UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
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RELACIONES BIOLÓGICAS, ECOLÓGICAS Y FILOGENÉTICAS EN LAS ÁREAS DE ENDEMISMO DE LOS MAMÍFEROS NEOTROPICALES

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS BIOLÓGICAS

PRESENTA:

M. en C. ELKIN ALEXI NOGUERA URBANO

TUTORA PRINCIPAL DE TESIS: DRA. TANIA ESCALANTE ESPINOSA
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AGRADECIMIENTOS INSTITUCIONALES

Al **Posgrado en Ciencias Biológicas (PCB) de la Universidad Nacional Autónoma de México**, por el apoyo brindado durante el proceso de mi formación académica, para el desarrollo y culminación de la presente disertación.

A los **Jurados Dr David Espinosa Organista, Dra Ella Vázquez Domínguez, Dr Juan José Morrone, Dra Livia León Paniagua,** y **Dr Octavio Rojas Soto** por los aportes realizados y todas sus sugerencias, las cuales fueron muy acertadas.

Al **Consejo Nacional de Ciencia y Tecnología (CONACYT)** por el apoyo económico brindado, mediante la beca de posgrado (N° 262582) y **Beca Mixta** (Becas Mixtas 2016 - MZO 2017 Movilidad en el Extranjero) para desarrollar una estancia de investigación en Argentina, lo cual fue fundamental para la realización del Doctorado.

Al **Programa de Apoyo de Estudios de Posgrado (PAEP) de la UNAM** por las becas otorgadas:

> Beca PAEP 2016, para participación en el 35th Annual Meeting of The Willi Hennig Society and XII Reunión Argentina de Cladística y Biogeografia en la Ciudad de Buenos Aires, Argentina (5-8 de octubre de 2016).
>
> Beca PAEP (2017), Convocatoria de Mejoras de la tasa de graduación del Doctorado en Ciencias del Posgrado en Ciencias Biológicas (PCB), participación en: VI Simposio Colombiano de Biología Evolutiva, Universidad del Valle, Cali, Colombia (17-19 de agosto de 2017).
>
> Beca PAEP (2017), Convocatoria de Mejoras de la tasa de graduación del Doctorado en Ciencias del Posgrado en Ciencias Biológicas (PCB), participación en: I Congreso Latinoamericano de Biogeografía, Universidad Regional Amazónica, Tena, Ecuador (19 a 24 de noviembre del 2017).

Programa **UNAM-DGAPA-PAPIIT**, Proyecto IN217717: “Planeación Sistemática de la Conservación en la Faja Volcánica Transmexicana”.

A la **Facultad de Ciencias, y Grupo de Investigación de Biogeografía de la Conservación, UNAM**, por brindarme apoyo y permitirme desarrollar esta investigación en sus instalaciones.

A **José Gerardo Rodríguez Tapia** del Instituto de Ecología, UNAM por el apoyo técnico.

A la **Dra. Tania Escalante Espinosa, Facultad de Ciencias, UNAM**, tutora principal, por su valioso apoyo, comentarios y ayuda, durante el desarrollo y finalización de esta investigación.

A los **Doctores Fernando Cervantes (Instituto de Biología, UNAM) y Octavio Rojas (Instituto de Ecología, A.C. INECOL)**, por su valioso apoyo, aportes, comentarios y ayuda, durante el desarrollo y finalización de esta investigación.

AGRADECIMIENTOS PERSONALES

A los Doctores Fernando Cervantes, Octavio Rojas, David Espinosa, Juan José Morrone, Joaquín Arroyo Cabrales, Irene Goyenechea Mayer, Adolfo Navarro a Ignacio Ferro (INECOA), por el tiempo, consejos e ideas, siempre útiles y oportunos.

A Lilia Espinosa, Lilia Jiménez, Patricia Oliva Estrella, Ernesto Armando Rodríguez y Antonio Suarez por el apoyo recibido durante el desarrollo del Doctorado.

A la gente del INECOA: Marco y familia, José, Juan, Carlos, Andrea, Nohelia, Mauricio, y muchos otros que me recibieron muy bien en Argentina. Excelentes asados.

A Rubén Barquez y Mónica Díaz por facilitar mi viaje por San Juan, Argentina. Lindos paisajes.

A Ana, Nacho y sus padres, Lety, por acogerme en sus casas durante mi estancia en Argentina.

