its geographical position, Costa Rica has played a key role in the Great Continental Interchange [21, 22] and has a mixture of Neotropical and Neartic faunas [23-25]. Costa Rica has nearly 238 mammal species, including >200 terrestrial species within 140 genera and 44 families [24, 26].

Data sources

Species geographic distributions were obtained from the 2008 Global Mammal Assessment [27] available through the IUCN Red List of Threatened Species (S1 Table, S2 Table; [27, 28]). Each range was delineated, assessed and revised by a group of mammalogists from the respective countries where the species are present [27] and represented the best information available. We classified each species as 'native', 'extant' and 'possibly extant', checking for consistency with the most recent species list for the country [24]. We also obtained the conservation status of each species [28], which included Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). Finally, we identified endemic species (n = 18), defined as those unique to Costa Rica or distributed only in Costa Rica-Panama or Costa Rica-Nicaragua [24, 26]. Taxonomic changes that occurred since the last Costa Rican mammal list update were considered for our analyses (S1 Text).

We obtained spatial information regarding protected areas from the Sistema Nacional de Áreas de Conservación – SINAC (Conservation Areas National System), the most current database for protected areas in Costa Rica that contained sub-national level areas not included in the World Database for Protected Areas [29]. We used only those protected areas (n = 198) with an IUCN Protected Areas management category [29, 30] (Table 1). Based on land cover data for the country [31], we estimated that 88.03% of protected areas consist of natural ecosystems, with 11.56% considered non-forested areas (secondary growth and regeneration), and 0.39% classified as agricultural and urban areas.

Table 1. Protected areas of Costa Rica classified by IUCN categories, its corresponding national category, number of areas in each category and area covered for effectiveness assessment for mammal conservation.

IUCN Category	Costa Rica Category	Abb.	Number of areas	Area (km^2)
I	Biological Reserves	BR	8	216.0
II	Absolute Natural Reserve	ANR	1	13.0
	National Park	NP	32	6274.8
IV	Wildlife Refuges	WR	90	2338.7
	National Wetland	NT	21	302.0
VI	Forestry Reserve	FR	11	2166.2
	Protected Zone	PZ	35	1575.0

Effectiveness of protected areas in representing species richness

To assess the effectiveness of protected areas for protecting total species richness, we determined the complementarity and representativeness of all mammal species in the protected areas system. We defined complementarity as the gain in representativeness of mammal species when a site is added to an existing set of protected areas [32, 33]. We overlaid the protected areas map with the distribution polygons of all 208 species and extracted the number and identity of each species for each protected area by protected area category. We then sorted the protected areas by year of establishment using the SINAC database and generated a species accumulation curve. We assessed complementarity, high or low redundancy, by generating an accumulation curve for the randomized pooled protected areas and assessed similarities in species composition (*i.e.,*species identity) among protected areas and categories through a cluster analysis using the Jaccard similarity coefficient; Jaccard coefficients measures spatial turnover by comparing all pairs sites, clustering similar sites until a complete dendrogram is constructed [34, 35]. Considering the variation in size among protected areas, we tested for the relationship between the extent of each protected area and the number of species protected using a simple linear regression.

Effectiveness of protected areas for protecting mammal species ranges

We used a digital vector map of Costa Rica to determine the geographic range of each species within its boundaries [31]. We then overlaid the range polygons of the 208 mammal species with the protected areas polygons and estimated the proportion of each species' range currently within the protected areas by category. We assessed the progression of species' range protection according to year of establishment by chronologically ordering the range proportion of each species added per area created each year. We used simple Pearson correlation tests to assess relationships between the geographic extent of each category and the mean range protected and to test if the proportion of range protected was associated with total species range.

To assess if a species is "underprotected" (i.e., if it has an insufficient coverage of its geographic range), we followed the targets proposed by Rodrigues et al. [36] but adapted to Costa Rica: restricted-range species (<1000 km^2) were expected to be 100% protected while large range species (>25,550 km^2, half the country´s total extent) were expected to be protected in at least 10% of their range, and a linear decline in the target between these two extremes [37]. We plotted the current range for each species, the proportion of its range protected and the a priori representation targets and identified as underprotected those species below this target.

Conservation gaps and priority areas

To determine conservation gaps and priorities we overlaid all species distribution polygons with a grid containing 83 km^2 cells and from each cell we extracted the species present in each cell, evaluating the total number of species and the number of species on each IUCN Red List category. We defined our mapping unit as this cell size considering the mean range of the five smallest species ranges in the country, thus ensuring that each of these species could be considered in at least one cell. We overlaid this grid with the protected areas digital layer and identified those cells with number of species and threatened species (i.e., Critically Endangered, Endangered, Vulnerable and Data Deficient) not covered by any protected area as well as those areas with the highest numbers of underprotected species according to the a priori targets. We included Data Deficient species among those threatened since this category represents those species with not sufficient information to be properly assessed but acknowledges the possibility that future research will indicate that a threatened category may be appropriate [38]. We considered a cell to be protected when it was partially overlapping with at least one protected area. We tested for differences ($\alpha = 0.05$) in total species richness and number of endemic and threatened species between protected and unprotected cells using non-parametric Kruskal Wallis tests and Conover post-hoc multiple comparison tests [39]. All statistical analyses were performed using Infostat software [39] and all spatial analyses with ArcGIS 10.2 [40]. Means are reported with + 1 SD unless otherwise noted.

Results

Representativeness of mammal species richness in protected areas

Most species (98.5%; 205 spp.) are represented in the NPAS. Only three species, *Coendou rothschildi*, *Peromyscus gymnotis* and *Reithrodonthomys paradoxus*, do not have any portion of their range protected. Of the 18 endemic species, all occur within at least three protected areas (Mean±SD= 25.72 ± 16.41), with *Sturnira mordax* and *Cryptotis nigrescens* the best represented (59 and 55 protected areas, respectively) and *Orthogeomys cavator* and *Sigmodontomys aphrastus* the poorest represented (3 and 4 protected areas, respectively; Table 2). Three protected areas contained 12 endemic species (Cordillera Volcánica Central Forestry Reserve and La Amistad and Chirripó National Parks). For threatened species, the mean number of protected areas for all species is greater for Endangered (153.00 ± 0.00), than Data Deficient (73.43 ± 75.40) and Vulnerable (69.35 ± 56.00) species. La Amistad and Chirripó National Parks and Los Santos Forestry Reserve each harbor 11 threatened species. *Leopardus tigrinus*, *Cryptotis gracilis* and *Saimiri oerstedii* (VU) represented in 48, 39 and 37 protected areas, respectively, and *Cryptotis orophila*, *Sylvilagus dicei* and *Sigmodontomys aphrastus* (DD) represented in 38, 13 and 4 protected areas, respectively, are the least represented of all threatened species.

About 82% of mammal species were represented in at least one protected area by 1961 and 97% were represented by 1975 (Figure 1). In 2014, the mean number of species per protected area is 123 (± 19) species (Median = 126), with the maximum number of species (n = 172) in La Amistad National Park and a minimum number of species (n = 93) in Costa Esmeralda Wildlife Refuge. More than 100 species are represented in >100 protected areas and 58 species in >140 protected areas; 76 species are protected in <60 protected areas (Figure 2). Although there is a significant positive relationship between the size of protected areas and the number of species, only 26% of the variation in the number of protected species is explained by the area of the reserve (R^2= 0.26, p>0.0001). Considering protected areas categories, National Parks contain the greatest species richness (98.10%), followed by Wildlife Reserves (97.60%), while National Absolute Reserves protect the fewest species (48.10%; Figure 3). National Parks and Protected Zones protect all endemic species, while National Wetlands and Absolute Natural Reserves protect 4 and 0 species, respectively. Considering threatened species, all protected area categories include all Endangered species (2 species). National Parks and Protected Zones protect all Data Deficient species (7 species) and these protected areas, along with Wildlife Refuges, include all Vulnerable species (4 species).

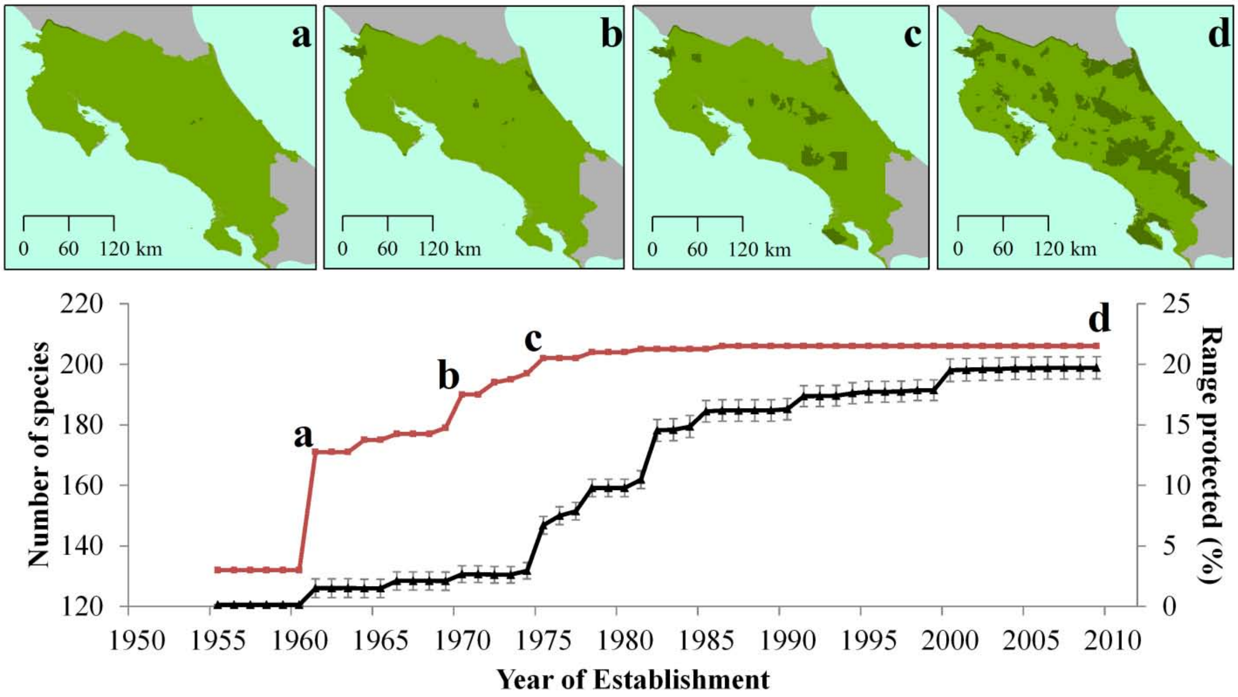

Figure 1. Chronology of protected areas establishment and number of mammal species represented in protected areas (red line), and mean percentage species ranges within protected areas (black line + SE) in Costa Rica. Inset maps denote locations of protected areas for each major increase in number of species protected in a) 1960, b) 1970, c) 1975 and d) 2009 as also indicated in the graph.

Table 2. Endemic and threatened species representativeness and range protected in the protected areas system of Costa Rica. Endemic species to Costa Rica (CR), to Costa Rica-Panama (CR-P) and to Costa Rica-Nicaragua (CR-N) are indicated by E. Species classified according to the IUCN Red List Criteria [28] as Endangered (EN), Vulnerable (VU), Data Deficient (DD), Near Threatened (NT) and Least Concern (LC) are indicated by RL (Red List).

Species	Range protected (%)	Protected Areas	Endemics			Red List status				
			CR	CR-P	CR-N	EN	VU	DD	NT	LC
Reithrodontomys paradoxus	0.00	0						*RL*		
Orthogeomys cherriei	4.88	22	E							*RL*
Orthogeomys heterodus	9.13	11	E							*RL*
Reithrodontomys brevirostris	12.31	28			E					*RL*
Mazama temama	19.21	153						*RL*		
Ateles geoffroyi	19.26	153				*RL*				
Tapirus bairdii	19.26	153				*RL*				
Cabassous centralis	19.26	153						*RL*		
Lontra longicaudis	19.26	153						*RL*		
Myrmecophaga tridactyla	19.63	153					*RL*			
Cryptotis orophila	23.68	38						*RL*		
Sturnira mordax	24.90	59		E					*RL*	
Saimiri oerstedii	25.54	37					*RL*			
Orthogeomys underwoodi	27.65	36	E							*RL*
Cryptotis nigrescens	32.39	55		E						*RL*
Reithrodontomys rodriguezi	34.18	14	E							*RL*
Leopardus tigrinus	35.98	48					*RL*			
Cryptotis gracilis	37.63	39		E			*RL*			
Heteromys oresterus	40.08	9	E							*RL*
Reithrodontomys creper	41.76	34		E						*RL*
Rheomys raptor	43.63	39		E						*RL*
Scotinomys xerampelinus	51.16	16		E						*RL*
Syntheosciurus brochus	57.22	26		E					*RL*	
Sylvilagus dicei	61.57	13		E				*RL*		
Sigmodontomys aphrastus	61.83	4		E				*RL*		
Orthogeomys cavator	62.06	3		E						*RL*
Rheomys underwoodi	68.44	18		E						*RL*

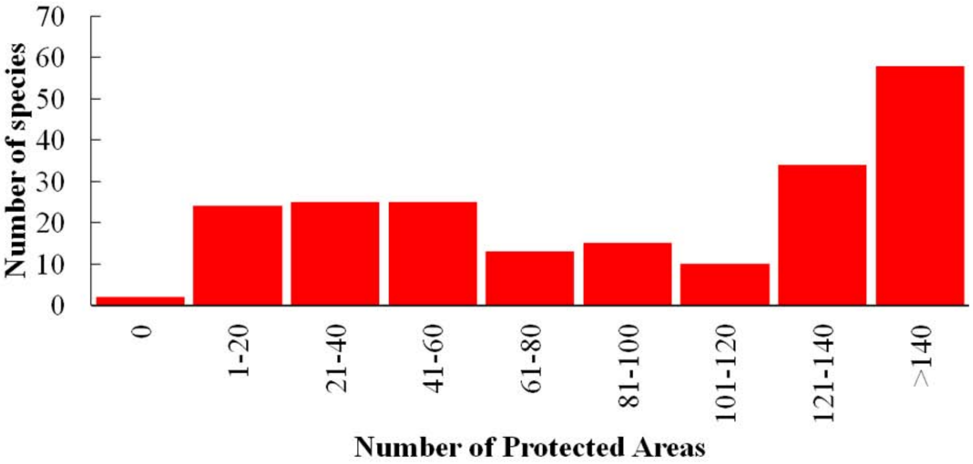

Figure 2. Frequency distribution of mammal species represented in all protected areas of Costa Rica. Note that most species were represented in at least 1 protected area and 48% of all species (100 species) were represented in more than 100 protected areas.

We found low complementarity (i.e., high redundancy) among protected areas for representing mammal species, as evidenced by a mean Jaccard similarity coefficient of 0.68 (± 0.13). This complementarity was even lower within protected area categories, with a mean Jaccard coefficient of 0.80 (± 0.18). Diversity similarities regarding protected area categories indicated three main groups, where National Absolute Reserves and National Wetlands differed from each other and from the remaining categories (Jaccard coefficient = 0.69 and 0.38, respectively) and protected fewer species, while Protected Zones, National Parks, and Wildlife Refuges were similar and protect the greatest number of species (Figure 4a). Even when protected areas included a high overall percentage of mammal species richness, the total number of species protected was achieved with comparatively few protected areas (Figure 4b).

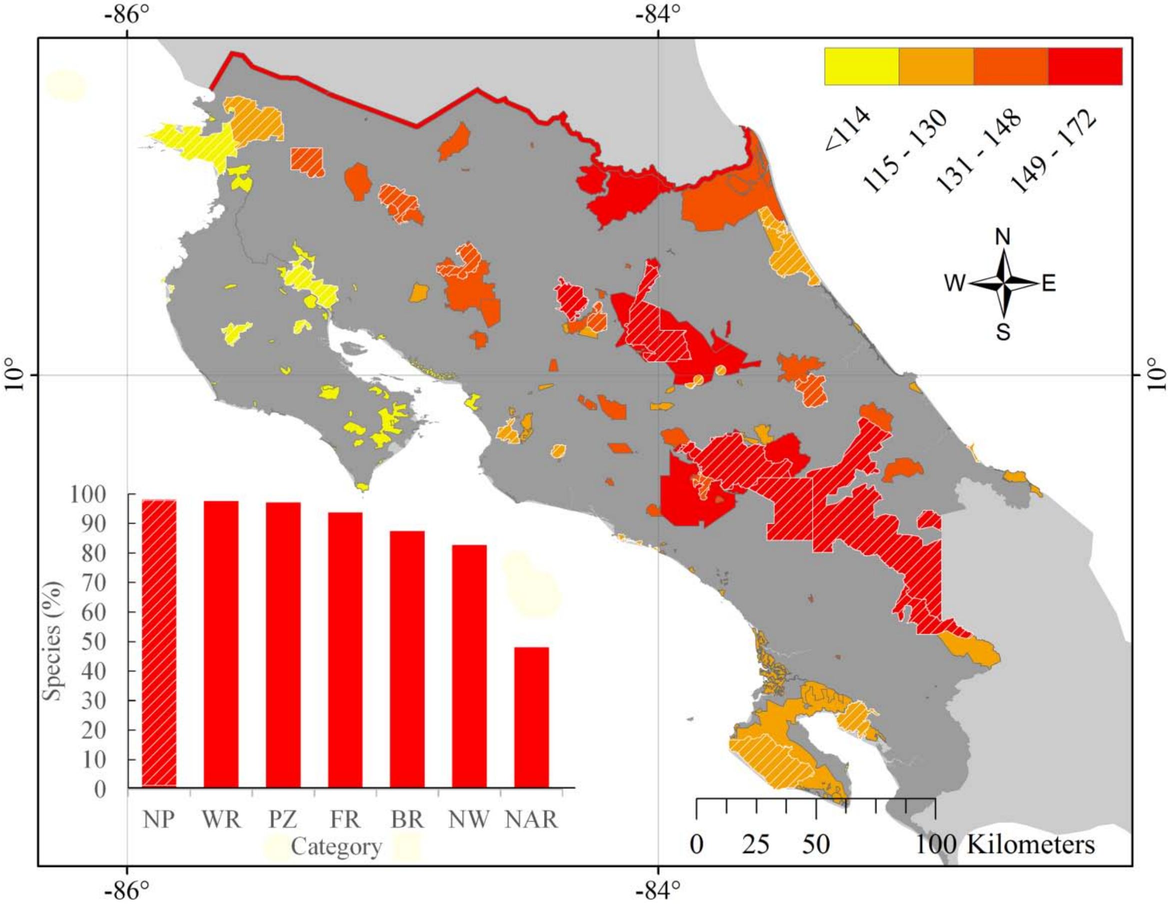

Figure 3. Number of mammal species by protected area and category in Costa Rica. The color scale at the top right indicates the number of species on each protected area. Protected areas with diagonal lines are National Parks. The inset figure indicates the percentage of mammal species in each protected area category (National Parks (NP), Wildlife Refuges (WR), Protected Zones (PZ), Forest Reserves (FR), Biological Reserves (BR), National Wetlands (NW) and Natural Absolute Reserves (NAR)).