A Lalo y su familia. A Laura, Ángel, Erick, Oscar, Gerardo, Leslie, Ana, Alejandra, Kevin, Luis, Niza y muchas otras personas de las que recibí siempre algo, apoyo, colaboración, amistad e ideas, que permitieron adaptarme a esta ciudad y culminar con éxito el reto propuesto.

A Tania Escalante, la paciencia y tranquilidad, por el apoyo brindado antes y durante el proceso que me lleva a alcanzar esta meta. Gracias por ser maestra, tutora y amiga.

A Silvia y su familia, por su apoyo, cariño, respeto y colaboración antes, durante y después de este proceso……y sobre todo por acompañarme en la distancia; gracias por seguirme en la consecución de este sueño. A Jhon Jairo Calderón por el apoyo desde la distancia.

A toda mi familia, especialmente a mi Padres María Jesús y Alfredo; a mis herman@s Cristina, Francis, Danny y Franklin, sobrin@s Ivon, Sofia, Luisa, Mathias, Emiliano, Santiago, y cuñad@s por todo el apoyo, confianza, amistad, amor durante el desarrollo de mi carrera y mi vida entera. Viajé a México cuando tenía una sobrina, ahora regreso a Colombia cuando son seis. A ellos debo todo lo que soy, son participes de mis triunfos y conocedores de todos nuestros recuerdos, alegrías y retos. Siempre serán la guía en mi camino y la verdadera bendición en mi vida.

A la vida misma por permitirme descubrir su belleza con cada paso y regalarme una familia y amigos maravillosos. El reto de ser biólogo es vivir y poder apreciar la vida en compañía.

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RESUMEN

La identificación de áreas de endemismo (AE) es uno de los primeros pasos en los análisis biogeográficos. Las AE se consideran unidades biogeográficas definidas por taxones codistribuidos e integrados evolutivamente, y su identificación se realiza básicamente a partir de la superposición de las áreas de distribución de dos o más taxones. Esto ha llevado a que se dificulte su caracterización de las AE o que existan vacíos en la identificación de sus propiedades, como lo es su dinámica evolutiva. Por lo tanto, esta investigación tuvo como objetivo principal analizar las relaciones biológicas, ecológicas y filogenéticas en las áreas de endemismo de mamíferos del Neotrópico. Para tal fin se integraron conceptos y herramientas biogeográficas de análisis de AE, modelos de nicho ecológicos y distribuciones de especies, en un contexto multitemporal; así como métodos de análisis filogenéticos de comunidades y procesos de análisis espacial. Los resultados indican que las AE persisten y mantienen su nivel jerárquico biogeográfico a lo largo del tiempo, es decir, las áreas que presentan menor tamaño actualmente, se han mantenido así desde el pasado; mientras que las áreas actuales de mayor tamaño, fueron las mayores en el pasado. Por otra parte, la inclusión de información filogenética y espacial permitió concluir que los factores que han afectado la dinámica de las AE (cambios de tamaño y composición) son el número de especies endémicas, la diversidad filogenética, la edad de las especies y el número de órdenes taxonómicos, como un *proxy* de la variabilidad biológica de las especies endémicas. Para la región Neotropical, la diversidad filogenética (DF) y la latitud afectan las tendencias ecológicas de las áreas de endemismo, encontrándose la mayor diversidad filogenética de la región Neotropical en latitudes cercanas al ecuador terrestre. Además, este patrón está caracterizado por un agrupamiento filogenético, soportado en su mayoría por linajes de murciélagos que evolucionaron en el Neotrópico. Para las subregiones y provincias, la generalidad es la ausencia de patrones filogenéticos, probablemente porque las áreas de endemismo están integradas por linajes múltiples y distantes. Por otra parte, las áreas de endemismo han sido y continúan siendo afectadas por los factores climáticos. Así las AE actuales que se encuentran en las Zonas de Transición Mexicana y Sudamericana (ZTM y ZTS), están afectadas principalmente por la isotermalidad; mientras que en la Zona de Integración del Bosque Atlántico (entre dominios Paranaense y Chaqueño), la mayor

influencia es ejercida por la precipitación del trimestre más cálido. Para las tres zonas, la precipitación del trimestre más cálido es un predictor importante del endemismo; sin embargo, la heterogeneidad topográfica y climática condiciona la alta riqueza de endemismos, lo cual indica que hay una fuerte influencia de la topografía sobre las áreas de distribución de las especies. Las áreas de endemismo son unidades biogeográficas que responden a la evolución tectónica de la tierra y sus variaciones climáticas. Las especies endémicas se integran temporalmente de manera sincrónica o asincrónica, dependiendo de su tiempo de evolución y su dinámica biológica. Las AE, al ser "fotografías" actuales e históricas de patrones de integración temporal y espacial de las especies, se modifican (1) al expandirse la distribución geográfica de las mismas, (2) al extinguirse, o (3) cuando se modifica por la dinámica interna de las poblaciones. Finalmente, se concluye que las AE están afectadas tanto por factores biológicos, ecológicos y filogenéticos, a cualquier nivel dentro de la jerarquía biogeográfica. Por lo tanto, las áreas de endemismo persisten en el tiempo, pero a la vez son dinámicas y evolucionan con la superficie de la Tierra.

ABSTRACT

The identification of areas of endemism (AE) is one of the first steps in the biogeographic analyses. The AE are biogeographical units defined by co-distributed and evolutionary integrated taxa. The identification of AE is based on the geographical overlap of distributional areas of two or more taxa. Then, some difficulties in the characterization and description of other properties of the AE have been recognized, such as their evolutionary dynamism. Therefore, the main goal of this research was to analyze the biological, ecological and phylogenetical relationships into the areas of endemism of Neotropical mammals. Regarding this, conceptual and biogeographical tools to analyze AE, ecological niche modeling in a multitemporal framework; as well as tools of phylogenetic community ecology and spatial analysis process. The results indicated that the AE persist and maintain their biogeographical level along the time, it is mean that small current AE, also were small in the past; while the big current areas had big sizes in the past. In other way, the inclusion of phylogenetical and spatial information to describe AE, allowed to conclude that the number of endemic species, the phylogenetical diversity, the evolutionary age of the endemic species, and the number of taxonomical orders as a *proxy* of the functional diversity, have affected the dynamism (changes of size and structure) of the AE. For the Neotropical region, the phylogenetical diversity and the latitude affect the ecological tendencies of the AE, found a core of high number of endemic species in equatorial terrestrial latitudes. Moreover, endemic species integrate a phylogenetical cluster, which is supported by bats that evolved in Neotropical habitats. For subregions and provinces, the generality of the phylogenetical patterns was the absence of phylogenetical clustering; may be due to the AE are integrated by several and distant lineages of mammals. On other hand, the AE have been affected by climate factors and also it currently occurs. Thus, the current areas of endemism belonging to transitional zones, like the Mexican (MTZ) and South American (SATZ) transition zones, are mainly affected by the isothermality; while in the Atlantic Forest Integration Zone, the precipitation of the warmest quarter was the stronger variable. Only one explicative variable was shared by the three transitions zones: the precipitation of the warmest quarter. However, the topographic and climatic heterogeneity affect the high richness of endemic species, which indicate a stronger influence of the topography on the distributional areas of the endemic

species in the three zones. Then, the AE are biogeographical units resulting from the evolution of the Earth tectonics and the climate. The endemic species are synchronous or asynchronous integrated, depending on their evolutionary age and biological dynamism. Because the areas of endemism are historical and current “snapshots” of integrative temporal and spatial patterns, their shape and size is modified when one or more species (1) expand their distributional area, (3) they appear or disappear, and (3) when the distributional areas of the species are modified by population dynamism. Finally, I conclude that the AE are affected by biological, ecological and phylogenetical factors, at any biogeographic level. Therefore, the areas of endemism persist along the time, but they are dynamic and evolve with the Earth surface.

INTRODUCCIÓN GENERAL

La biogeografía estudia los patrones de distribución en el tiempo y en el espacio de la biota actual y pasada (Wiley 1981, Espinosa et al. 2001). En particular, la biogeografía evolutiva propone una incorporación de evidencia de diversas disciplinas como climatología, filogenética, geología, biología molecular y paleontología, para descubrir los patrones de distribución geográfica y evaluar los cambios históricos que los han formado (Wiens & Donoghue 2004, Morrone 2007, Weeks et al. 2016). Algunos de los principales cuestionamientos en este enfoque, se han referido a la identificación de áreas de endemismo y sus relaciones (Nelson y Platnick 1981, Humphries y Parenti 1986). Los taxones *endémicos* son aquellos que se encuentran restringidos a un área geográfica (Candolle 1820, Anderson 1994), y el patrón de codistribución de dos o más taxones constituye un *área de endemismo* (Platnick 1991, Anderson 1994, Morrone 1994, Espinosa et al. 2001).