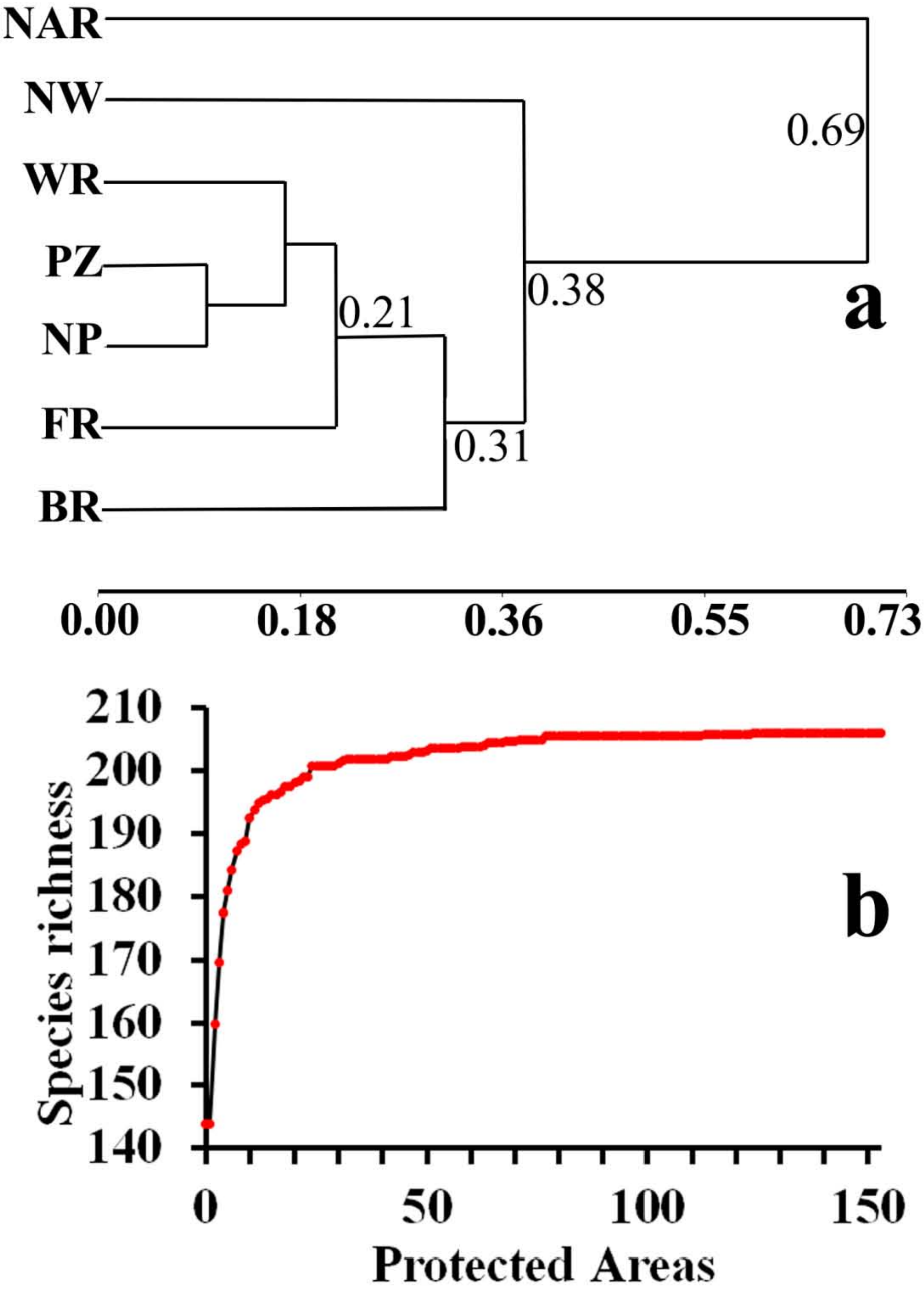

Figure 4. Complementarity of protected areas for representing mammal species richness in Costa Rica. a) Cluster analyses of species diversity using the Jaccard index between protected area categories (National parks (NP), Wildlife Refuges (WR), Forest Reserves (FR), Protected Zones (PZ), National Wetlands (NW) and Biological Reserves (BR)) and b) cumulative number of species protected.

Representativeness of mammal species ranges in protected areas

Though 98.50% of mammal species occur in at least one protected area, the geographic ranges of species protected within Costa Rica is considerably low. Considering all species, the mean percentage of protected range is 28.33 ± 13.85%, with National Parks protecting the greatest proportion of species ranges (14.27 ± 0.71%), followed by Wildlife Reserves (5.26 ± 0.66%). We found a strong correlation between the mean range of all species and the area covered by each category ($r = 0.99$, $p <0.001$). For four of the five remaining categories, mean percentage of species´ range protected was <5% (Figure 5). The temporal accumulation of mean species ranges within protected areas differed from that of the species richness. By 1960 only 1.50 ± 10.19% of the mean range of all mammals was protected, followed by 6.70 ± 10.40% by 1975 and reaching 19.72 ± 13.18% by 2009 (Median = 16.63%; Figure 1). Considering all species, 52 (25%) are underprotected in terms of range coverage by protected areas according to the a priori targets (Figure 6a). As for all endemic species, the overall mean range coverage is 38.70 ± 19.20%, with 10 endemic species under the proposed target (Table 2). Species classified as Data Deficient had on average 42.67 ± 27.55% of their geographic ranges protected, while the mean range protected for Vulnerable and Endangered species was 28.75 ± 13.32% and 25.00 ±0.01%, respectively (Figure 6b). Three species, *Cryptotis orophila* (DD), *Sigmodontomys aphrastus* (DD) and *Saimiri oerstedii* (VU) were considered underprotected according to our a priori targets. We found an inverse correlation between the total size of the species´ ranges in Costa Rica and the proportion protected ($r = -0.76$, $p < 0.001$).

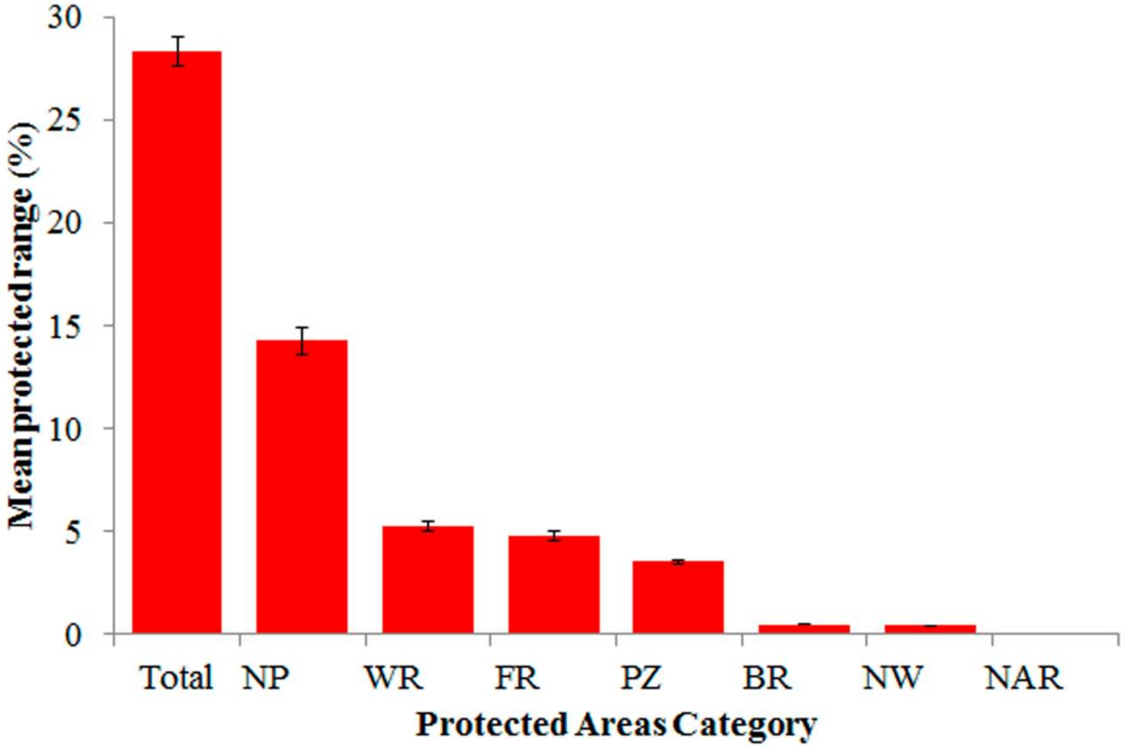

Figure 5. Percentage (±SE) of mammal species ranges within protected areas in Costa Rica. Mean percentage species ranges protected overall and in National Parks (NP), Wildlife Refuges (WR), Forest Reserves (FR), Protected Zones (PZ), Biological Reserves (BR), National Wetlands (NW) and National Absolute Reserves (NAR).

Conservation gaps and priority areas

Forty-three percent of cells are not currently included in any protected area. Mean species richness was significantly lower in cells without protected areas (121.41 ± 32.51) than in cells with >1 protected area (124.99 ±17.28; H = 5.51, p = 0.019). Unprotected areas include the Valle del General in the southern part of the country and the piedmont of the Tilaran Mountains in the north (Figure 7a). Also, a higher number of threatened species was estimated in cells with at least one protected area (7.38 ± 1.66) than in cells with none (6.47 ± 1.88; H = 42.94, p <0.0001; Figure 7b). A lower number of endemic species was estimated in unprotected (1.82 ± 2.38) than protected (3.16 ± 3.75) cells (H = 14.96, p < 0.001).

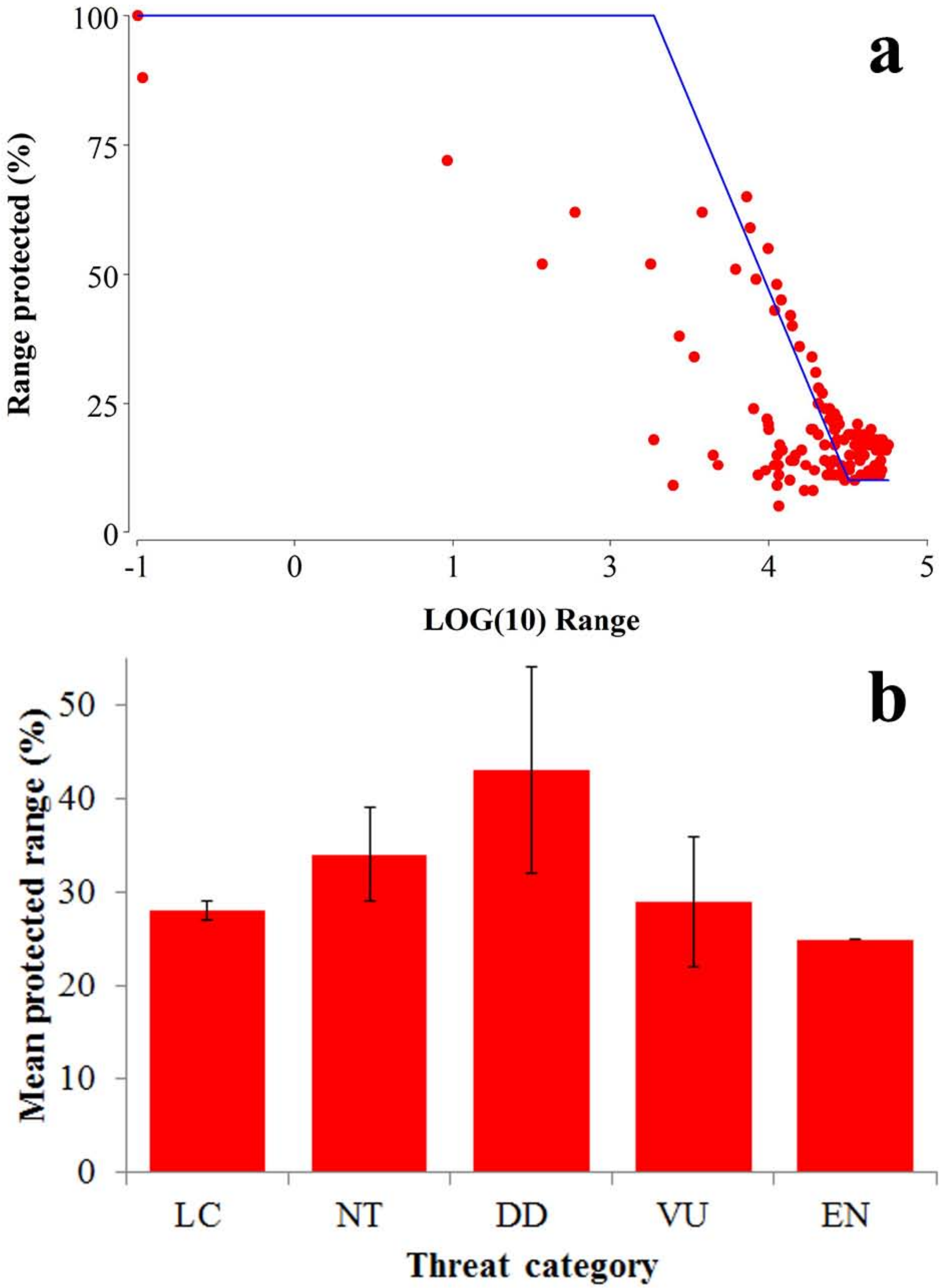

Figure 6. a) Mammal species range and percentage of each species range protected indicating a priori conservations targets (blue line) and b) percentage (±SE) of mammal species ranges protected in Costa Rica based on IUCN Red List of Threatened Species category (LC = Least Concern, NT = Near Threatened, DD = Data Deficient, VU = Vulnerable and EN = Endangered). Species located below the a priori target (see Methods) were identified as underprotected.

Priority areas to consider for filling gaps in range coverage for underprotected species (i.e., based on the a priori targets) were mostly in the Northern region and in the Valle del General of southern Costa Rica (Figure 7c). In general, most unprotected cells contained larger number of species, whereas Biological Reserves and National Wetlands contained the lowest number of species (Figure 7d).

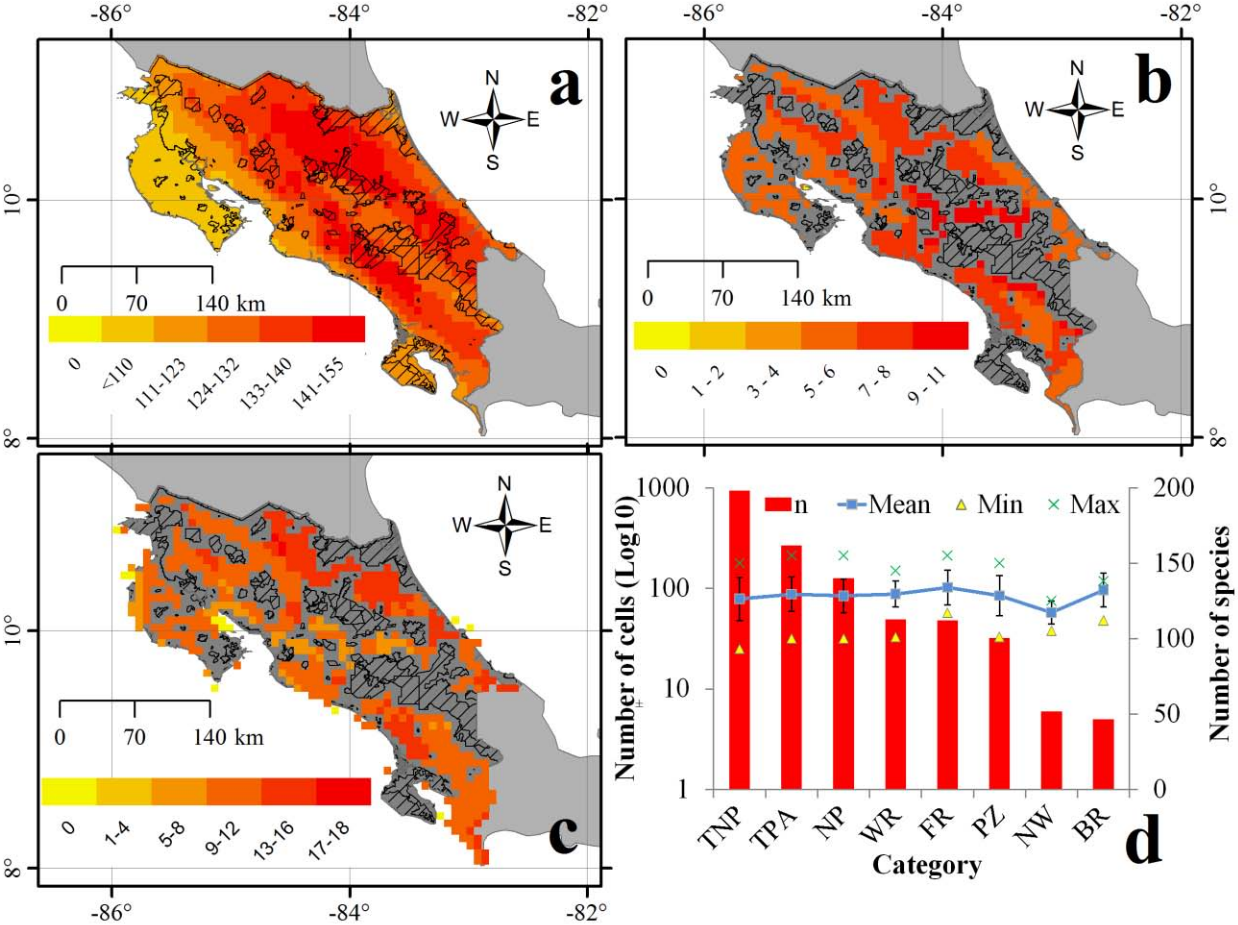

Figure 7. Mammal species richness within 83 km^2 grid cells in Costa Rica and protected areas (dashed polygons). a) Total species richness; b) number of threatened (VU, EN, CR and DD) species in cells not covered by protected areas; c) number of underprotected species (according to a priori targets; see Methods) in cells not covered by protected areas, and; d) number of cells not protected (TNP), cells in all protected areas (TPA), and cells on each protected area category (National Parks (NP), Wildlife Refuges (WR), Forest Reserves (FR), Protected Zones (PZ), National Wetlands (NW) and Biological Reserves (BR)). Secondary Y axis indicates the mean (blue line + SD), minimum (triangles) and maximum (x) number of species protected by cell in each category.

Discussion

Costa Rica´s protected areas system is one of the most extensive in Latin America, and is considered a management success [8], yet its representativeness and efficiency for biodiversity has been poorly studied. Protected areas contained 98.5% of terrestrial mammal species but we found low complementarity among these, with several areas contributing similarly to species richness and range coverage. A large proportion of species had substantial portions of their range protected, yet 25% of all species appear underprotected. Both endemic and threatened species were represented in at least a few protected areas, but species ranges were not adequately protected, especially for endemic species (10 species below the target).