La identificación de áreas de endemismo (AE) es uno de los primeros pasos en los análisis biogeográficos, las cuales están compuestas por taxones coexistentes e integrados espacio-temporalmente (Morrone 2007). En AE se considera el supuesto de la existencia de una historia biogeográfica común entre los taxones que las componen (Platnick 1991, Espinosa et al. 2001, Szumik et al. 2002). Así, especies aún con medios de dispersión diferentes están relacionadas en el espacio y el tiempo (Nelson y Platnick 1981), resultado de procesos diferentes al azar (Morrone 1994). La identificación de las AE se realiza básicamente a partir de la superposición de las áreas de distribución de dos o más taxones (Platnick 1991, Morrone 1994, Szumik et al. 2002), bucando alta congruencia espacial. De esta manera, la alta congruencia espacial representa la respuesta paralela y simultánea de los taxones endémicos a factores históricos y actuales, lo cual podría reflejar concordancia ecológica y evolutiva entre ellos (Szumik et al. 2002).

Croizat (1964) propuso que hay tres dimensiones de la biodiversidad: el espacio, el tiempo y la forma. Sin embargo, en la identificación de las AE se considera sólo al espacio como dimensión central de análisis, dejando a un lado el tiempo de evolución de las especies endémicas que las estructuran. Es decir, la identificación de AE esta soportada fundamentalmente en la congruencia espacial de las especies endémicas. Lo cual conlleva a problemas de tipo metodológico (Hovenkamp 1997), debido a que los valores de congruencia espacial son relativos a la escala del universo de estudio o al método de graficado de las áreas de distribución (Roig-Juñent et al. 2002). En algunos casos la congruencia espacial puede ser resultado del azar (Nelson y Platnick 1981). Esto ha llevado a que existan dificultades en la caracterización de las AE (Domínguez et al. 2006) o se ponga en duda su existencia (Hovenkamp 1997).

Las AE constituyen hipótesis de homología biogeográfica primaria y son puestas a prueba mediante análisis de biogeografía cladística u homología biogeográfica secundaria (Morrone 2001, Morrone 2007). Para ello se contrastan las relaciones espaciales entre áreas, a partir de cladogramas, además se proponen explicaciones sobre las causas que las relacionan y su evolución (Nelson y Platnick 1981, Morrone 2001, Morrone 2007). Sin embargo, son pocas las explicaciones sobre la naturaleza de aquellas interconexiones (Nelson y Platnick 1981) o la congruencia temporal de los taxones que integran a las AE (Cunningham y Collins 1994).

Algunos factores que influyen en la congruencia espacial de los taxones que conforman a las AE son el clima (temperatura y precipitación), los tipos de vegetación y ciclos climáticos, entre otros (Crisp 2001, Emerson y Gillespie 2008, Cardillo y Meijaard 2010). Por lo tanto, las AE podrían ser dinámicas y responderían al ambiente como lo hacen las áreas de distribución (Gámez et al. 2014, Aguado y Escalante 2015), de acuerdo con reglas que rigen la dinámica ecológica de las comunidades (Murray y Crother 2016). Sin embargo, se desconoce las variaciones en la congruencia espacial entre especies endémicas y los factores históricos y ecológicos que afectan la dinámica de las áreas de endemismo. Además, el conocimiento sobre las tendencias de las áreas de endemismo con respecto al tamaño y posición geográfica o la descripción de patrones filogenéticos en las áreas de endemismo es escaso. Se suma a ello, los vacíos conceptuales y empíricos sobre la integración temporal de las especies endémicas en las áreas de endemismo. La profundización en dichos aspectos permite explicar los procesos de integración de las especies endémicas en las áreas de endemismo, así como su dinámica (ampliación, contracción y extinción de las áreas de endemismo).

La presente tesis tuvo como objetivo principal analizar las relaciones biológicas, ecológicas y filogenéticas en las áreas de endemismo de mamíferos del Neotrópico. Para tal fin se usaron herramientas biogeográficas como el Análisis de Endemicidad (Szumik et al.

2002), modelos de distribución (Philips et al. 2006), métodos de análisis filogenéticos de comunidades (Webb 2000, Webb et al. 2002) y herramientas de análisis espacial. Durante el proceso de desarrollo de la tesis se realizaron revisiones de literatura y se han abordado diferentes perspectivas de investigación, las cuales se incluyen en tres capítulos.

Capítulo I. Se presenta una revisión de los conceptos de endemismo y áreas de endemismo en el documento "El endemismo: diferenciación del término, métodos y aplicaciones" (Noguera-Urbano 2017), además se describe la congruencia espacial, considerada la principal dimensión de análisis actual de las AE, se indican los cambios que pueden tener las áreas de distribución y se puntualiza la necesidad de incorporar la dimensión filogenética para explicar las tendencias ecológicas y evolutivas de las AE. Posteriormente se presenta el manuscrito "*Dynamism of the areas of endemism in neotropical mammals: differential effects of historical and ecological factors*" (Noguera-Urbano et al. Enviado), en el cual se analiza el efecto de factores como el número de especies endémicas, el número de órdenes, la diversidad filogenética, estructura filogenética) y otros factores sobre la dinámica de las mismas. La dinámica fue medida como los cambios de tamaño y persistencia a lo largo de tres periodos de tiempo: presente, Holoceno Medio y Última Interglaciación. Los resultados indican una relación positiva del tamaño de las áreas de endemismo entre los tres periodos, es decir, las áreas que presentan menor tamaño se han mantenido así desde el pasado, mientras que las áreas de mayor tamaño, fueron las mayores en el pasado. Esto indica que las unidades biogeográficas tienden a persistir en el tiempo, conservando una proporción equivalente en cada periodo; y además que los regímenes climáticos y la fisiogeografía de las áreas de endemismo presentan barreras substanciales a la dispersión de las especies endémicas, relativas al tamaño de cada AE. Los factores que influyeron con mayor importancia sobre los cambios del tamaño de las áreas de endemismo fueron: (1) el número de especies endémicas, (2) la diversidad filogenética, (3) la edad de las especies y (4) el número de órdenes taxonómicos como un *proxy* de la variabilidad biológica de las especies endémicas. Esto indica que AE con mayor diversidad tienden a presentar mayor tamaño; en consecuencia, presentan mayores cambios en el tamaño a lo largo del tiempo. Esto posiblemente se deba a que las AE con mayor diversidad, están integradas por especies que presentan diferentes adaptaciones a la dispersión y a la variabilidad de condiciones climáticas, así como también diferentes parámetros poblacionales. Con respecto a la estructura filogenética, la mayoría de las AE están compuestas por múltiples linajes de mamíferos que se han integrado asincrónicamente sin definir ningún tipo de patrón filogenético. En general, los dos manuscritos de este capítulo indican que las AE de los mamíferos neotropicale, cambian en forma y composición de acuerdo con los cambios individuales de las áreas de distribución de las especies endémicas, pero como generalidad, los patrones de endemismo persisten una vez las especies se han integrado en el espacio geográfico. De esta manera se comprueba la hipótesis propuesta: considerando que las áreas de endemismo representan patrones históricos, dichos patrones se mantendrán como tal a lo largo del tiempo; por ejemplo, durante eventos de glaciaciones e interglaciares.

Capítulo II. En este capítulo se describen las AE que estructuran a la región Neotropical, así como las tendencias macroecológicas de los patrones de endemismo y los patrones filogenéticos de las especies de mamíferos endémicos que las componen. Los artículos “Boundaries of the Neotropical region based on areas of endemism of mammals (Noguera-Urbano y Escalante 2017)” y “Phylogenetical and ecological relationships into the Neotropical areas of endemism (Noguera-Urbano y Escalante Enviado)” indican que existen múltiples límites de la región Neotropical. Además, el patrón general de superposición de AE a nivel de región biogeográfica y la diversidad filogenética (DF) de las especies endémicas, tienen una tendencia positiva con la latitud desde la línea ecuatorial hacia el norte del Neotrópico y una tendencia negativa desde la línea ecuatorial hacia el sur del Neotrópico. Esto corresponde con patrones macroecológicos propuestos para explicar la relación entre la riqueza de especies y la latitud, principalmente explicados por las altas tasa de colonización de los mamíferos en los trópicos, bajas tasas de extinción, múltiples eventos de dispersión, alta estabilidad climática, alta productividad y heterogeneidad espacial (Pianka 1966; Antonelli y Sanmartín 2011; Rolland et al. 2014). Por otra parte, existe agrupamiento filogenético de los mamíferos endémicos a nivel de región, lo cual indica hay una integración especial y filogenética de ellas. Esto posiblemente causado por procesos tales como especiación *in situ*, conservadurismo de nicho ecológico (Cardillo 2008, 2011) y especialización de linajes (Cantalapiedra et al. 2014), ya que las especies endémicas que caracterizan a la región Neotropical en este estudio, son principalmente murciélagos que evolucionaron en el Neotrópico (Teeling et al. 2005). Los resultados indican que la integración de los mamíferos endémicos en la región Neotropical posiblemente se ha realizado de manera asincrónica, ya que algunas especies endémicas se han expandido desde los trópicos hacia el norte y sur de la región Neotropical, otras desde América del Norte-América Central y las Antillas hacia el Neotrópico. Aunque el endemismo no predice totalmente la distribución geográfica ancestral de las especies endémicas, el 76% de las especies endémicas evolucionaron en América del Sur. Esto revela que el endemismo basado en congruencia espacial representa una integración asincrónica de linajes. Este capítulo sugiere que las especies endémicas se encuentran desagrupadas en la filogenia por lo tanto su congruencia espacial podría deberse a su respuesta similar a barreras ecológicas y fisiográficas comunes.