Protected areas in Costa Rica contained at least a small percentage of the geographic ranges of most mammal species since the 1970s. The establishment of new areas since and up to the mid-1980s significantly increased mammal range coverage, not species, and remained fairly steady up to the year 2000 (i.e., about 19% mean range covered); since then new areas have not appreciably contributed to mammal protection nor markedly increased protection of areas with high species richness or mammal ranges. A large number of endemic species remain underprotected and require attention to reduce the potential for population losses. That many endemic species do not appear adequately protected suggests the approach used to design and establish protected areas has not incorporated all conservation needs that should be considered at a national scale to maximize biodiversity across ecosystems [33].

Complementarity is a key consideration when planning for conservation [32]. Since the contribution of different areas to the system is necessary to ensure representativeness, assessing this complementarity for Costa Rica could potentially inform planning for expanding and improving the current system. We found low complementarity (*i.e.,*high redundancy) among protected areas for representing mammal species suggesting they have likely been established either opportunistically, without detailed information on species occurrence and distribution, or with emphasis on other taxonomic groups or different values (*i.e.,*many National Parks were established around volcanoes), or even based on political will and agendas [18]. The high dependence of the Costa Rican NPAS on small reserves such as Wildlife Refuges (18% of all protected areas with a mean area of <26 km^2), areas without complete protection (i.e., protected zones and forest reserves) and the lack of connectivity between them could compromise their potential for protecting many mammal populations and perhaps species. Thus, we highlight the importance of National Parks in protecting mammal diversity, as they include nearly 98.5% of all species in at least one area. Protection of endemic and threatened species is also of importance and highlights the need for systematic planning [33] that considers their protection. We note that although National Parks protected at least part of the range of almost all species, 25% of these species remain under the a priori target. Other categories of protected areas are generally in areas of the country least represented by National Parks and therefore could play an important role in protecting additional portions of species ranges.

In the absence of information regarding species population ecology, density or abundance, we considered range as the best available proxy for species´ populations, especially for an area as small as Costa Rica [5]. Conservation of wildlife, including mammals, is often based on conservation at the species and population levels [41], where population losses can adversely affect ecosystem function and services [5, 42]. We found for Costa Rica that at least 25% of all species are currently underprotected, a pattern similar to global analyses [6, 37]. However, the percentage of species underprotected in Costa

Rica is greater than at global scale. More importantly, 55% of endemic and 23% of threatened species are currently underprotected, considerably greater than global values. This is of special concern for endemic species such as Orthogeomys cherriei, O. heterodus and Reithrodontomys brevirostris, which have a low percentage of their ranges currently protected (4.9, 9.1 and 12.3%, respectively). Protection of species richness depends on the extent of the protected area system as well as the range sizes of species. In Costa Rica, the relationship between range size and range protected was highly similar with global scales [37]; for species with small ranges, a general tendency to be either fully protected or drastically underprotected was observed, while species above our large range threshold (>25,550 km^2) were well covered by the entire protected areas system.

The selection of potential additional areas for protection remains a complex task for Costa Rica. Considering the already extensive system in the country, few remaining areas appear to have largely intact ecosystems and are not currently dedicated to agriculture activities [11, 43, 44]. Nevertheless, these areas could represent a good investment by contributing to protecting ranges of underprotected species or species of conservation concern. Moreover, considering the low complementarity among categories, and the important role of small protected areas, conservation strategies could consider expanding current protected areas or ensuring connectivity corridors among these areas [45-47]. Previous assessments of gaps within the Costa Rican NPAS indicated that nearly 50% of life-zones were represented in only 2% of the protected areas, which highlights high biodiversity risks for these systems and the species that inhabit them [11]. Our approach incorporated not only the species presence but species range representativeness that can be used to emphasize potential risk for many species. For instance, special consideration should be given for species in the orders Carnivora, Didelphimorphia, Primates and

Eulipotyphla considering the proportionally large number of threatened and declining species in these groups. Due to geographic extent constraints, few reserves in Costa Rica can likely harbor viable populations of many species, especially large mammals [48]. Therefore, incorporating species´ range into reserve planning or country-side conservation schemes [49] seems warranted to maintain mammal diversity in the country. Biological corridors have been identified as potential alternatives to protected areas in the country [45, 50], and thinking “outside the park” seems a necessary alternative to consider in light of potential mammal population losses [5, 49]. Already 26% of the country is under protection, but reserve size, isolation and anthropogenic pressures on these areas requires further evaluation of the protected areas system scheme [6, 14, 51]. Prioritization of expanded and connected reserve networks based on systematic conservation planning at landscape scales could help overcome the risks to perpetuate the representativeness of this protected areas system [52].

Costa Rica is an important area for continental mammal conservation [17, 24, 53, 54]; however, our results highlight the need for greater complementarity and representativeness [4, 55-58]. We have demonstrated the need for additional prioritization based on species and their geographic ranges, supporting the need for systematic conservation planning [59, 60]. The GRUAS II project (Technical proposal for territorial zoning for biodiversity conservation in Costa Rica) has identified several important areas for connectivity and species representation [61]. Though their analyses relied heavily on floristic components, several proposed areas were similar to areas we identified as important. Although in many respects highly successful, the Costa Rica NPAS would benefit from further protection schemes to ensure not only species richness, but species population viability, to better address the most serious threats in global biodiversity [5, 41].

We assessed the effectiveness of a protected areas system for one group of species. Our approach to identify protected area gaps in species and species' range, including threatened and endemic species, could be applied to other taxa. Our results, together with assessments of other taxa could be used to help refine conservation priorities by incorporating additional levels of surrogacy and ecosystem level variations [62].

Acknowledgements

This paper constitutes a partial fulfillment of the Graduate Doctoral Degree Program in Biomedical Sciences (Programa de Doctorado en Ciencias Biomédicas; PDCB) of the National Autonomous University of México (UNAM) for the first author. J.F. González-Maya acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT) and UNAM (scholarship 255983) and the support of the PDCB. We thank E. Martínez-Meyer, R.A. Medellín, and J. Schipper for insightful comments and support throughout this research.

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Supporting Information

S1 Text. Taxonomic information.

S1Table. List of Costa Rican mammal species used for analyzes classified by order and with its corresponding conservation status according to the IUCN Red List of Threatened Species.

S2 Table. Species Richness, number of species on each category of the IUCN Red List of Threatened Species by taxa for Costa Rican mammals used for assessing their representativeness in protected areas.

Supporting Information - SI

Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica

José F. González-Maya, Luis R. Víquez-R, Jerrold L. Belant & Gerardo Ceballos

S1 Text. Taxonomic information

We used 208 species of mammals within 36 families and 11 orders (Table S1). The order with greatest number of species was Chiroptera (107 spp.) followed by Rodentia (50 spp.); Perissodactyla had the lowest species richness (Table S2). At the family level, Phyllostomidae (59 spp) had the greatest number of species followed by Cricetidae (31 spp); nine families contained only one species. Regarding conservation status, 185 species were considered Least Concern, 10 Near Threatened, 9 as Data Deficient and six were classified as threatened (4 Vulnerable and 2 Endangered). Population trends of 99 species were considered stable, 27 decreasing, 10 increasing and 74 as unknown. Perissodactyla, Carnivora and Cetartiodactyla were the orders with the greatest percentages of decreasing populations (100, 55 and 50% respectively), while Primates and Eulipotyphla have the greatest percentages of threatened species (50 and 25%, respectively; Table S2).

Taxonomic changes for the final list of species used in our analyses included our recognition of *Handleyomys alfaroi*, *Nephelomys devius* (endemic to Costa Rica and Panama), *Sigmodontomys alfari*, *S. aphrastus*, *Transandinomys bolivaris*, and *T. talamancae* from the former *Oryzomys* genus following Weksler et al. [28]. We followed Musser and Carleton [1] for including former *Sigmodon hispidus* as *Sigmodon hirsutus*. *Spilogale angustifrons* was previously considered *S. putorius* [2]. Rodríguez-H et al. [3]

excluded *Bassarycion pauli* and *B. lasius* as their taxonomy is unresolved, even though specimens were confirmed for the country and recent evidence suggests they all belong to *B. gabbii* [4]. Therefore, we retained only *B. gabbii* for analyses. For bats we recognized *Cynomops mexicanus* instead of *C. greenhalli* according to Peters et al. [5], *Natalus stramineus* is now recognized as *N. mexicanus* [6], *Lonchophylla mordax* was included as *L. concava* [7], *Mimon cozumelae* was previously a subspecies of *M. benneti* and *Sturnira ludovici* is now used instead of *S. hondurensis* [6]. *Vampyressa pusilla* is now *V. thyone* [8] and *Cryptotis parva* is now considered *C. orophila* [9].

S1 Table. List of Costa Rican mammal species used for analyzes classified by order and with its corresponding conservation status according to the IUCN Red List of Threatened Species. Least Concern (LC), Near Threatened (NT), Data Deficient (DD), Vulnerable (VU) and Endangered (EN).

Order	Family	Species	IUCN Red List				
			LC	NT	DD	VU	EN
Carnivora	Canidae	*Canis latrans*	X				
		Urocyon cinereoargenteus	X				
	Felidae	*Leopardus pardalis*	X				
		Leopardus tigrinus				X	
		Leopardus wiedii		X			
		Panthera onca		X			
		Puma concolor	X				
		Puma yagouaroundi	X				
	Mephitidae	*Conepatus semistriatus*	X				
		Spilogale angustifrons	X				
	Mustelidae	*Eira barbara*	X				
		Galictis vittata	X				
		Lontra longicaudis			X		
		Mustela frenata	X				
	Procyonidae	*Bassaricyon gabbii*	X				
		Bassariscus sumichrasti	X				
		Nasua narica	X				
		Potos flavus	X				
		Procyon cancrivorus	X				
		Procyon lotor	X				
Cetartiodactyla	Cervidae	*Mazama temama*			X		
		Odocoileus virginianus	X				
	Tayassuidae	*Pecari tajacu*	X				
		Tayassu pecari		X			
Chiroptera	Emballonuridae	*Balantiopteryx plicata*	X				
		Centronycteris centralis	X				
		Cormura brevirostris	X				
		Cyttarops alecto	X				
		Diclidurus albus	X				
		Peropteryx kappleri	X				
		Peropteryx macrotis	X				
		Rhynchonycteris naso	X				
		Saccopteryx bilineata	X				
		Saccopteryx leptura	X				
	Furipteridae	*Furipterus horrens*	X				
	Molossidae	*Cynomops mexicanus*	X				
		Eumops auripendulus	X				
		Eumops glaucinus	X				
		Eumops hansae	X				
		Eumops underwoodi	X				
		Molossus coibensis	X				
		Molossus currentium	X				
		Molossus molossus	X				
		Molossus pretiosus	X				
		Molossus rufus	X				
		Molossus sinaloae	X				
		Tadarida brasiliensis	X				
	Mormoopidae	*Pteronotus davyi*	X				
		Pteronotus gymnonotus	X				
		Pteronotus parnellii	X				
		Pteronotus personatus	X				
	Natalidae	*Natalus mexicanus*	X				
	Noctilionidae	*Noctilio albiventris*	X				
		Noctilio leporinus	X				

… Continue S1Table…

Order	Family	Species	LC	NT	DD	VU	EN
Chiroptera	Phyllostomidae	*Anoura cultrata*		X			
		Anoura geoffroyi	X				
		Artibeus aztecus	X				
		Artibeus jamaicensis	X				
		Artibeus lituratus	X				
		Artibeus phaeotis	X				
		Artibeus toltecus	X				
		Artibeus watsoni	X				
		Carollia castanea	X				
		Carollia perspicillata	X				
		Carollia sowelli	X				
		Carollia subrufa	X				
		Chiroderma salvini	X				
		Chiroderma trinitatum	X				
		Chiroderma villosum	X				
		Choeroniscus godmani	X				
		Chrotopterus auritus	X				
		Desmodus rotundus	X				
		Diaemus youngi	X				
		Diphylla ecaudata	X				
		Ectophylla alba		X			
		Enchisthenes hartii	X				
		Glossophaga commissarisi	X				
		Glossophaga leachii	X				
		Glossophaga soricina	X				
		Glyphonycteris sylvestris	X				
		Hylonycteris underwoodi	X				
		Lampronycteris brachyotis	X				
		Lichonycteris obscura	X				
		Lonchophylla concava		X			
		Lonchophylla robusta	X				
		Lonchorhina aurita	X				
		Lophostoma brasiliense	X				
		Lophostoma silvicolum	X				
		Macrophyllum macrophyllum	X				
		Mesophylla macconnelli	X				
		Micronycteris hirsuta	X				
		Micronycteris microtis	X				
		Micronycteris minuta	X				
		Micronycteris schmidtorum	X				
		Mimon cozumelae	X				
		Mimon crenulatum	X				
		Phylloderma stenops	X				
		Phyllostomus discolor	X				
		Phyllostomus hastatus	X				
		Platyrrhinus helleri	X				
		Platyrrhinus vittatus	X				
		Sturnira lilium	X				
		Sturnira ludovici	X				
		Sturnira luisi	X				
		Sturnira mordax		X			
		Tonatia saurophila	X				
		Trachops cirrhosus	X				
		Trinycteris nicefori	X				
		Uroderma bilobatum	X				
		Vampyressa nymphaea	X				
		Vampyressa thyone	X				
		Vampyrodes caraccioli	X				
		Vampyrum spectrum		X			
	Thyropteridae	*Thyroptera discifera*	X				
		Thyroptera tricolor	X				

…Continue S1Table…

Order	Family	Species	LC	NT	DD	VU	EN
Chiroptera	Vespertilionidae	*Bauerus dubiaquercus*		X			
		Eptesicus brasiliensis	X				
		Eptesicus furinalis	X				
		Eptesicus fuscus	X				
		Lasiurus blossevillii	X				
		Lasiurus cinereus	X				
		Lasiurus ega	X				
		Lasiurus intermedius	X				
		Myotis albescens	X				
		Myotis elegans	X				
		Myotis keaysi	X				
		Myotis nigricans	X				
		Myotis oxyotus	X				
		Myotis riparius	X				
		Rhogeessa io	X				
		Rhogeessa tumida	X				
Cingulata	Dasypodidae	*Cabassous centralis*			X		
		Dasypus novemcinctus	X				
Didelphimorphia	Didelphidae	*Caluromys derbianus*	X				
		Chironectes minimus	X				
		Didelphis marsupialis	X				
		Didelphis virginiana	X				
		Marmosa mexicana	X				
		Metachirus nudicaudatus	X				
		Philander opossum	X				
		Micoureus alstoni	X				
Lagomorpha	Leporidae	*Sylvilagus brasiliensis*	X				
		Sylvilagus dicei			X		
		Sylvilagus floridanus	X				
Perissodactyla	Tapiridae	*Tapirus bairdii*					X
Pilosa	Bradypodidae	*Bradypus variegatus*	X				
	Cyclopedidae	*Cyclopes didactylus*	X				
	Megalonychidae	*Choloepus hoffmanni*	X				
	Myrmecophagidae	*Myrmecophaga tridactyla*				X	
		Tamandua mexicana	X				
Primates	Atelidae	*Alouatta palliata*	X				
		Ateles geoffroyi					X
	Cebidae	*Cebus capucinus*	X				
		Saimiri oerstedii				X	

…Continue S1Table…

Order	Family	Species	LC	NT	DD	VU	EN
Rodentia	Cricetidae	*Handleyomys alfaroi*	X				
		Melanomys caliginosus	X				
		Nephelomys devius	X				
		Nyctomys sumichrasti	X				
		Oecomys trinitatis	X				
		Oligoryzomys fulvescens	X				
		Oligoryzomys vegetus	X				
		Oryzomys couesi	X				
		Ototylomys phyllotis	X				
		Peromyscus gymnotis	X				
		Peromyscus mexicanus	X				
		Reithrodontomys brevirostris	X				
		Reithrodontomys creper	X				
		Reithrodontomys fulvescens	X				
		Reithrodontomys gracilis	X				
		Reithrodontomys mexicanus	X				
		Reithrodontomys paradoxus			X		
		Reithrodontomys rodriguezi	X				
		Reithrodontomys sumichrasti	X				
		Rheomys raptor	X				
		Rheomys underwoodi	X				
		Scotinomys teguina	X				
		Scotinomys xerampelinus	X				
		Sigmodon hirsutus	X				
		Sigmodontomys alfari	X				
		Sigmodontomys aphrastus			X		
		Transandinomys bolivaris	X				
		Transandinomys talamancae	X				
		Tylomys nudicaudus	X				
		Tylomys watsoni	X				
		Zygodontomys brevicauda	X				
	Cuniculidae	*Cuniculus paca*	X				
	Dasyproctidae	*Dasyprocta punctata*	X				
	Echimyidae	*Hoplomys gymnurus*	X				
		Proechimys semispinosus	X				
	Erethizontidae	*Coendou rothschildi*	X				
		Sphiggurus mexicanus	X				
	Geomyidae	*Orthogeomys cavator*	X				
		Orthogeomys cherriei	X				
		Orthogeomys heterodus	X				
		Orthogeomys underwoodi	X				
	Heteromyidae	*Heteromys desmarestianus*	X				
		Heteromys oresterus	X				
		Liomys salvini	X				
	Muridae	*Mus musculus*	X				
	Sciuridae	*Microsciurus alfari*	X				
		Sciurus deppei	X				
		Sciurus granatensis	X				
		Sciurus variegatoides	X				
		Syntheosciurus brochus		X			
Soricomorpha	Soricidae	*Cryptotis gracilis*				X	
		Cryptotis merriami	X				
		Cryptotis nigrescens	X				
		Cryptotis orophila			X		

S2 Table. Species Richness, number of species on each category of the IUCN Red List of Threatened Species (EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, and DD = Data Deficient) by taxa for Costa Rican mammals used for assessing their representativeness in protected areas.