Capítulo III. Este capítulo está enfocado en analizar otras dos dimensiones de las áreas de endemismo. La primera dimensión que se analiza es la ecológica, para lo cual se discute la relación que existe entre las áreas de endemismo y los factores bioclimáticos. La segunda dimensión que se analiza es la histórica, al proponer una síntesis sobre la integración espacial y temporal de las especies endémicas. Los manuscritos "Environmental factors related to biogeographical transition zones of Neotropical mammals' areas of endemism", de Noguera-Urbano y Ferro (2017) y "Areas of endemism: travelling through space and the unexplored dimension" de Noguera-Urbano (2016), indican que las áreas de endemismo son unidades biogeográficas que también están afectadas por los factores climáticos. Por ejemplo, las áreas de endemismo que se encuentran en las Zonas de Transición Mexicana y Sudamericana (ZTM y ZTS), están afectadas por la isotermalidad, la precipitación del trimestre más frío, la precipitación del trimestre más cálido y la heterogeneidad topográfica. Mientras que aquellas AE que hacen parte de la Zona de Integración del Bosque Atlántico (entre dominios Paranaense y Chaqueño), están afectadas por variables como la precipitación del trimestre más cálido, el intervalo de temperaturas diurnas y la heterogeneidad topográfica. Lo anterior demuestra que las dos grandes zonas de transición están influenciadas por condiciones climáticas similares. Para las tres áreas, la estructura espacial es un predictor importante del endemismo, lo cual indica que hay una fuerte influencia de procesos geológicos que han estructurado el paisaje de las áreas de endemismo en las tres zonas. La dimensión histórica de las AE se describe en el manuscrito "Areas of endemism: travelling through space and the unexplored dimensión" (Noguera-Urbano 2016). Dado que las áreas de endemismo son unidades biogeográficas que responden a la evolución geológica, históricos y las variaciones del clima, las especies se integran temporalmente de manera sincrónica o asincrónica, dependiendo de su tiempo de evolución y la dinámica de sus áreas de distribución. Las áreas de endemismo pueden considerarse 'fotografías' actuales e históricas de patrones de integración temporal y espacial de las especies, las cuales se modifican al expandirse la distribución geográfica de una o más especies que la constituyen, pero también si esas especies se extinguen, o cuando las áreas de distribución se modifican por la dinámica interna de sus poblaciones. Es decir, las AE son afectadas tanto por factores ecológicos, como biológicos y filogenéticos de las especies endémicas, lo cual supone que las áreas de endemismo son dinámicas y evolucionan a lo largo del tiempo.

Las conclusiones que se obtuvieron durante el desarrollo de la presente tesis pueden permitir trazar nuevas líneas de investigación y cuestionamientos para el avance del conocimiento acerca de las áreas de endemismo y sus especies endémicas.

CAPÍTULO I. CONGRUENCIA ESPACIAL DE LAS ESPECIES ENDÉMICAS

I.I El endemismo: diferenciación del término, métodos y aplicaciones.

I.II Dynamism of the areas of endemism in neotropical mammals: differential effects of historical and ecological factors (Enviado *Journal of Biogeography*).