Taxa	Species Richness	IUCN Red List				
		LC	NT	DD	VU	EN
Carnivora	**20**	**16**	**2**	**1**	**1**	
Canidae	2	2				
Felidae	6	3	2		1	
Mephitidae	2	2				
Mustelidae	4	3		1		
Procyonidae	6	6				
Cetartiodactyla	**4**	**2**	**1**	**1**		
Cervidae	2	1		1		
Tayassuidae	2	1	1			
Chiroptera	**107**	**101**	**6**			
Emballonuridae	10	10				
Furipteridae	1	1				
Molossidae	12	12				
Mormoopidae	4	4				
Natalidae	1	1				
Noctilionidae	2	2				
Phyllostomidae	59	54	5			
Thyropteridae	2	2				
Vespertilionidae	16	15	1			
Cingulata	**2**	**1**		**1**		
Dasypodidae	2	1		1		
Didelphimorphia	**8**	**8**				
Didelphidae	8	8				
Eulipotyphla	**4**	**2**		**1**	**1**	
Soricidae	4	2		1	1	
Lagomorpha	**3**	**2**		**1**		
Leporidae	3	2		1		
Perissodactyla	**1**					**1**
Tapiridae	1					1
Pilosa	**5**	**4**			**1**	
Bradypodidae	1	1				
Cyclopedidae	1	1				
Megalonychidae	1	1				
Myrmecophagidae	2	1			1	
Primates	**4**	**2**			**1**	**1**
Atelidae	2	1				1
Cebidae	2	1			1	
Rodentia	**50**	**47**	**1**	**2**		
Cricetidae	31	29		2		
Cuniculidae	1	1				
Dasyproctidae	1	1				
Echimyidae	2	2				
Erethizontidae	2	2				
Geomyidae	4	4				
Heteromyidae	3	3				
Muridae	1	1				
Sciuridae	5	4	1			
Country Total	**208**	**185**	**10**	**7**	**4**	**2**

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7.2. Spatial patterns of species and functional diversity in Costa Rican terrestrial mammals: implications for conservation

Running head: Costa Rica mammal diversity

Spatial patterns of species and functional diversity in Costa Rican terrestrial mammals: implications for conservation

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Abstract

Aim Understand the spatial relationships of mammal species richness and functional diversity, and their implications in ecology and conservation biology. Functional diversity is a relatively recent approach to quantify species diversity and potentially provides a better understanding of the linkages between biological diversity and ecosystem function.

Location Costa Rica (8° 0′–11° 14′ N and 82° 32′–85° 56′ W)

Methods We evaluated spatial patterns of species richness and functional diversity for terrestrial mammals in Costa Rica using regression techniques, and assessed the influence of environmental, biological, and anthropic factors on those patterns.

Results Environmental and anthropic factors influenced both species richness and functional diversity, whereas biological factors influenced functional diversity only. Species richness effects on functional diversity clearly identified three regions within the country defined by ecosystem type and the occurrence of bats and rodents. The best supported model for species richness demonstrated considerable spatial variation and local models performed better than the overall country model. However, for functional diversity, the overall regional models performed better than did local models.

Main conclusions Both diversity measures varied spatially, with the effects of determinant variables locally driven for species richness and its influence over functional diversity variable by region within Costa Rica. Conservation planning should incorporate regional variation into priorities definitions since anthropic variables affect species diversity measures differentially depending on the region and interaction of environmental variables.

Keywords Costa Rica, functional diversity, ordinary least squares, geographically weighted regression, spatially-explicit patterns, species richness, terrestrial mammals.

(A) INTRODUCTION

Knowledge of biological diversity is fundamental for understanding ecological and anthropogenic processes useful for conservation planning (Brooks & Helgen, 2010). The loss of a single species or a population can have major irreversible effects on ecosystem functioning and services (Ceballos & Ehrlich, 2002). Given the accelerated rates of species and population losses and the current biodiversity crisis (Ceballos et al., 2010), characterizing spatial patterns of species diversity in relation to regions relevant to conservation actions (e.g., ecoregions) is critical to inform decision-making and assess ecological patterns (Safi et al., 2011; González-Maya et al., 2012). Traditional and recent studies of biological diversity and their patterns have focused mainly on basic measure of species richness (Petchey & Gaston, 2002; Rondinini et al., 2011b). Information regarding global species distribution and its patterns has recently become more available, allowing practitioners to understand trends in species risk and develop priorities to aid conservation planning (Ceballos et al., 2005; Schipper et al., 2008; Brooks et al., 2010; Boitani et al., 2011). However, more recent measures of diversity; such as genetic, phylogenetic, and functional traits; provide additional knowledge (Magurran & McGill, 2011) and can improve our understanding of diversity itself and associated ecological processes (Tilman, 2001; Petchey & Gaston, 2002) .

Functional diversity (FD), is a recent approach that provides a measure of taxonomic diversity and species' roles in ecosystem functioning (Tilman et al., 1997; Tilman, 2001). Functional diversity has gained increasing attention among ecologists and has been used to characterize the provisioning of ecosystem services (Daily et al., 1997; Dias et al., 2013). The concept of functional diversity was originally applied to plants (Tilman et al., 1997; Tilman, 2001) but has since been used to quantify diversity of other taxa, including animals (Blaum et al., 2011; Cardoso et al., 2011). For mammals, several recent studies have assessed FD in relation to dispersion and pollination from regional (Stevens et al., 2004) to global (Kunz et al., 2011; Safi et al., 2011) scales. However, many aspects of patterns and determinants of functional diversity are not understood (Blaum et al., 2011).

Functional diversity as linked to the concept of functional richness is defined as the "amount of functional trait space filled by species in the community" (Mason et al., 2005), and can influence ecosystem and community productivity and in turn functionality and resilience (Tilman et al., 1997; Petchey, 2003). Since FD is directly related to ecosystem resilience and services (Mouchet et al., 2010), it is fundamental to understand the underlying processes and scales at which these processes operate (Wright et al., 1998; Kraft & Ackerly, 2010; Messier et al., 2010; Belmaker & Jetz, 2011) to facilitate conservation planning (Boitani et al., 2011; Rondinini et al., 2011a). Furthermore, despite global approaches providing clues for conservation priority definition (Brooks et al., 2006; Brooks et al., 2010), conservation planning typically occurs at local or regional scales (Groves et al., 2002). Therefore, finer scale analyses can provide tools for regional planning and understanding of local processes (Belmaker & Jetz, 2013). Scale is critical to ecological and biogeographical processes (Koleff & Gaston, 2002), however, information at appropriate resolutions is not always available (Rondinini et al., 2011b), or not used for conservation planning (Boitani et al., 2011). Therefore, analyzing regional patterns may be necessary to appropriately inform conservation at typical planning scales.

We compared species richness and FD patterns of terrestrial mammals at a national scale for Costa Rica. Given that Costa Rica has played a key role in ecological, evolutionary and biogeographical processes at continental scales for mammals (Sánchez-

Azofeifa et al., 2001; Rodríguez-H et al., 2002), we considered the country a model system for analyses of biodiversity patterns. Since local extinctions or mammal population losses can adversely affect ecosystem processes, assessing the determinant variables, both anthropogenic and environmental, and the effects of spatial scale can inform decision making and priorities definition. Our objectives were 1) to assess spatial patterns of terrestrial mammal species richness and FD; 2) to evaluate the influence of environmental, biological, and anthropic factors on species richness and FD; and 3) to assess the effect of local and regional variation on variables influencing species richness and FD compared to overall (country) models.

(A) METHODS

(B) *Study area*

Costa Rica is located in Central America (8°0′–11°14′ N, 82°32′–85°56′ W), with a continental area of 51,100 km^2 bordering Nicaragua on the north and Panama on the southeast. Due to its geographical position and geological history, Costa Rica has been a key connection for distributions of Neartic and Neotropical faunas, linking North and South America with the Panama isthmus (Sánchez-Azofeifa et al., 2001; Rodríguez-H et al., 2002). This location, together with a complex geography (Sánchez-Azofeifa et al., 2001), makes Costa Rica a highly diverse country with about 4% of the known global biodiversity in only 0.03% of the global continental area (Obando, 2008). Costa Rica contains 238 mammal species, including 207 terrestrial species (18 endemic) in 140 genera and 44 families (Rodríguez-H et al., 2002; Rodríguez-H et al., 2012), approximately 4.5% of all known mammal species globally (Schipper et al., 2008) and 11.3% and 28.7% of globally known genera and families, respectively (Wilson & Reeder, 2005).

(B) *Mammal data sources*

We assessed the spatial patterns and determinants of Costa Rican mammal diversity based on species distribution data, life traits, and environmental and human factors. Using global data on mammal distribution provided by the IUCN Red List of Threatened Species (International Union for the Conservation of Nature, 2011), we extracted all species recorded as present in Costa Rica assessed by the 2008 Global Mammal Assessment (Schipper et al., 2008) and validated these standardized distribution maps using the last updated list of species for the country (Rodríguez-H et al., 2002). Our database included 206 terrestrial mammal species from Costa Rica, differing from the 208 reported by Rodríguez-H et al. (2002). Differences between these lists was a consequence of taxonomic and distribution changes. Four species recorded for the country from Rodríguez-H et al. (2002) did not have updated distribution information, two were synonymized recently (Helgen et al., 2013) and we included four species with marginal distributions in Costa Rica, thus maintaining consistency with the species distribution polygons used for analyses. Taxonomy followed (Wilson & Reeder, 2005) with posterior changes. For each of the 206 species derived from the combination of both lists, we compiled information regarding functional traits including body mass, trophic niche (*i.e.,*herbivore, carnivore and omnivore), and habitat mode (*i.e.,*terrestrial, aquatic, arboreal, fossorial, and volant) from published databases (Jones et al., 2009), previous published works (Davidson et al., 2009), and other published information sources for species not included in these databases. When no information existed for a species (~4%), we used data from the most similar and related species within the same genus (Davidson et al., 2009). We assessed the dominance of each trait according to mammalian orders by plotting the percentage of species on each trait category.

We obtained information on environmental (*i.e.,*bioclimatic, ecosystem, and topographic) and anthropogenic variables from global databases and our own estimation of natural landcover (Table 1), generated as the proportion of undisturbed landcover in each cell (see below; Table 2). For biological variables we considered species richness (for functional diversity analyses) and the evolutionary origin of each species. To estimate evolutionary origin, we compiled information on the possible origin of each taxon at the lowest taxonomic level where information was available (Eisenberg, 1981; Lim, 2009; Wilson & Mittermeier, 2009; Wilson & Mittermeier, 2011; Morgan & Czaplewski, 2012; Mittermeier et al., 2013). We then classified each species to its proposed origin (North or South America) and estimated the proportion of species from each continent of origin for each cell (see below for details on the grid).

Table 1 Description of biological, environmental and human influence variables potentially related with terrestrial mammals species richness and functional diversity in Costa Rica. All variables were scaled to the same resolution by averaging in case of coarser resolution of our study grid; higher resolution from richness estimated from distribution polygons will likely increase spatial autocorrelation but will not increase analytical performance.

Type of variable	Variable	Description	Resolution	Source
Biological	S	Species Richness: number of mammal species per cell	Grid resolution (83 km^2)	This study
	N.A.Orig.	Proportion of species (from total) of North American origin	Grid resolution (83 km^2)	This study
	S.A.Orig.	Proportion of species (from total) of South American origin	Grid resolution (83 km^2)	This study
Environmental	Elevation	The mean elevation value per cell derived from a Digital Elevation Model	1 km^2	U. S. Geological Survey (2012)
	Aspect	Terrain orientation degree regarding North derived from a Digital Elevation Model	1 km^2	U. S. Geological Survey (2012)
	AMT	Annual Mean Temperature value averaged per cell	~ 1 km	Hijmans et al (2005)
	AP	Annual Precipitation mean value averaged per cell	~ 1 km	Hijmans et al (2005)
	PS	The coefficient of variation for precipitation per cell (Precipitation seasonality)	~ 1 km	Hijmans et al (2005)
	TS	The standard deviation of temperature *100 per cell (Temperature seasonality)	~ 1 km	Hijmans et al (2005)
	NPP	The net amount of solar energy converted to plant organic matter through photosynthesis averaged per cell (Net Primary Productivity)	0.25 decimal degrees	Imhoff et al (2004a)
	PET	The Potential Evapo-transpiration mean per cell	~ 1 km	Trabucco and Zomer (2009)
Human influence	NLC	The proportion of natural land cover (NLC) respecting the intervened cover (including crops, cities, roads and highways)	Grid resolution (83 km^2)	This study based on Instituto Tecnológico de Costa Rica (2008)
	HANPP	Human appropriation of net primary productivity (HANPP) through the consumption of food, paper, wood and fiber, alters the composition of the atmosphere, levels of biodiversity, energy flows within food webs and the provision of important ecosystem services averaged per cell	0.25 decimal degrees	Imhoff et al (2004b)
	HD	Estimates of human population for the years 1990, 1995, and 2000 averaged per cell.	2.5 arc-minute	CIESIN - Columbia University (2005)

(B) *Spatial data*

We generated a grid of 617 ~83 km^2 cells adjusted to geography by clipping cells to the land edge which comprised the entire mainland area based on equal lat-long degrees. We selected this cell size as our mapping unit based on the mean range of the five species with the smallest ranges in the country, ensuring these species were included in at least one cell center and therefore FD estimations. Though species polygons were in vector format and could be used at finer resolutions, we used this semi-coarse resolution based on our definition of minimum mapping unit and because finer resolutions based on richness estimated from these distribution polygons would likely increase spatial autocorrelation but not improve analytical performance (Safi et al., 2011).

We overlaid this grid on the mammal distribution layers and extracted data for the species present within each cell. We linked data on taxonomic classification and traits with the species list from each cell. We calculated species richness and FD (see below) for each cell to explore spatial patterns. We estimated environmental variables for each cell using the mean value for each cell derived from the global datasets in raster formats; variables at finer resolution were scaled to the same resolution by averaging to the coarser resolution of our study grid. Since most environmental variables (*i.e.,*climatic) are actually based on interpolation between sampling stations, we considered our scale would ensure sufficient accuracy (Belmaker & Jetz, 2011) and good performance with the species´ distribution data. We estimated conserved habitat by extracting the mean value from global dataset rasters and calculating the proportion of natural land-covers from each cell using national data (Instituto Tecnológico de Costa Rica, 2008). All spatial analyses were performed in ArcGIS 10.2 (Environmental Systems Research Institute, 2013) and the overlapping of distributions (presence-absence) was performed using Hawth's tools available for ArcGIS 9.x (Beyer, 2004).

(B) *Data analysis*

We first explored country-wide spatial patterns of species richness and FD using the grid of cells. We estimated species richness as the total number of species for each cell. We estimated a FD index (FDI) based on Petchey and Gaston's Functional Traits Diversity index (Petchey & Gaston, 2002) using the species richness and associated traits from each cell. The selected traits are considered to better represent niche dimensions and resource use requirements of species (Flynn et al., 2009; Safi et al., 2011), therefore driving biodiversity and ecosystem function relationship (Flynn et al., 2009), are readily available for most species (Davidson et al., 2009; Jones et al., 2009; Dalerum, 2013), and have been used successfully for exploring functional diversity and threats in mammals (Marquet & Cofre, 1999; Davidson et al., 2009; Safi et al., 2011). The FD index is defined as the sum of the dendrogram branch distances necessary to connect all species in the functional space and does not account for abundance (Casanoves et al., 2011; Safi et al., 2011). A distance matrix was estimated and a functional dendrogram was built using the Gower distance (unweighted pair group with arithmetic averages) and we summed the branches necessary to connect all species within each cell. Comparative high FD index values indicate high complementarity (*i.e.,*species are distant in trait-space), while low values indicate low complementarity (*i.e.,*species are more similar). We selected this functional diversity metric as it can be used and performs appropriately with multiple traits, does not depend on abundance data, and also have significant interaction with species richness but perform well for high species richness communities (Mason et al., 2012).

To test for correlation between both measures, we plotted species richness and FD values in all cells. From scatterplots we identified three groups as defined by different intercepts; we selected the cells in each group and assigned these cells to different regions. For each region we tested the relationship between species richness and FD using simple linear regression. For each region we explored which variables could explain the groupings, both by dominant biomes/major habitat types (Olson et al., 2001) and by plotting species richness of dominant groups such as rodents and bats.

To explore spatial relationships between species richness and functional diversity with environmental and biological determinants and human intervention, we performed ordinary least squares (OLS) regressions (Comont et al., 2012; Barnagaud et al., 2014) to identify the best models and variables that explain species richness and FD. We generated OLS models for species richness at the country scale and for each of the three regions. All variables except natural landcover proportion were log (10) transformed to reduce the magnitude and variation of values as variables had different scales. We generated independent models with all possible variable combinations without interaction terms and selected the best model using the lowest Akaike Information Criterion corrected for small samples (AIC; Burnham et al. (2011)) and AIC weights of the competing models (Wagenmakers & Farrell, 2004) and R^2 to assess how much variation in the data the model explained (*i.e.,*higher R^2 values were preferred). In case of competing models (difference <2 in AIC units) we averaged the selected models (Fotheringham et al., 2002). Once selected we tested for spatial autocorrelation of the model and as an indicator of significant differences of the model results from random, we used the Moran's I spatial autocorrelation test of the residuals (Brunsdon et al., 2010). We evaluated overall model performance and explanatory power using R^2 and coefficients of each variable and then we used Koenker's statistic to assess heterocedasticity and nonstationarity of the model and the Jarque-Bera test for normality (Brunsdon et al., 2010). To assess multicollinearity, we used the Variance Inflationary Factor (VIF) to see which variables are potentially redundant; as a rule-of-thumb, VIF values >7.5 have potential redundancy in a model (Fotheringham et al., 1998).

Once a model was selected and nonstationarity identified, we performed a geographically weighted regression (GWR) to identify spatial variation in variables and clusters of high and low predictability or mismatch (Brunsdon et al., 1998; Fotheringham et al., 1998; Foody, 2003; Brunsdon et al., 2010). Geographically weighted regression estimates separate equations for each variable and incorporate dependent and independent variables within a defined bandwidth (Fotheringham et al., 1998). We defined our bandwidth based on kernel-based adaptive selections with corrected AIC which defines the number of neighborhood features for analyses as an adaptive function of the spatial context (Gaussian function) and selects the best smoothing factor. As the influence of different variables is likely spatially defined, we selected GWR as an appropriate method capable of identifying nonstationary patterns at our spatial scales (Brunsdon et al., 2010). Geographically weighted regression also allows exploring the spatial influence of any linear model at different resolutions, comparing an overall model (such as ordinary least squares) with a geographically weighted factor, indicating local differences and the influence of resolution on the modeled relationship (details on GWR: (Brunsdon et al., 1998; Fotheringham et al., 1998; Foody, 2003; Brunsdon et al., 2010). Geographically weighted regressions were performed when fitted models were found both for overall species richness and for the regions identified with differing functional diversity. All statistical analyses were performed using the R platform for windows (R Team

Development Core, 2008) and ArcGIS 10.2, including the spatial analyst extension (Environmental Systems Research Institute, 2013).

(A) RESULTS

(B) *Spatial patterns of species and functional diversity*

Percentage trait categories varied among mammalian orders with trophic niche dominated overall by carnivore and herbivore species and habitat mode dominated by terrestrial and volant species (Fig.1a, b). Body mass for mammals was predominantly small and small-medium species, largely corresponding to the orders Chiroptera and Rodentia (Fig.1c). Species richness was heterogeneous across the country (Fig. 2a) and dominated by species groups such as bats and rodents which accounted for~75% of all species. Greatest species richness was in and near the Talamanca cordillera piedmont and the Central Volcanic range, with a mean number of species (± SD) for all grid cells in the country of 128 ±18. Functional diversity varied also with a mean (± SD) index value of 3.26 ± 0.561 for the country. Greatest values were concentrated in northeastern Costa Rica (Guanacaste Province) near the Nicaraguan border and lowest values were in the central Caribbean plains (Fig. 2b). We identified three distinct groupings when plotting species richness versus functional diversity, identified by different intercepts (Fig. 3a). These groupings were represented regionally as the Caribbean and Central and Southern Pacific lowlands (Region 1), the high elevation areas of the country (Talamanca, Central Volcanic and Monteverde ranges), and the northern lowlands (Region 2) and the Nicoya Peninsula in the northeastern portion of the country (Region 3; Fig. 3c). Regression analyses for the three groups indicated a significant and positive influence of species richness over functional diversity with Region 3 having the strongest relationship (coefficient=0.03, $p < 0.0001$,

R^2=0.95), followed by Region 1 (coefficient = 0.01, $p < 0.0001$, $R^2 = 0.73$) and Region 2 (coefficient = 0.02, $p < 0.0001$, $R^2 = 0.39$). Intercepts also varied among regions; 1.03, 0.40 and 0.20 for regions 1, 2 and 3, respectively. Regions 1 and 2 are dominated by Tropical Moist Forests (98% each) whereas Region 3 is composed of Tropical Moist forests and Dry forests (46% and 50%, respectively) and influenced by the relationship between rodents and bats effects on functional diversity indexes (Fig. 3b). Spatially, high species richness overlapped with high FD areas.

The best model for species richness identified eight environmental and human influence variables (Table 2). Precipitation and temperature seasonality, natural land use and human density were negatively associated with species richness, while remaining variables were positively associated (Table 3). The selected model had high variation explained ($R^2 = 0.714$, AIC = 4232.7); we identified heterocedasticity and nonstationarity in the model (Koenker = 17.5, $p = 0.025$) but not bias and no clustering of the residuals of regressor variables (Moran's I = 0.41). The VIF values for all variables showed no autocollinearity or variable redundance (Table 3). As OLS tests for the global overall species richness response to variables, we generated a GWR to test for the influence of local relationships (lower resolution) and found substantial improvement of model performance (AIC = 4058.87) and improved explanatory power of dependent variable variation ($R^2 = 0.80$), indicating a significant influence of regional patterns, with elevation contributing to this greater influence. Greater association of determinant variables occurred in southern (Osa Peninsula) and northwestern (Tortuguero) Costa Rica, with an additional area in the Tilarán mountains (Fig. 4a). Higher coefficients were also distributed towards the Central Valley and areas with higher human density, while negative influence was concentrated in the areas with higher R^2 values (Fig. 4b).

Table 2 Results for best competing and selected ordinary least squares models for species richness and functional diversity (FD) of mammals using an 83 km^2 grid, Costa Rica. No. Par indicates the number of estimated parameters for each model, log(L) is the natural logarithm of the maximum likelihood value; AIC is Akaike Information Criterion value, ΔAIC is the difference between the model and best supported model, and w is the Akaike weights. * indicates the selected models.

Variable	Model	No. Par	log(L)	AIC	ΔAIC	w_i	R^2
			Richness				
Species richness	S1	8	0.113	4237.06	4.36	0.08	0.712
	S2	8	0.139	4236.65	3.95	0.09	0.713
	S3	7	0.235	4235.60	2.90	0.16	0.710
	S4	8*	1.000	4232.70	0.00	0.67	0.714
			Functional Diversity				
Region 1	FD1	6*	1.000	-434.52	0.00	1.00	0.786
	FD2	9	1.1E-43	-236.77	197.75	<0.01	0.460
	FD3	9	1.1E-43	-236.77	197.75	<0.01	0.395
	FD4	7	0.00	1800.75	2235.27	N/E	N/E
Region 2	FD1	4*	1.000	-98.17	0.00	0.65	0.499
	FD2	5	0.156	-94.45	3.72	0.10	0.500
	FD3	5	0.243	-95.34	2.83	0.16	0.506
	FD4	7	0.133	-94.13	4.04	0.09	0.510
Region 3	FD1	7*	1.000	-360.11	0.00	0.93	0.960
	FD2	10	<0.01	-334.22	25.89	<0.01	0.960
	FD3	6	0.073	-354.87	5.24	0.07	0.960
	FD4	10	<0.01	-334.22	25.89	<0.01	0.960

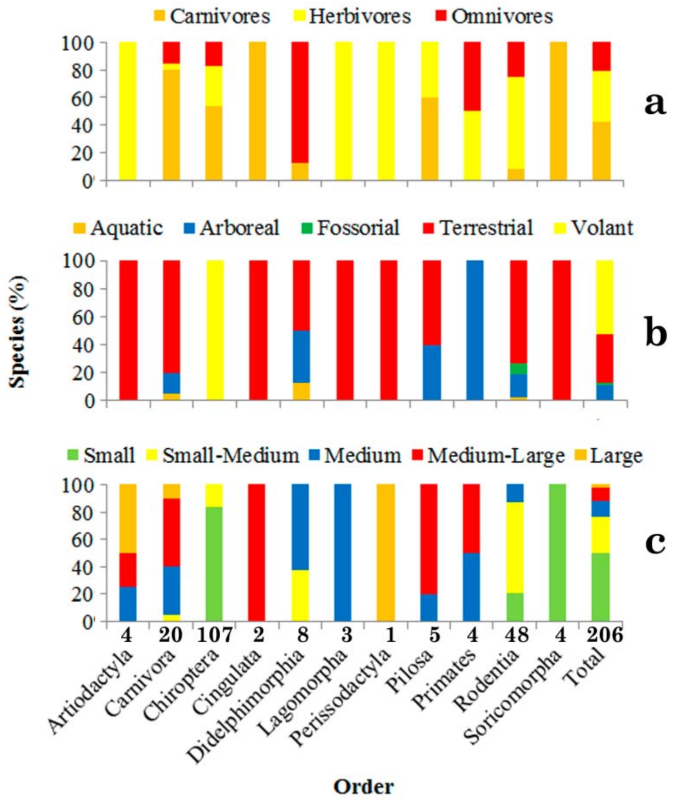

Figure 1 Distribution of species percentage on trait categories grouped by taxonomic order. a) trophic niche; b) habitat mode, and; c) body size. Bold numbers under X-axis on graph c indicate the total number of species per order. Legends are indicated on top of each plot.

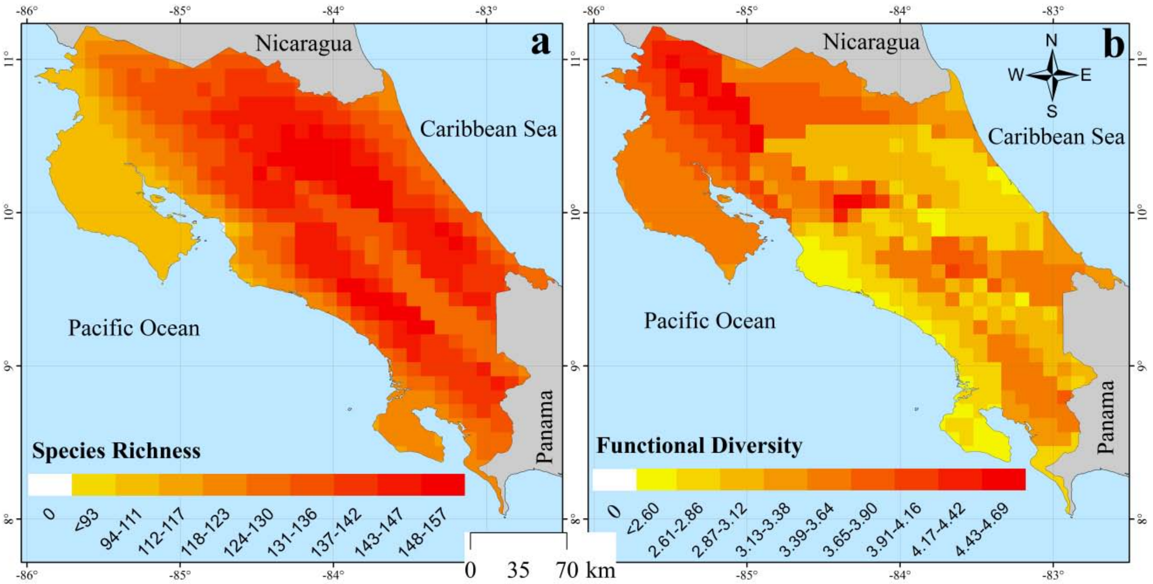

Figure 2 Terrestrial mammal species richness (a) and functional diversity (b) using an 83 km^2 grid, Costa Rica. Note the pattern for high species richness toward the mountain range piedmonts.

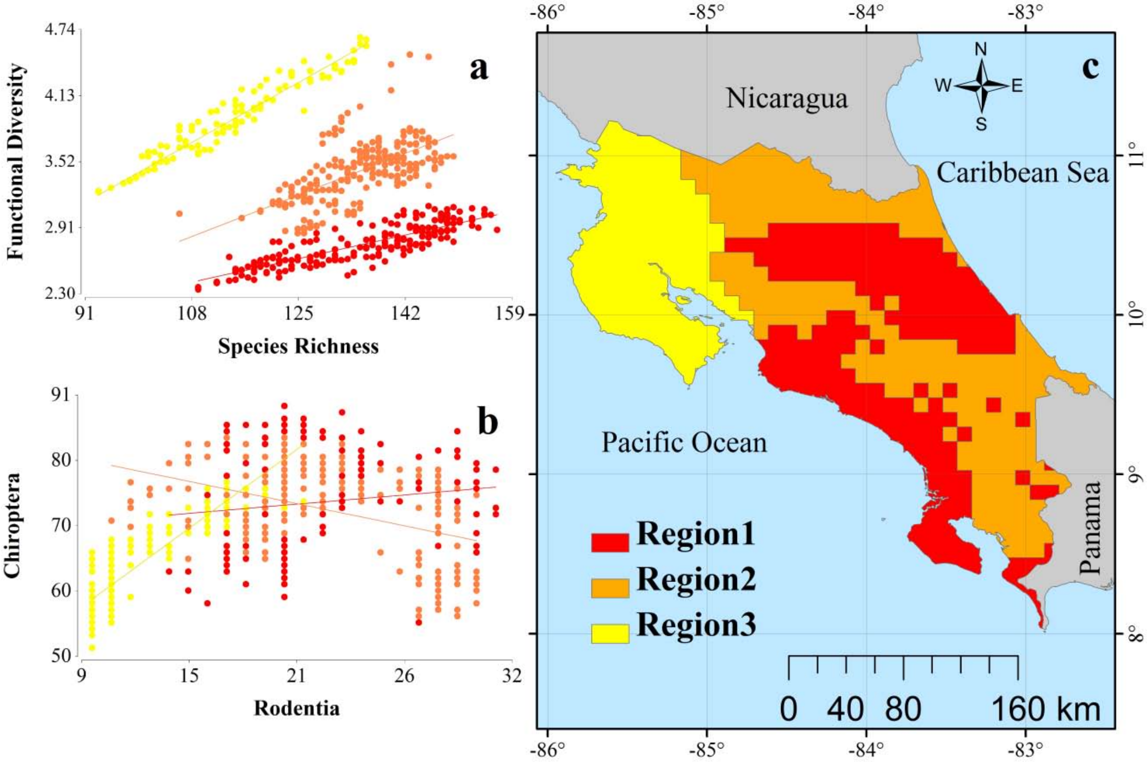

Figure 3 Data dispersion comparing species richness and functional diversity of mammals in Costa Rica. (a) Functional diversity versus species richness, (b) species richness of Chiroptera versus Rodentia orders and (c) spatial distribution of the three regions.

Table 3 Ordinary least squares regression results between terrestrial mammal species richness and functional diversity with environmental and human intervention determinants using an 83 km^2 grid, Costa Rica. See Table 1 for variable definitions.

Diversity Measure		Variable type	Variable	Coeficient	Std Error	T	p	Variance Inflation Factor
Species Richness		Environmental	Intercept	321.71	39.81	8.08	<0.001	
			Elev.	4.99	0.68	7.31	<0.001	2.14
			AP	22.88	3.59	6.37	<0.001	1.88
			PS	-44.29	2.83	-15.66	<0.001	1.83
			TS	-96.18	9.75	-9.86	<0.001	2.12
			NPP	2.59	1.18	2.2	0.028	1.35
		Human influence	Interv.	-15.42	1.29	-11.92	<0.001	1.41
			HANPP	4.73	1.38	3.43	<0.001	2.92
			HD	-4.19	1.41	-2.98	0.0033	2.39
Functional Diversity	Region1	Biological	Intercept	-2.77	0.64	-4.31	<0.001	
			SR	0.02	0.00	20.48	<0.001	2.40
			S.A. Orig	-1.15	0.27	-4.28	<0.001	2.35
		Environmental	AMT	0.28	0.11	2.52	0.013	1.50
			AP	0.29	0.08	3.60	0.0004	2.23
			PS	0.24	0.06	4.37	<0.001	2.41
			TS	0.71	0.19	3.83	0.0001	2.77
	Region2	Biological	Intercept	-2.41	0.44	-5.43	<0.001	
			SR	0.02	0.00	13.29	<0.001	1.01
		Environmental	AMT	0.85	0.12	6.94	<0.001	1.13
			PS	0.40	0.10	3.98	0.0001	1.14
		Human influence	HD	0.09	0.03	2.78	0.006	1.10
	Region3	Biological	Intercept	-2.16	1.25	-1.72	0.09	
			SR	0.04	0.00	33.02	<0.001	3.93
			N.A. Orig	3.13	0.70	4.46	<0.001	1.52
		Environmental	AMT	-1.29	0.40	-3.19	0.002	2.96
			PS	0.94	0.16	5.79	<0.001	3.37
			TS	0.71	0.33	2.15	0.03	2.18
		Human influence	NLC	-0.10	0.03	-2.94	0.004	1.53

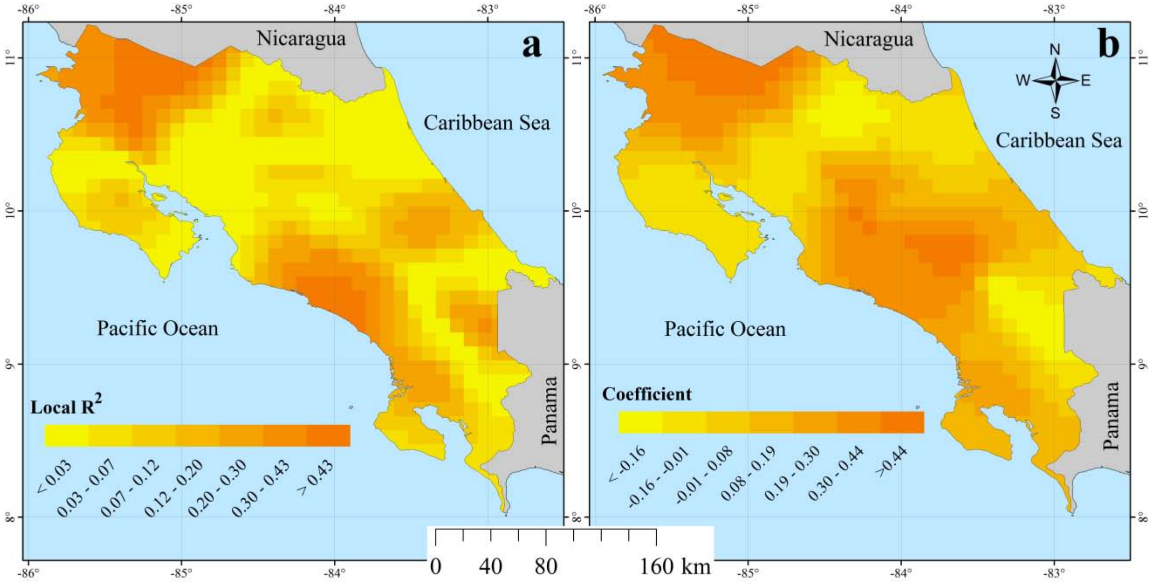

Figure 4 Geographically weighted regression for terrestrial mammal species richness as influenced by environmental, biological, and anthropic factors using an 83 km^2 grid, Costa Rica. (a) Local R^2 values and (b) local coefficient values.

Ordinary least squares regression for functional diversity in the three regions suggested that biological, environmental, and human influence variables influenced FD patterns. In Region 1, species richness and South American origin, annual mean temperature and annual precipitation, and precipitation and temperature seasonality were selected with no influence of human intervention variables (Table 2). Overall model FD variation explained by these variables was high ($R^2 = 0.73$) and tested significantly for heterocedasticity and nonstationarity (Koenker´s = 76.12, $p < 0.001$) with no clustering of regressor residuals (Moran's I = 0.27); no significant VIF were detected for any variable in the model (Table 3). The Region 2 model identified species richness, annual mean temperature, precipitation seasonality, and human density as the most influential variables (Table 3). Functional diversity variability explained by selected variables was not as high for Region1 ($R^2=0.49$). This model had significant heterocedasticity and nonstationarity (Koenker=53.47, $p<0.001$), but no clustering of regressor residuals (Moran's I= 0.31) and no VIF was identified. Finally, the Region 3 model contained species richness, North American Origin, annual mean temperature, precipitation and temperature seasonality and natural land-covers. Variation explained by these regressor variables was the highest of the three regions ($R^2 = 0.95$), and tested significant for heterocedasticity and nonstationarity (Koenker = 14.24, $p = 0.02$), with no clustering of regressor residuals (Moran's I = 0.25) and no VIF identified. We generated GWR for the three regions to evaluate if there was a spatial influence and pattern in the evaluated relationship. Georgraphically weighted regression models performed considerably better than OLS for Region 1 (AIC = -444.57), but not for Regions 2 and 3 (AIC = -51.74 and -222.51, respectively), with variation explained slightly improved for Region 1 ($R^2 = 0.79$), and lesser for Regions 2 and 3 ($R^2 = 0.46$ and 0.95, respectively; Fig. 5a, b).