ISSN 0065-1737 ActaZoológicaMexicana (NUEVA SERIE) 33(1) 2017

Ensayo
Essay

EL ENDEMISMO: DIFERENCIACIÓN DEL TÉRMINO, MÉTODOS Y APLICACIONES

ENDEMISM: DIFFERENTIATION OF THE CONCEPT, METHODS AND APPLICATIONS

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Recibido: 08/04/2016; aceptado: 12/01/2017
Editor responsable: Octavio Rafael Rojas Soto

Noguera-Urbano, E. A. (2017) El endemismo: diferenciación del término, métodos y aplicaciones. *Acta Zoológica Mexicana (n. s.)*, 33(1), 89-107.

RESUMEN. El endemismo es un concepto comúnmente usado para identificar a taxones nativos o grupos biológicos con área de distribución restringida. Sin embargo, el endemismo tiene diferentes interpretaciones de acuerdo a la aproximación usada para los análisis biogeográficos (ecológico o histórico). Los múltiples usos del endemismo han llevado a proponer otros conceptos relacionados con las áreas geográficas ocupadas por los taxones endémicos (área endémica, área de endemismo, centro de endemismo). En algunos casos los resultados de las técnicas y protocolos usados para evaluar el endemismo son malinterpretados, ya que en la literatura los tres términos son usados como sinónimos. En este orden de ideas, esta revisión discute el concepto de endemismo y su aplicación en múltiples campos del conocimiento. Además, se comparan y discuten las técnicas y protocolos usados para evaluar el endemismo. Se concluye que es necesario el uso de un concepto unificado del endemismo, lo cual podría facilitar su interpretación tanto en ecología como en conservación y biogeografía.

Palabras clave: Biogeografía, Conservación, distribución restringida, endémico, Ecología.

Noguera-Urbano, E. A. (2017) Endemism: differentiation of the concept, methods and applications. *Acta Zoológica Mexicana (n. s.)*, 33(1), 89-107.

ABSTRACT. Endemism is a concept commonly used to identify native taxa or biological groups with restricted range. However, the endemism has different interpretations according to the approach used in the biogeographic analysis (ecological or historical). The multiples interpretations of endemism have led to propose other concepts related with the geographical areas occupied by the endemic taxa (endemic area, area of endemism, center of endemism). In some cases, the results of the technics and protocols used to evaluate the endemism are misinterpreted because in the literature endemic area, area of endemism and center of endemism are used as synonyms. In this order of ideas, this review discusses the concept of endemism, and its application in multiples knowledge fields. The technics and protocols to evaluate the endemism are discussed and compared. It is concluded that it is necessary to use a unified concept of endemism, which could facilitate the interpretation of the endemism in ecology, conservation and biogeography.

Key words: Biogeography, Conservation, Ecology, endemic, restricted range.

¿QUÉ ES EL ENDEMISMO?

La importancia del endemismo radica en la necesidad de conocer y proteger los atributos biológicos e historia evolutiva que representan los taxones endémicos y sus patrones biogeográficos. El endemismo toma un valor ecológico e histórico, si se considera que define zonas geográficas donde hay taxones integrados espacio-temporalmente (Nelson & Platnick 1981; Stattersfield *et al.* 1998; Morrone 2009).

La palabra "endémico" proviene del griego "*endēmios* = nativo". Fue transferido por Candolle (1820) desde la medicina a la botánica para indicar taxones nativos que se distribuyen en un lugar y no en otro (Anderson 1994; Hobohm & Tucker 2014). Aunque los variados usos y aplicaciones del endemismo han ocasionado confusiones en su interpretación (Anderson 1994), las definiciones coinciden en que el "endemismo" es una implicación de restricción geográfica.

Es evidente que para aplicar el término "endemismo" se necesita relacionar un área geográfica de restricción, ya que el endemismo es dependiente de la escala geográfica del área en la que se distribuya el taxón (Cracraft 1985). Por ejemplo, el área de distribución del jaguar (*Panthera onca* [Linnaeus 1758]) se extiende desde México hasta el norte de Argentina (Caso *et al.* 2008), por lo tanto esta especie se puede considerar endémica del Neotrópico (Fig. 1). En otro caso el mapache pigmeo (*Procyon pygmaeus* Merriam 1901), restringido a la Isla de Cozumel en México, es endémico para esa isla (Cuarón *et al.* 2008) (Fig. 1). En comparación con el jaguar, el mapache pigmeo presenta una distribución reducida a sólo una parte del Neotrópico. Por lo tanto, cada una de las especies es endémica dentro del área geográfica con la que se relaciona su distribución, Neotrópico e Isla de Cozumel, respectivamente.