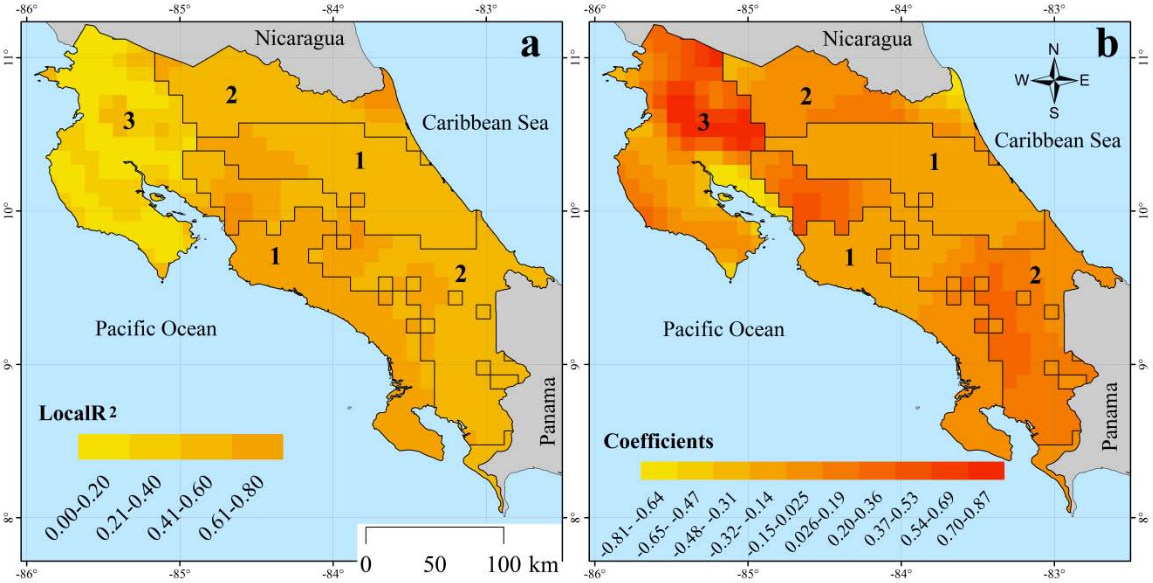

Figure 5 Geographically weighted regression for terrestrial mammal functional diversity as influenced by environmental, biological, and anthropic factors in the three functional diversity regions using an 83 km^2 grid, Costa Rica. (a) Local R^2 values and (b) local coefficient values.

(A) DISCUSSION

Both species richness and FD were heterogeneous across Costa Rica with clear spatial clustering of both measures in different regions. Species richness showed a continuous gradient across the country with greater concentrations at intermediate elevations, especially in mountain piedmonts on the Pacific slopes of Talamanca and across the Central Volcanic Range. In contrast, FD was patchily distributed with greater values in the northwestern portion of Costa Rica. High FD occurred mostly in Tropical Dry Forests with some intermediate values concentrated in the northernmost portion of the Talamanca range and near the Monteverde area (central Costa Rica). Lowlands of the Pacific and Caribbean slopes and the northern region contained a gradient of typically low functional diversity values. Spatially, high species richness overlapped with high FD areas since a significant positive relationship is expected from both measures based on the FD metric used in our analyses (Mouchet et al., 2010; Safi et al., 2011; Mason et al., 2012; Pavoine et al., 2013).

Species richness was typically greater at mid-elevations on mountain slopes as generally proposed (Brown, 2001), and previously found for small mammals in Costa Rica (McCain, 2004).

Environmental turnovers can significantly influence species turnovers on global scales, which seem to operate at different scales than in our study (Buckley & Jetz, 2008). We found that environmental variables best explained species richness at our scale, as found in multi-scale studies of species-environment interactions (Belmaker & Jetz, 2011) and general species richness (Andrews & O'Brien, 2001). Most of the variation in species richness was explained by these environmental variables and clustered spatially, while FD was better explained at the regional level, with overall models for the country performing better when weighted by geographic region. Areas with higher FD values were more spatially related and explained by these factors but were stationary; FD patterns did not respond better to local geographic scales (*i.e.,*grid cell) variation but to regional scales, thus highlighting the effect of scales on FD in general and the operation of large ecological pools on these trends (Belmaker & Jetz, 2011). The three human influence variables (*i.e.,*human density, natural land-cover and human appropriation of net primary productivity) were also significant, as expected from previous studies (Fox & Fox, 2000; Michalski & Peres, 2007; Flynn et al., 2009; Biswas & Mallik, 2010). Greater species richness typically occurred in areas with lower human intervention (Cuarón, 2008). Instead, FD showed a heterogeneous pattern of human influence, with only two regions influenced by these variables with lower variation explained, and likely stationary effect, towards the dry forests and mountains. Environmental filtering is probably more important for explaining these patterns than human intervention at this scale, with evolutionary or biogeographic factors together with ecosystem productivity potentially having a more important role (Andrews & O'Brien, 2001).

The three regions identified for FD were moderately defined by dominant habitat types which corresponded to ecoregions for the country (Olson et al., 2001). Variables that influenced regional FD were dominated by species richness and secondarily influenced by annual mean temperature and precipitation seasonality; previous studies at global scales also identified these factors as a main predictor of FD for mammals (Safi et al., 2011). Interestingly, species of South American origin influenced FD for Region 1, this region shares Amazon forest structure and species affinities (Sanchez-Azofeifa et al., 2002), therefore South American origin influence on FD makes sense for similar ecosystems and species composition. In contrast, species of North American origin only influenced FD in Region 3 which is the southernmost limit of the Mesoamerican Dry Forests (Gillespie et al., 2000), potentially indicating the coincidence of southernmost limits of many Nearctic mammal distributions in this region. Species evolutionary origin for countries such as Costa Rica with mixed mammal fauna assemblages (*i.e.,*Neartic 47% and Neotropical 53%; (Rodríguez-H et al., 2002; Rodríguez-H et al., 2012)) seems to substantially influence FD, having the same effect of evolutionary history and biogeographic scales already mentioned (Andrews & O'Brien, 2001), and potentially contributing to a functional regionalization of the country.

Patterns of FD and species richness we identified for Costa Rica are similar to global patterns (Safi et al., 2011), with our study having greater spatial clustering and influence of environmental variables. Spatial clustering across proportionately large regions likely reflects similar species compositions and therefore similar evolutionary and environmental-filtering effects across large areas (Swenson et al., 2012). Similar effects of environmental variables across similar ecoregions also could indicate similar species assemblages and ecoregional variation across scales from the ecological pool (Belmaker & Jetz, 2013). Likely, similar evolutionary history of species assemblages (*i.e.*,phylogenetic diversity) over these regions could influence functional diversity, and not only environmental filtering (Messier et al., 2010), as previously found at global scales (Safi et al., 2011). Both species richness and functional diversity were considerably influenced by rodent and bat richness which accounted for ~75 % of species richness, therefore ecosystem and habitat structure would likely affect both measures as determined by factors influencing these group´s richness and functional complementarity (Rodríguez & Ojeda, 2014). Many factors have been proposed to influence species richness gradients (Buckley et al., 2010; Belmaker & Jetz, 2013), however, little information exists regarding what factors affect functional diversity. Our results indicate functional diversity was influenced at regional scales and varied among habitat types, species assemblages, and extent of human intervention. Thus FD was influenced by species' evolutionary history and assembly rules across scales (Belmaker & Jetz, 2011; Safi et al., 2011; Belmaker & Jetz, 2013).

Overall, species richness and functional diversity showed markedly different patterns and relationships with environmental, biological and human intervention factors. While species richness patterns have already been demonstrated for mammals (Brown, 2001; McCain, 2004, 2005) FD has an opposite pattern, with greater values associated with certain ecosystem types, influenced both by species origin and climatic variation. Additionally, FD has higher spatial match, higher stationary patterns, and was more regionally driven than species richness. The greater regional variation observed in FD is likely a consequence of large evolutionary scales and species assembly rules as a response to ecosystem heterogeneity, as similar FD patterns can be found in regions with similar environmental and ecological features (Tilman et al., 1997; Bengtsson et al., 2002).

Understanding the spatial patterns of diversity and its congruence with environmental and anthropic factors at multiple scales is of great importance and at the forefront of ecological, biogeographical, and even conservation research (Ricklefs, 1987; Ricklefs & Schluter, 1993; Bengtsson et al., 2002; McCain, 2005; Buckley et al., 2010). Information on spatial patterns and understanding mechanisms influencing these patterns can serve as the basis for conservation planning, reserve networks design, and decision-making (Ceballos et al., 2005), by providing the scientific basis for planning (Kraft & Ackerly, 2010; Boitani et al., 2011; Rondinini et al., 2011a; Amori et al., 2013). We provide an assessment of species richness and FD of terrestrial mammals in Costa Rica at a scale suitable for scientific inquiry and conservation planning (Boitani et al., 2011; Rondinini et al., 2011b) and believe our results could be used to aid national conservation planning and assess the representativeness of current conservation schemes in Costa Rica.

(A) Acknowledgements

This paper constitutes a partial fulfillment of the Graduate Doctoral Degree Program in Biomedical Sciences (Programa de Doctorado en Ciencias Biomédicas) of the National Autonomous University of México (UNAM) of the first author. J.F. González-Maya acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT), and UNAM (scholarship 255983). Partial support was provided by The Sierra to Sea Institute and The Mikelberg Family Foundation. We thank E. Martínez-Meyer, R.A. Medellín and J. Schipper for insightful comments and support throughout the research.

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7.3. Environmental drivers and spatial mismatch of mammal diversity in Colombia

Environmental drivers and spatial mismatch of mammal diversity in Colombia

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Abstract
The inclusion of complementary biological measures into ecological and conservation studies should improve our ability to link species assemblages to ecosystems. Recent measures such as phylogenetic and functional diversity have furthered our understanding of ecosystem and species´ assemblage patterns, allowing improved inference of ecosystem function and history and to benefit conservation. We evaluated spatial patterns of taxonomic, phylogenetic and functional diversity of mammals in Colombia and identified their main environmental determinants, as well as interrelationships and spatial mismatch among the three measures. We developed coarse-scale estimates of these three measures using distribution polygons for all terrestrial mammals in Colombia. We used ordinary least squares and geographically weighted regressions to assess environmental variables affecting each measure, assess inter-relationships, and analyze the spatial mismatch among the three measures. We found significant effects of elevation and precipitation on species richness, slope and species richness on phylogenetic diversity and slope and phylogenetic diversity on functional diversity. We also identified spatial mismatch of the three measures in some areas of the country; 12% of the country for species richness and 14% for phylogenetic and functional diversity. Using complementary measures to account for assemblage history and ecosystem function in spatial analyses of diversity could facilitate selection of priority areas for conservation, especially when mismatch among measures occur. Our results highlight the importance of including species relationships with environmental drivers with biogeographical and distribution analyses of species diversity.

Keywords: functional diversity, geographically weighted regression, ordinary least squares, phylogenetic diversity, species richness

Introduction

The measurement of biological diversity has become a major research challenge in the increasingly interdisciplinary fields of ecology and conservation biology [1,2]. Traditional measures have emphasized species richness and evenness [3]; but recently, more sophisticated measures including evolutionary history and species function within ecosystems have been employed [4,5]. These new measures purportedly allow more precise and comprehensive assessments of ecological and conservation issues related to biodiversity across spatial and temporal scales [4,6,7]. However, interpreting the results of phylogenetic and functional diversity remains a challenge, particularly understanding potential mechanisms responsible for observed patterns [8], which hinders what could otherwise be considered a substantive advance in comprehensive conservation planning [9-11].

Phylogenetic diversity is a measure of evolutionary history, such as diversity within an assemblage [12]. It provides insights into the evolutionary distinctiveness of an assemblage and can be used to estimate future ecosystem performance [9]. In contrast, functional diversity incorporates elements of biodiversity that represent how ecosystems function [13], and is important for understanding current ecosystem dynamics, resilience and services [14,15]. Continued environmental degradation places growing pressure on the world´s biodiversity [16], which has led some authors to suggest we are facing the sixth mass extinction [17,18]. As the complexities of ecosystems and species interactions are unraveled, comprehensive and interdisciplinary conservation schemes are needed which can account for the dynamic and interwoven patterns in the tapestry of the world´s natural capital [9,11,19,20]. Incorporating multiple measures of species diversity including species richness, but more importantly evolutionary history and ecosystems functioning into planning, would be a major advance in conservation [9].

The Neotropical region has high biodiversity [21], but is one of the least biologically known regions of the world [22,23]. This knowledge gap represents a constraint for comprehensive conservation planning [24,25], exacerbated by our limited knowledge of how environmental drivers influence species diversity [26-28]. As a first step to further our understanding of biodiversity patterns, we provide the first nation-wide assessment of terrestrial mammal diversity in the mega-diverse country of Colombia using a new generation of measurement tools. Specifically, we assessed spatial patterns of species richness, functional and phylogenetic diversity and the influence of environmental factors on these patterns.

Materials and Methods

We first developed a grid of 127 1 x 1 degree cells over the country. We selected this coarse resolution to match the scale of global distribution maps for mammal species developed for the IUCN Red List of Threatened Species [29,30] since the country lacks information for finer resolution. As these species distribution maps were developed for the global scale, we considered this spatial resolution most appropriate for analyses. We used the distribution polygons for mammal species present or potentially present in the country and calculated the centroid of each cell (cell geographic center) and extracted all species overlapping each centroid as a proxy of the species assemblage present in each cell [31]. For cells overlapping the edge of the country, we estimated the centroid after clipping the perimeter of the country over the grid.

For each cell assemblage we calculated species richness and phylogenetic and functional diversity. Phylogenetic diversity (PD) was estimated using the Bininda-Emonds et al. (2007) phylogenetic tree and Faiths phylogenetic diversity index (Faith, 1992), which is based on the sum of the branches connecting all species in phylogenetic space for a given species assemblage. Functional diversity (FD) was calculated using the Petchey and Gaston FD index [31,32]; where the FD index is defined as the sum of the branches necessary to connect all species in trait space; for this we first estimated a matrix of distances based on the Gower distance (because we used both qualitative and quantitative traits) and built a dendrogram with this distance matrix. Finally, we summed the distance of all branches within the tree for each assemblage [32]. High FD values indicate high complementarity of species functions, therefore low redundancy based on the traits used, and low values indicate lower diversity of species functions, thus higher redundancy [31]. We used Pearson’s correlation to assess the degree of lineal relationships of the three variables.

We determined functional traits for each species using the PanTHERIA database (Jones et al., 2009), updates by Davidson et al. [33] and our own revision, including activity (i.e., diurnal, nocturnal, crepuscular, or cathemeral), diet (i.e., insectivore, frugivore, herbivore or carnivore), habits (*i.e.,*terrestrial, arboreal, aquatic, fossorial or scansorial) and body mass (g).

To assess the effects of environmental variables on diversity measures, we estimated mean cell annual precipitation and temperature, elevation and slope. Precipitation and temperatures were calculated from the Worldclim database [34] based on estimates representative from 1950-2000 at 30 arc-seconds, while elevation and slope were derived from Hydro 1k Digital Elevation Model for South America also at 30 arc-seconds [35]. We used ordinary least squares regression to assess the influence of environmental variables on species richness, the influence of the environmental drivers and species richness on phylogenetic diversity, and the influence of environmental variables, species richness and phylogenetic diversity on functional diversity. For each measure we generated all possible variable combinations without interaction of model terms, including 15 models for species richness, 31 for phylogenetic diversity and 63 for functional diversity (Table S1).

We identified the best performing models using Akaike Information Criterion corrected for small samples (AICc) [36]. We used adjusted R^2 values to estimate the proportion of variation in the dependent variable explained by the model variables. After selecting the best models according to AICc we identified the variables of the best performing models and we calculated the variable coefficients and Variance Inflation Factor (VIF) of best performing models to assess potential correlation among variables; models containing variables with scores >7.5 considered correlated [37]. As we ran all main effect model combinations, when this occurred we discarded those models and selected the model with the next lowest AICc value [37].

We estimated the Koenker studentized Breusch-Pagan statistic (K(BP)) to assess the reliability of standard errors when heteroskedaticity is present. If the K(BP) was significant, we used the robust probability instead of the raw probability estimation [38,39]. Heterokedasticity and non-stationarity indicates that the relationship between the dependent variable and the drivers would not change with changes in the magnitude of the drivers, and the relationship is not equal across geographic space, respectively. Moran´s I tests were used for testing for residuals clustering; clustered residuals indicate come variables or terms were missing from the model [40].

To explore where spatial mismatching occurred and where selected models did not perform adequately (indicating at least one important variable was missing from the model) we performed a hot-spots analyses using the residuals of the selected models based on the Getis-Ord Gi* statistic, estimating z-scores and p-values for each cell [41,42]. Hot spots are those where z-cores are significant ($p>0.05$), therefore where high clustering occurs. P-values are considered significant when z-scores estimated with the cell and its neighbors differ from expected when compared proportionally to the sum of all features. Significant z-scores in a cell ($p>0.05$) indicates clustered residual patterns and suggests one or more explanatory variables are missing in the model for that cell, in turn indicating spatial mismatch of the measures, overall model and the explanatory variables [41,42]. We mapped cells with high levels of residual clustering that were significant ($p>0.05$), therefore the spots of significant spatial mismatch of the terms of the model. All geographic and statistical analyses were performed using ArcGIS 10.2 [43] and R software [44].

Results

We found a heterogeneous distribution of the three diversity measures of mammals in Colombia. Species richness is concentrated near the center of the country, specifically towards the Andes piedmont, while the lowest values are concentrated in the Northern Llanos region (Eastern Colombia) and the northernmost portion of the country (i.e., Guajira Peninsula; Figure 1A). Phylogenetic and functional diversity were similarly distributed with greater values towards the southern Andes (FD) and the Eastern and Western Andes cordilleras in the north (FD); lowest values were found for Eastern Colombia (i. e. Llanos) and an apparent homogenous distribution of both PD and FD also for Eastern Colombia, with homogeneous PD for the Llanos and homogeneous FD for the Amazon regions (Figure1B, C). The three measures were highly related; species richness and phylogenetic diversity were highly correlation (Pearson=0.96, $p<0.001$), as were phylogenetic and functional diversity (Pearson=0.95, p<0.001) and species richness and functional diversity (Pearson=0.90, p<0.001).

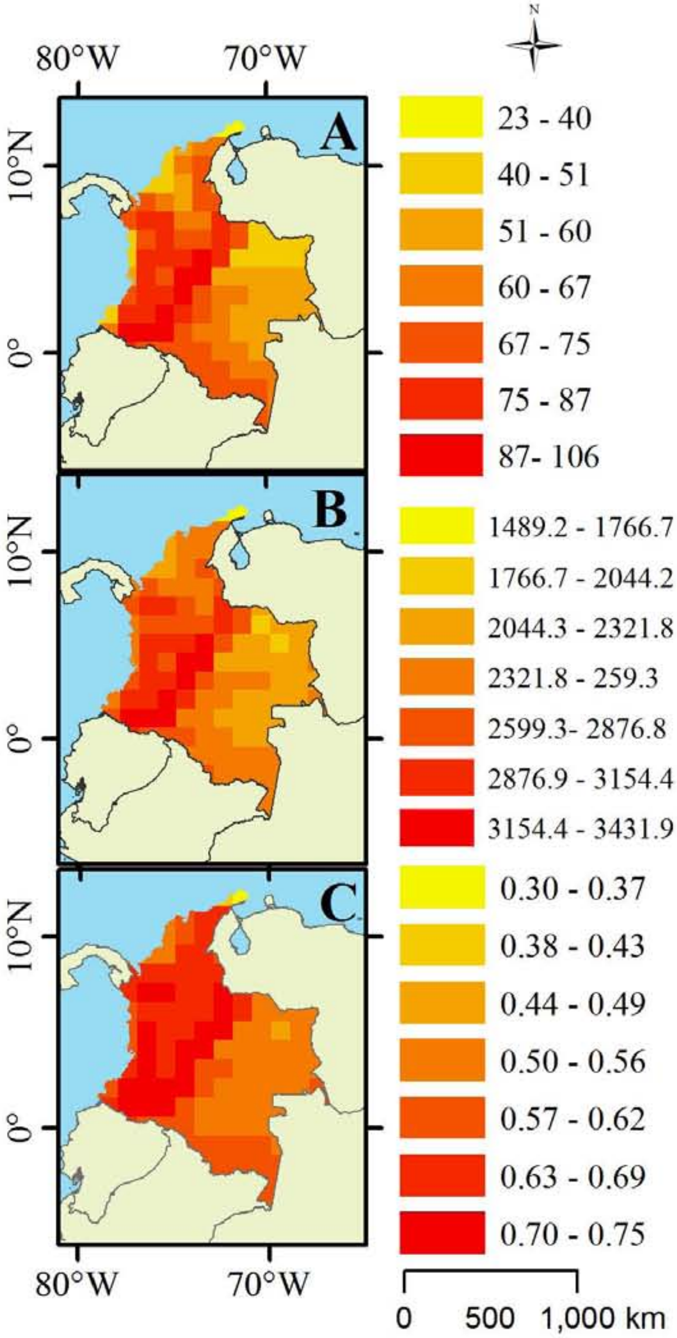

Figure 1. Spatial residuals clustering graphed as standard deviations indicating spatial mismatch of models explaining the influence of environmental drivers on mammal (A) species richness, (B) phylogenetic and (C) functional diversity over a grid of 1 x1 degree cells in Colombia.

For species richness, the best model (Table 1) included elevation and precipitation as the most important drivers of species richness (Table 2). Nevertheless, Moran´s I test was positive for clustering of the residuals (Moran´s Index=0.37, $p<0.001$) and the overall proportion of variation in the dependent variable explained was low ($R^2=0.45$). The K(BP), indicating non-stationarity of the model (K(BP)=2.36, p=0.0381). Therefore, we used robust probabilities (Table 2). For phylogenetic diversity, the best model included species richness and slope, with a high proportion of the variability explained ($adjR^2=0.94$). Moran´s I (Moran´s Index=0.005, p=0.15) and K(BP) tests were not significant, indicating the change in relationship between the dependent variable and the drivers will not change when the magnitude of drivers change and that this relationship is constant across geographic space (Table 2). For functional diversity the best model (Table 1) included phylogenetic diversity and slope, with a high proportion of variability explained by the model ($adjR^2=0.94$), and indicated non-clustering of the residuals (Moran´s Index=-0.032, p=0.09). Stationarity and heteroskedaticity are also found for phylogenetic diversity (Table 2). The variable slope in both cases had a lesser influence on phylogenetic and functional diversity than did species richness and phylogenetic diversity.

Spatial mismatch for the three models identified areas where the models failed to explain the different diversity measures. For species richness, model mismatches occurred in the southern Andean region and Guajira peninsula in the northernmost part of the country, covering ~12% of the country (Figure 2A). A clear mismatch between environmental drivers and phylogenetic diversity occurred along the southern Pacific coast and on lesser extent in a portion of the Amazon basin (~14%; Figure 2B). Greatest clustering and mismatch for functional diversity occurred in the Sierra Nevada de Santa

Marta, Paramillo Complex and Guajira peninsula of the Caribbean region (~14%; Figure 2C).

Table 1. Best competing ordinary least squares models of environmental drivers over mammal species richness, phylogenetic and functional diversity in Colombia. AICc: Akaike Information Criterion corrected, SE: Standard Error, VIF: Variance Inflation Factor, and p: significance of the variable in the model.

Model	Variables	Coefficient	SE	p	VIF	R^2	cAIC
Species richness	Elevation	0.02	0.00	0.00	**7.09**	0.45	972.83
	Slope	-0.02	0.01	0.12	**7.17**		
	Precipitation	0.00	0.00	0.01	**1.10**		
	Elevation	0.02	0.00	0.00	**7.80**	0.45	973.24
	Slope	-0.02	0.01	0.11	**7.23**		
	Temperature	-0.36	0.29	0.22	**1.99**		
	Precipitation	0.00	0.00	0.00	**1.19**		
	Elevation	0.02	0.00	0.00	**1.08**	0.45	973.40
	Precipitation	0.00	0.00	0.00	**1.08**		
	Elevation	0.01	0.00	0.00	**1.84**	0.46	973.44
	Temperature	-0.35	0.29	0.24	**1.97**		
	Precipitation	0.00	0.00	0.00	**1.17**		
Phylogenetic diversity	Richness	20.60	0.62	0.00	**1.65**	0.95	1485.62
	Slope	0.24	0.05	0.00	**2.06**		
	Temperature	-3.49	2.14	0.10	**1.92**		
	Precipitation	0.02	0.01	0.00	**1.27**		
	Richness	20.92	0.68	0.00	**1.99**	0.95	1486.18
	Elevation	-0.04	0.04	0.24	**9.40**		
	Slope	0.33	0.09	0.00	**7.45**		
	Temperature	-4.05	2.19	0.07	**2.03**		
	Precipitation	0.02	0.01	0.00	**1.28**		
	Richness	21.27	0.62	0.00	**1.47**	0.94	1495.42
	Slope	0.23	0.04	0.00	**1.47**		
Functional diversity	Phylogenetic diversity	0.00	0.00	0.00	**2.00**	0.92	-598.49
	Elevation	0.00	0.00	0.00	**8.32**		
	Slope	0.00	0.00	0.00	**7.11**		
	Phylogenetic diversity	0.00	0.00	0.00	**2.24**	0.91	-596.52
	Elevation	0.00	0.00	0.00	**8.51**		
	Slope	0.00	0.00	0.00	**7.23**		
	Precipitation	0.00	0.00	0.86	**1.23**		
	Phylogenetic diversity	0.00	0.00	0.00	**2.32**	0.91	-594.52
	Elevation	0.00	0.00	0.00	**8.98**		
	Slope	0.00	0.00	0.00	**7.29**		
	Temperature	0.00	0.00	0.95	**2.06**		
	Precipitation	0.00	0.00	0.88	**1.36**		
	Phylogenetic diversity	0.00	0.00	0.00	**1.69**	0.91	-587.30
	Slope	0.00	0.00	0.00	**1.69**		
	Phylogenetic diversity	0.00	0.00	0.00	**2.03**	0.91	-596.50
	Elevation	0.00	0.00	0.00	**8.89**		
	Slope	0.00	0.00	0.00	**7.19**		
	Temperature	0.00	0.00	0.91	**1.87**		

Table2. Best performing models testing for environmental drivers influence on mammal species richness (SR), phylogenetic (PD) and functional diversity (FD) in Colombia. AICc: corrected Akaike Information Criterion, SE: Standard Error, VIF: Variance Inflation Factor, K(BP): Koenker's studentized Breusch-Pagan Statistic.

Model	Variable	Coefficient	SE	P	Robust t	Robust p	VIF	K(BP)
SR	Intercept	50.816	2.63	<0.01	15.92	0.00	*	2.36
R^2=0.445	Elevation	0.016	0.0016	<0.01	8.94	0.00	1.08	p=0.0381
AICc=973.40	Precipitation	0.002	0.0008	0.01	2.31	0.02	1.08	
PD	Intercept	1099.117	37.72	<0.01	25.75	0.00	*	6.54
R^2=0.941	SR	21.269	0.62	<0.01	29.76	0.00	1.47	p=0.307
AICc=1495.42	Slope	0.226	0.04	<0.01	4.13	0.00	1.47	
FD	Intercept	0.11085	0.018	<0.01	3.99	0.00	*	3.48
R^2=0.907	PD	0.00019	0.00001	<0.01	16.64	0.00	1.69	p=0.175
AICc=-587.29	Slope	0.00004	0.00001	0.001	3.27	0.00	1.69	

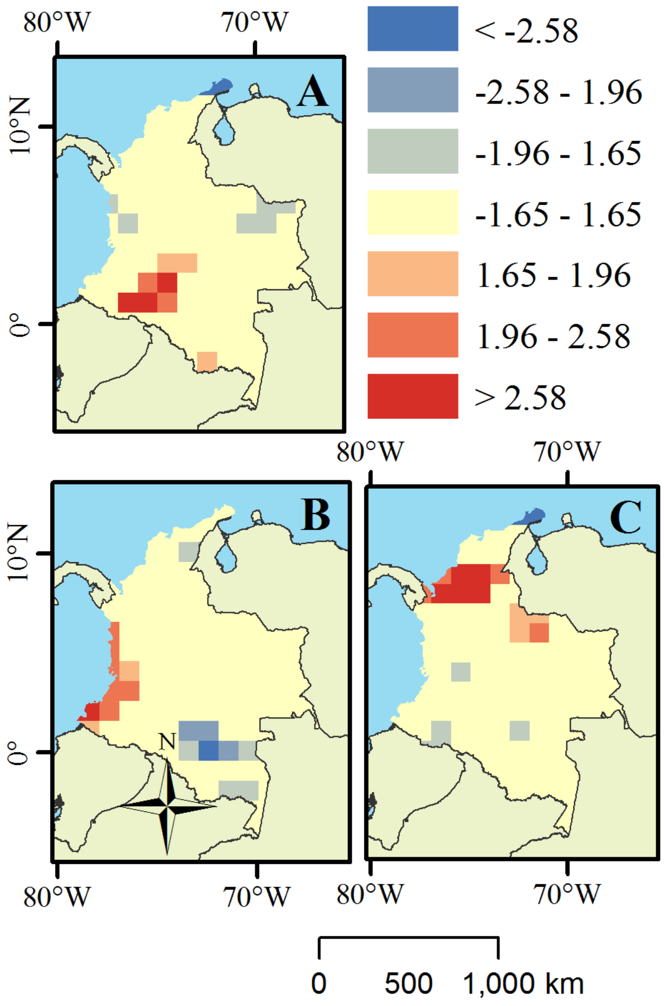

Figure 2. Spatial residuals clustering graphed as standard deviations indicating spatial mismatch of models explaining the influence of environmental drivers on mammal (A) species richness, (B) phylogenetic and (C) functional diversity over a grid of 1 x1 degree cells in Colombia.

Discussion

We provide the first quantification of phylogenetic and functional diversity of terrestrial mammals in Colombia. Our results demonstrate a high degree of relatedness among biodiversity measures, including high similarity in spatial patterns, similar to large scale analyses in other latitudes [45,46]. The evaluation of these complementary measures demonstrates how different attributes of biodiversity can be used simultaneously to better understand the assembly of species communities [46]. Furthermore, previous works have identified how both phylogenetic and functional characteristics can explain species co-occurrence at regional and global scales [45]. Our results highlight that even when the taxonomic, phylogenetic and functional diversity significantly overlap, some areas will differ among the three measures (*i.e.*,spatial mismatch) suggesting other factors are affecting assemblage composition and species co-occurrence.

The three diversity measures were strongly correlated, supporting how taxonomic richness drives phylogenetic diversity [9,31], which in turn is a key driver of functional diversity [31]. Assemblages with larger or shorter evolutionary histories can markedly effect functional diversity and stability of those assemblages [31]. However, for global analyses of these measures on mammals [31], spatial mismatches occur at different scales and geographic localities where additional factors or distinctive evolutionary histories has an unidentified effect on both measures [11,20]. This is clear for areas previously identified having high endemisms and singularity in the country like Sierra Nevada de Santa Marta and Southern Andes [47,48]. Our results further indicate that selecting the areas with species-rich assemblages for conservation priorities will typically directly affect other biodiversity measures [9], and that areas identified as mismatches require further assessment and strong consideration for conservation.

Environmental drivers, or environmental filtering, determines a substantial proportion of the basic diversity measure, namely species richness [46,49], while the effect of these variables on other measures was less influential than expected. Previous studies of trait- and phylogenetic-based diversity measures have proposed environmental filtering as the most likely driver of these measures [31,46,49,50]. However, in our study these drivers were not sufficient to fully explain variation in species richness. Safi et al. [31] evaluated these three measures of diversity at a global scale and found they have a significant degree of surrogacy. Nevertheless, there appears to be considerable spatial mismatch across geographic scales, suggesting greater support to local and environmental factors influencing species assembly at taxonomic, functional and evolutionary levels. Local drivers, such as assemblage time, environmental constraints and biogeographic scale, have been proposed to explain phylogenetic and functional diversity patterns [51,52], which in our study seems to be a key aspect; environmental constraints significantly affect species richness, slope, as a locally-defined variable affects functional and phylogenetic diversity and assemblage time affects functional diversity . Our identification of slope as an important determinant of phylogenetic and functional diversity has been previously identified for substantially different systems and taxonomic groups [53,54]. In this study, as a locally-constrained variable, it is likely representative of locally-defined conditions of species assemblage.

Our results can certainly be refined since both phylogenetic and functional diversity measures are highly influenced by the phylogeny and traits used, respectively, and the method used to estimate both measures [9]. Our selection of both measures was based on using similar dendrogram-based measures, so the comparison and simultaneous evaluation of both measures was congruent [9,32,55]. As previously stated for concepts such as redundancy [56-58], as more information becomes available and we further understand evolutionary and ecological aspects of a group, analyses on diversity measures can be further refined. Nevertheless, as the first effort to map phylogenetic and functional diversity for Colombia, our results could be incorporated into conservation schemes and facilitate further exploration of these topics in Colombia and other Neotropical countries.

The inclusion of complementary diversity measures into species assemblage patterns analyses allows further understanding of species assemblages by incorporating not only species richness but species evolutionary history and attributes [4,59], and therefore mechanisms linking species to environment, ecosystem processes and vulnerability [32,51,60,61]. Phylogenetic diversity accounts for species evolutionary history influencing species assemblage while functional diversity accounts for species roles in ecosystems [4], therefore, incorporating multiple dimensions of biological diversity beyond species richness, and how these measures interact, may better explain patterns and processes of biodiversity [62], potentially informing more adequately conservation planning and ecological and evolutionary history of assemblages and ecosystems [45]. Our results contribute to the understanding of diversity patterns in Colombia, and our preliminary mapping could help define priorities for complementarity and singularity [11,20]. Despite the potential surrogacy of the three measures used, identifying areas with high values of the three measures would likely result in more comprehensive and integral conservation planning accounting for taxonomic, evolutionary and ecosystem function singularities and important areas for the country. The variation in three important biodiversity measures, and that no one measure best represented species assemblages, suggests species assemblages are best represented using multiple metrics. Using multiple metrics in turn will help ensure that areas for conservation are more likely to be correctly identified based on the conservation objectives.

Acknowledgements

This paper constitutes a partial fulfillment of the Graduate Doctoral Degree Program in Biomedical Sciences of the National Autonomous University of México (UNAM) of the first author. J.F. González-Maya acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT), and UNAM (scholarship 255983). The authors would like to thank R. Medellin, E. Martínez-Meyer and N. Mancera for constant support through the development of this project. Partial support was provided by The Sierra to Sea Institute and ProCAT Colombia.

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Supporting Information

Table S1. All possible driver independent variable combinations of ordinary least squares models for mammal species richness, phylogenetic and functional diversity in Colombia, including variables, R^2 and corrected Akaike Information Criterion (cAIC). Variables: P: Precipitation, T: Temperature, E: Elevation, S: Slope, R: Species Richness and PD: Phylogenetic diversity.

Model	Variables	R^2	cAIC
Species richness	P	-0.01	1048.09
	T	0.19	1019.80
	E	0.41	979.64
	S	0.30	1002.55
	P, T	0.23	1015.06
	P, E	0.45	973.40
	P, S	0.32	998.37
	T, E	0.41	981.48
	T, S	0.31	0.31
	E, S	0.42	978.24
	P, T, E	0.45	973.24
	P, T, S	0.35	993.84
	P, E, S	0.45	972.83
	T, E, S	0.42	979.99
	P, T, E, S	0.45	973.24
Phylogenetic diversity	P	0.00	1855.00
	E	0.48	1771.80
	S	0.39	1791.83
	R	0.93	1520.69
	T	0.24	1819.86
	P, E	0.48	1773.27
	P, S	0.44	1782.31
	P, R	0.93	1521.34
	P, T	0.30	1811.10
	E, S	0.48	1773.46
	E, R	0.94	1505.71
	E, T	0.48	1773.27
	S, R	0.94	1495.42
	S, T	0.40	1790.23
	R, T	0.93	1513.55
	P, E, S	0.52	1762.13
	P, E, R	0.94	1499.56
	P, E, T	0.54	1758.88
	P, S, R	0.94	1497.09
	P, S, T	0.40	1790.23
	P, R, T	0.94	1508.34
	E, S, R	0.94	1496.26
	E, S, T	0.47	1774.89
	E, R, T	0.94	1506.69
	S, R, T	0.94	1497.09
	P, E, S, R	0.94	1497.52
	P, E, S, T	0.53	1760.81
	P, E, R, T	0.94	1497.83
	P, S, R, T	0.95	1485.62
	E, S, R, T	0.94	1497.52
	P, E, S, R, T	0.95	1486.18

…Continue S1Table…

Functional diversity	P	-0.01	-285.80
	R	0.82	-501.54
	E	0.46	-365.51
	PD	0.90	-578.16
	T	0.24	-320.78
	S	0.44	-360.45
	P, R	0.82	-499.54
	P, E	0.50	-372.86
	P, PD	0.90	-577.15
	P, T	0.28	-326.64
	P, S	0.48	-368.65
	R, E	0.83	-511.81
	R, PD	0.90	-577.97
	R, T	0.82	-506.19
	R, S	0.86	-532.21
	E, PD	0.90	-577.58
	E, T	0.46	-364.15
	E, S	0.47	-365.61
	PD, T	0.90	-576.98
	PD, S	0.91	-587.30
	T, S	0.45	-360.50
	P, R, E	0.83	-511.31
	P, R, PD	0.90	-577.25
	P, R, T	0.82	-505.40
	P, R, S	0.86	-534.48
	P, E, PD	0.90	-575.93
	P, E, T	0.50	-373.76
	P, E, S	0.51	-374.27
	P, PD, T	0.90	-575.43
	P, PD, S	0.91	-585.36
	P, T, S	0.50	-372.26
	R, E, PD	0.90	-577.06
	R, E, T	0.83	-510.53
	R, E, S	0.87	-542.76
	R, PD, T	0.90	-576.53
	R, PD, S	0.91	-585.56
	R, T, S	0.86	-530.27
	E, PD, T	0.90	-575.70
	E, PD, S	0.92	-598.49
	E, T, S	0.46	-364.15
	PD, T, S	0.91	-585.84
	P, R, E, PD	0.90	-575.67
	P, R, E, T	0.83	-510.86
	P, R, E, S	0.87	-544.06
	P, R, PD, T	0.90	-575.33
	P, R, PD, S	0.91	-583.58
	P, R, T, S	0.86	-532.61
	P, E, PD, T	0.90	-573.96
	P, E, PD, S	0.91	-596.52
	P, E, T, S	0.51	-375.10
	P, PD, T, S	0.91	-583.84
	R, E, PD, T	0.90	-575.13

…Continue S1Table…

Functional diversity (continue)	R, E, PD, S	0.91	-596.60
	R, E, T, S	0.87	-541.14
	R, PD, T, S	0.91	-584.10
	E, PD, T, S	0.91	-596.50
	P, R, E, PD, T	0.90	-573.67
	P, R, E, PD, S	0.91	-594.61
	P, R, E, T, S	0.87	-543.43
	P, R, PD, T, S	0.91	-582.11
	P, E, PD, T, S	0.91	-594.52
	R, E, PD, T, S	0.91	-594.62
	P, R, E, PD, T, S	0.91	-592.62

8. Discusión general

Entender los patrones de distribución de la diversidad y los procesos subyacentes que influencian estos patrones ha sido uno de los principales temas de interés de la ecología desde hace décadas (Buzas 1972; Klopfer & MacArthur 1961; MacArthur & MacArthur 1961; Ricklefs & Schluter 1993; Rosenzweig 1995; Turpie & Crowe 1994). Numerosas aproximaciones se han enfocado en describir y explicar los gradientes de diversidad, principalmente en términos de la riqueza de especies, siendo largamente explorados los patrones latitudinales de esta diversidad (Klopfer & MacArthur 1961; MacArthur 1969). En años recientes se ha avanzado significativamente en el entendimiento de la ecología de la diversidad, especialmente en términos de su medición, sus componentes y la interrelación entre diferentes aspectos de esta (Magurran & McGill 2011). Dentro de esta nueva concepción y comprensión de la diversidad, la identificación de sus principales atributos y determinantes, y la medición de diferentes aspectos, como el funcional y evolutivo, han ganado una importante fuerza teniendo implicaciones más profundas al relacionarla no sólo con su variedad sino con procesos históricos y ecosistémicos. Sin embargo, hasta años recientes pocos grupos biológicos habían sido evaluados dentro de estos nuevos conceptos, y la ecología de la diversidad ha ido poco a poco ampliándose a la mayoría de grupos taxonómicos a nivel global (Blaum et al. 2011; Devictor et al. 2010).

Los mamíferos, a pesar de ser considerado un grupo carismático, es de los que menos atención ha recibido, principalmente en términos funcionales, y es hasta años recientes que se empezó a evaluar los aspectos funcionales de su diversidad y los patrones a diferentes escalas (Belmaker & Jetz 2013; Safi et al. 2011). El entendimiento de los patrones globales de la diversidad de mamíferos resulta de gran importancia actualmente, no sólo por el interés e importancia científica, si no por los grandes retos de conservación a los que se enfrenta el grupo, entre muchos otros, a escala global (Devictor et al. 2010). Así, la evaluación de los patrones de distribución, determinantes ambientales y conservación de la diversidad funcional y taxonómica de mamíferos a múltiples escalas, es uno de los primeros pasos para entender los patrones y procesos que influencian la diversidad del grupo, teniendo fuertes implicaciones de conservación.

La distribución de la diversidad funcional de mamíferos a escala global está fuertemente influenciada por la riqueza de especies, como se había previamente probado (Mason et al. 2012; Mason et al. 2005; Mouchet et al. 2010; Safi et al. 2011), sin embargo, diferentes factores influencian estos patrones, así como existe cierto desajuste espacial entre las diferentes medidas. Así mismo, esta influencia varía de acuerdo a la región biogeográfica y el tipo principal de hábitat (*i.e.,*bioma); más sobresaliente aún, la diversidad funcional en diferentes ecoregiones de diferentes regiones biogeográficas, o ecozonas, parecen mantener una tendencia común independientemente de su ubicación o la identidad taxonómica de sus especies. Diferentes mecanismos pueden influenciar esta tendencia: por un lado es posible que el filtraje ambiental opere sobre los principales atributos ecológicos de las especies influenciando así el ensamblaje de especies dependiendo del tipo de ecosistema (Messier et al. 2010; Pavoine & Bonsall 2011; Swenson et al. 2012) o existe una extraordinaria convergencia de atributos ecológicos dentro los ensamblajes y esto está influenciado por la historia evolutiva y estructura de los ecosistemas (Safi et al. 2011). Adicionalmente, la influencia significativa del área, en términos de extensión geográfica, se respalda en hipótesis previas de la relación especies área (Holt et al. 1999; Scheiner 2003; Veech 2000), pero potencialmente determinada por una influencia diferencial a nivel de los atributos ecológicos de las especies (Franzén et al. 2012) y en función del contexto ecológico donde se dan estas relaciones (Matias et al. 2013).

Adicional a los procesos biogeográficos y macroecológicos subyacentes que influencian los patrones de distribución de la diversidad funcional, las implicaciones de conservación son aún más significativas. Dado que la diversidad funcional es una medida del nivel de complementariedad entre los atributos ecológicos de la especies en un ensamblaje (Mason et al. 2005; Petchey & Gaston 2002b), la composición de especies y su vulnerabilidad pueden representar un riesgo latente sobre la pérdida de diversidad funcional y por ende sobre la funcionalidad y capacidad de resiliencia de los ecosistemas (Barragán et al. 2011; Boyer & Jetz 2014; Flynn et al. 2009; Petchey & Gaston 2002a; Sundstrom et al. 2012; Worm et al. 2006). A nivel global las especies amenazadas ejercen una fuerte influencia sobre la diversidad funcional a escala de las ecoregiones. Estudios previos han demostrado que las especies raras juegan papeles fundamentales y únicos en el funcionamiento de los ecosistemas (Mouillot et al. 2013), pero adicionalmente, se ha demostrado que ciertos atributos ejercen una fuerte influencia sobre el riesgo de extinción en mamíferos (Davidson et al. 2009). A nivel global cerca del 60% de la diversidad funcional está explicado por las especies en riesgo, y esta relación varía considerablemente dependiendo del contexto ecológico (*i.e.,*biomas y ecoregiones), alcanzando cerca del 80% de la diversidad funcional explicada por las especies en riesgo para múltiples ecoregiones.

De acuerdo a la clasificación de la Lista Roja de Especies Amenazadas de UICN (IUCN 2012), las especies clasificadas como Vulnerables, Amenazadas o Críticamente Amenazadas, en general las llamadas especies en peligro, son aquellas con mayor riesgo de desaparecer a un corto plazo (*i.e.,*generaciones), y por ende son aquellas más vulnerables a la intervención, que en el caso de los mamíferos alcanza cerca del 25% de todas las especies (Schipper et al. 2008). Las implicaciones de esta influencia evidencian la vulnerabilidad de la estabilidad funcional de los ecosistemas y el riesgo potencial no sólo en términos de la pérdida de especies, pero de la pérdida funcional si las especies amenazadas desaparecen. Estos procesos sin embargo varían a escala global y a diferentes escalas geográficas, por lo que las ecoregiones donde las especies en riesgo ejercen mayor influencia sobre la diversidad funcional son aquellas que requieren acciones más urgentes de conservación.

Además de la variación global de la diversidad funcional, los patrones parecen mantenerse a escalas menores pero además a estas escalas es posible identificar de forma más precisa el impacto de las actividades humanas sobre este aspecto de la diversidad. Los resultados indican que a medida que se baja de escala es posible identificar más claramente patrones y gradientes a resoluciones más finas de la variación funcional y de atributos ecológicos que permiten entender continuos ecológicos y evolutivos. A escala global se identificaron los principales gradientes y conglomerados significativos de alta y baja diversidad funcional, pero a su vez, a escalas regionales es posible identificar como se dan esos gradientes en términos de variación de la composición de atributos funcionales. El ejemplo del continuo del istmo de Panamá-Chocó permite identificar como los gradientes operan a escalas finas, dándose recambios de atributos ecológicos entre las especies que conforman los ensamblajes, lo que incide directamente sobre su diversidad funcional (Belmaker & Jetz 2013; González-Maya et al. 2012). La evaluación de la variación a escala del Neotrópico parece mostrar además un impacto considerable de la intervención humana y de nuevo la fuerte influencia de las especies en riesgo sobre la diversidad funcional de mamíferos. Más importante aún, dada la degradación diferencial de las ecoregiones, al parecer a escala Neotropical múltiples ecoregiones han sufrido una degradación considerable de su diversidad funcional, donde los procesos de intervención pueden estar favoreciendo el papel que juegan especies tolerantes a la intervención. En múltiples regiones a escala global se ha probado como la intervención tiene efectos diferenciales sobre ciertas especies y sobre ciertos componentes de la diversidad (Barragán et al. 2011; Biswas & Mallik 2010; Biswas & Mallik 2011). El entendimiento de esta influencia diferencial sobre aspectos funcionales puede permitir así la identificación y selección de prioridades tanto geográficas como temáticas, de forma que se procure el mantenimiento de los procesos funcionales en las ecoregiones más intervenidas por medio de acciones dirigidas de conservación.

La aproximación ecoregional permite además entender los patrones macroecológicos de la diversidad funcional sobre una escala con sentido ecológico, al agrupar y evaluar estos patrones sobre gradientes y regionalizaciones basadas en tipos de ecosistemas y hábitats y con afinidades ecológicas y evolutivas claras (Funk & Fa 2010; Olson et al. 2001). Sin embargo, las ecoregiones implican también naturalmente una alta heterogeneidad al variar significativamente en términos de su extensión, y al generalizar grandes regiones ecológicas con afinidad estructural y biogeográfica, lo que se debe considerar en su análisis. Dado que a escala global fue posible identificar patrones claros de distribución, así como algunos procesos subyacentes, el paso lógico fue probar hipótesis acerca de la variación a escalas de país con el fin de entender la variación y los factores determinantes a escalas de planificación. La evaluación de los principales determinantes ambientales de la diversidad funcional, y la influencia de la escala y la variación geográfica, en Colombia y Costa Rica, muestran principalmente aspectos relacionados con el filtraje ambiental de la diversidad funcional (Messier et al. 2010; Swenson et al. 2012) y la influencia de la intervención a estas escalas. Variables ambientales como la temperatura y la precipitación parecen ejercer un efecto significativo sobre la diversidad funcional, como ya había sido previamente identificado a escala global (Safi et al. 2011). Sin embargo, los efectos más considerables fueron identificados para la intervención antropogénica y la historia evolutiva y biogeográfica.

Costa Rica, ubicado en la conexión entre Norte y Suramérica, contiene una biota conformada por elementos de Norte y Suramérica lo que lo hacen un país altamente diverso (Rodríguez-H et al. 2002). Esta conformación biogeográfica tiene implicaciones sobre su diversidad taxonómica, pero además ejerce un efecto fundamental sobre su diversidad funcional; por ejemplo, la composición de los ensamblajes en función del origen de las especies (Norte-Sur), ejercen una mayor o menor influencia dependiendo de la ubicación geográfica de los ensamblajes. Esta influencia diferencial es clara a nivel de país por la división geográfica en zonas con continuos más o menos claros de regiones funcionales, la cual está claramente influenciada por las especies de murciélagos y roedores, pero que permiten entender la variada composición de la diversidad del país. Sin embargo, a esta escala es posible también identificar la influencia de la intervención humana sobre esta diversidad como fue también identificada para el Neotrópico en general. Considerando el efecto de la intervención a escala de país, la evaluación de los esquemas actuales de conservación se hace necesaria para entender y priorizar las acciones requeridas para el mantenimiento de la diversidad.

Una de las principales herramientas de conservación histórica es la creación de áreas protegidas (Chape et al. 2005; Davey 1998; González-Maya et al. 2010; González-Maya et al. 2011; González-Maya et al. 2013; González-Maya et al. 2015), la cual en la mayoría de casos no ha sido sustentada en información de atributos ecológicos. Ya que la diversidad funcional está influenciada por la riqueza de especies (Mason et al. 2012), y que no sólo las especies en general pero las poblaciones son las que ejercen influencia sobre los ecosistemas, y estas sufren incluso en mayor magnitud un riesgo latente de extinción (Ceballos & Ehrlich 2002; Ceballos et al. 2005; Ceballos et al. 2010), entender la eficiencia de las áreas protegidas para mantener poblaciones y especies es una de las principales herramientas para planificar el territorio y de esta forma asegurar las funciones que ejercen las especies sobre los ecosistemas (Ceballos 2007; González-Maya et al. 2015). Para Costa Rica se identificó una clara redundancia del sistema de áreas protegidas, pero adicionalmente, vacíos considerables de protección de especies y poblaciones. La identificación de vacíos y áreas prioritarias permiten informar la toma de decisiones en conservación (Brooks et al. 2006; Rodrigues 2007; Watson et al. 2011), por ende, la evaluación para el país de la eficiencia de las áreas protegidas representa un avance significativo para mejorar la resolución en la toma de decisiones y una herramienta para alocar recursos, definir prioridades y expandir los esquemas de conservación y mantenimiento de las funciones y en general de la diversidad (González-Maya et al. 2015).

Recientemente, una de las principales discusiones en términos de planificación de conservación es la generación de herramientas para priorizar y definir acciones de conservación y esquemas de asignación y uso de los escasos recursos en conservación (Balmford et al. 2000; Carwardine et al. 2008; Ceballos et al. 2015; Joseph et al. 2009; Víquez-R et al. 2013). Dentro de esta evaluación, la selección de indicadores o sustitutos (*i.e.,surrogates* en inglés) apropiados que informen de manera adecuada la toma de decisiones es uno de los principales retos (Ceballos et al. 2015; Grantham et al. 2010; Rodrigues 2007; Víquez-R et al. 2013). La selección de prioridades en general ha estado históricamente relacionada con la evaluación de zonas con alta riqueza de especies, siendo especialmente conocidos la selección de “puntos calientes” de biodiversidad, como aquellas áreas con altas concentraciones de riquezas de especies (Faith & Walker 1996; Myers et al. 2000; Reid 1998). Más recientemente se han incorporado nuevas aproximaciones, principalmente enfocadas en entender los procesos subyacentes a estas zonas de alta diversidad (Lucifora et al. 2011; Ovadia 2003; Penner et al. 2011; Veech 2000) y en la identificación de áreas de conservación no sólo en términos de riqueza de especies pero también de singularidades y sitios de mayor riesgo potencial de extinción de especies (Butchart et al. 2010; Le Saout et al. 2013). Adicionalmente, el entendimiento de otros procesos y medidas de diversidad, en especial desde el punto de vista funcional y filogenético, han permitido identificar aquellas zonas prioritarias tanto por su funcionalidad como por su historia evolutiva (Buckley et al. 2010; Cardillo et al. 2008; Cardillo et al. 2006; Devictor et al. 2010; Faith 1992; Isaac et al. 2007; McGoogan et al. 2007; Pio et al. 2011). Estas nuevas aproximaciones sin embargo han abierto una serie de nuevas preguntas relacionadas sobre cuáles son los mejores indicadores, y la coincidencia entre las diferentes medidas con enfoque espacial (Ceballos et al. 2015; Devictor et al. 2010).

A diferentes escalas se ha identificado que no necesariamente las diferentes medidas de diversidad son buenas medidas sustitutas entre sí, y por ende deben considerarse aproximaciones complementarias que identifiquen prioridades desde todos los niveles de esta diversidad (Calba et al. 2014; Monnet et al. 2014; Munkemuller et al. 2014; Zupan et al. 2014). Como se encontró a múltiples escalas, la diversidad funcional no necesariamente es totalmente explicada a escala global y nacional por la riqueza de especies, a pesar de su relación cercana (Mouchet et al. 2010), por lo que es necesario entender otros procesos subyacentes que influencian la diversidad funcional y su distribución en el espacio. A escala global determinantes macroecológicos como el área, la escala y el tipo de ecosistema son algunas de las variables que influencian la distribución de la riqueza y la diversidad funcional, mientras a escalas menores operan otros factores, incluyendo aquellos de carcater ambiental, biogeográfico y antropogénicos, que potencialmente explican el claro desajuste (*i.e.,mismatch* en inglés) entre las medidas.

8.1 Conclusión general

En general, la distribución de la diversidad funcional de mamíferos presenta patrones relacionados tanto con factores macroecológicos, biológicos y evolutivos, donde actualmente la intervención humana, a escala estructural y sobre el riesgo de extinción de las especies, también influencia considerablemente estos patrones. Los patrones observados además responden a la escala, y la variación y congruencia a diferentes escalas es un indicativo de los procesos biológicos y evolutivos subyacentes, donde el filtraje ambiental y la convergencia de atributos parecen ser los principales conductores de estos patrones.

Estudios previos habían explorado y evidenciado algunos patrones de diversidad funcional de mamíferos, sin embargo, muchos de sus aspectos básicos relacionados con el efecto de la escala, el filtraje ambiental y la convergencia según ecosistemas permanecían sin ser propiamente abordados. Además de estos aspectos descriptivos básicos, los procesos subyacentes y determinantes a escalas de planificación no habían sido explorados adecuadamente, por lo que el avance en el entendimiento de estas relaciones y su variación espacial permiten una planificación de conservación a mejor resolución, entendiendo además el efecto de la intervención antrópica sobre esta medida de diversidad. Adicionalmente, la influencia de las especies amenazadas sobre la diversidad funcional, y sus implicaciones en términos de funcionamiento y resiliencia de los ecosistemas, representan un avance considerable, generando un nuevo mapa de riesgo no sólo para la pérdida de especies, si no del riesgo de los ecosistemas mismos a sufrir cambios funcionales irreversibles.

La aproximación multiescalar abordada en el presente trabajo aporta aspectos fundamentales de la naturaleza y patrones de la diversidad funcional, necesarios para entender su ecología y vulnerabilidad, y a su vez evalúa la pertinencia de la selección de las escalas y provee de argumentos para considerar esta medida en la priorización de acciones y regiones para conservación. La escala ejerce un efecto fundamental en la distribución y el efecto de la intervención sobre medidas como la diversidad funcional, y a pesar de que existen patrones que trascienden las escalas (*e.g.*, biogeográficos, filtraje ambiental), es necesario considerar el efecto de la variación espacial y escalar en la medición y análisis de sus patrones y procesos subyacentes, así como en el diseño de medidas de conservación.

Dado que la diversidad funcional no ha sido abordada para grupos diferentes a las plantas hasta años recientes, aún quedan numerosos aspectos de requieren análisis adicional. Por ejemplo, se debe explorar aún más los caracteres funcionales más importantes en mamíferos, principalmente aquellos que tienen más relevancia en el funcionamiento de los ecosistemas. Así mismo, análisis a escalas de paisaje, que involucren ensamblajes estimados a partir de datos de campo, pueden arrojar nuevas luces sobre los procesos de ensamblaje, la sobreposición de funciones y el recambio funcional como respuesta a la intervención humana.

Por último, la evaluación de la efectividad y eficiencia de los esquemas actuales de conservación, cómo las áreas protegidas, es una herramienta fundamental que aporta información necesaria para la toma de decisiones hacia el logro de metas globales y nacionales de conservación que aseguran la perdurabilidad de la biodiversidad al largo plazo. Así mismo, la diversidad funcional deberá ser una medida considerada en los futuros esquemas de conservación, y su entendimiento permitirá una mejor resolución para explorar patrones ecológicos y servirá de soporte para la toma de decisiones en conservación y manejo de la biodiversidad.

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