ENFOQUES EN LA APLICACIÓN DEL CONCEPTO

Los múltiples usos y aplicaciones del "endemismo" tienen como base la definición de Candolle (1820), al tomar a la unicidad geográfica para cualificar a un taxón como endémico. Las variantes del concepto son propuestas para la formalización de la relación entre la evolución de un taxón y su área de distribución, o la necesidad de un criterio práctico para definir objetos y/o áreas prioritarias de conservación. Por lo tanto, mantener el sentido que le dio Candolle (1820) al endemismo debería primar en las aplicaciones biogeográficas para todo tipo de organismos. Y cuando sea posible, se deberían emplear unidades geográficas naturales (ecosistemas, cuencas, provincias biogeográficas, regiones biogeográficas, etc.) en los análisis relacionados con el endemismo. Con ello se lograría usar un mismo contexto teórico del endemismo y se aclararía la combinación del "endemismo" con otros términos.

En algunos casos el endemismo ha sido interpretado con base en la rareza de poblaciones o comunidades (Major 1988), esto debido al conocimiento incompleto de las áreas de distribución (Kruckeberg & Rabinowitz 1985). La aplicación del concepto ha cambiado para ser aplicado a taxones (especies, géneros, familias, etc.), debido al progresivo aumento de los sitios de colecta y el desarrollo de hipótesis sobre áreas de distribución. Desde hace unos años el endemismo se relaciona con taxones restringidos a una sola área geográfica o que presentan área de distribución reducida (Polunin 1960; Anderson 1994; Peterson & Watson 1998). Pese a ello, una de las críticas en los procedimientos para la definición de los taxones endémi-

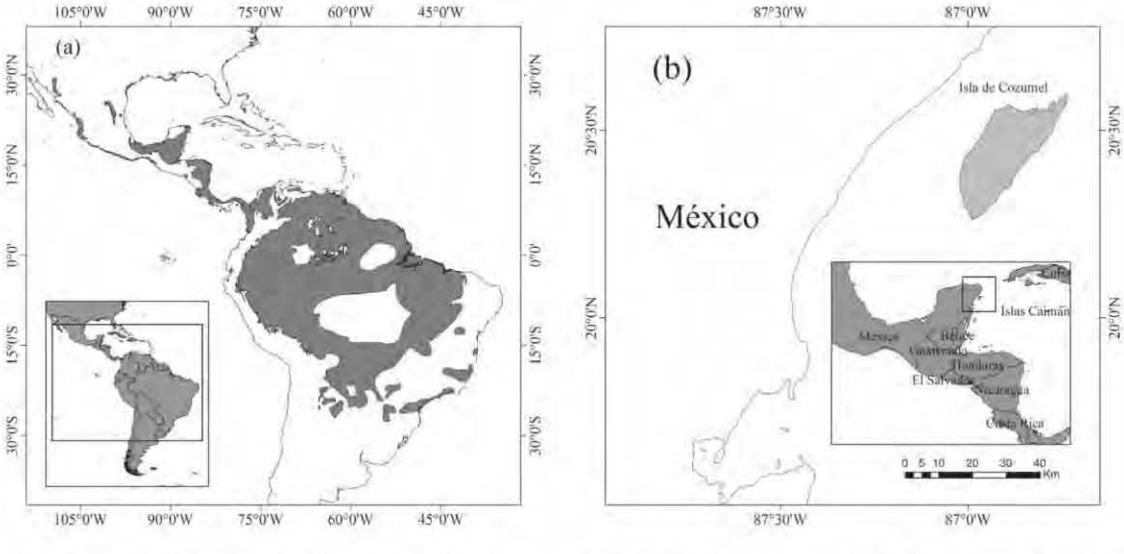

Figura 1. Endemismo a diferentes escalas y diferentes límites geográficos. (a) Distribución geográfica del jaguar (*Panthera onca*) y (b) mapache pigmeo (*Procyon pygmaeus*). Cada una de las especies es endémica al área geográfica de referencia, el jaguar al Neotrópico y el mapache pigmeo a la Isla de Cozumel. En cada área geográfica que se tome como referencia hay uno o más taxones que pueden ser considerados endémicos.

cos fue la ausencia de un criterio práctico (Stattersfield *et al.* 1998; Bruchmann & Hobohm 2014). En este contexto, se han propuesto múltiples enfoques para determinar el criterio de restricción y/o relacionar el endemismo con la evolución de los taxones.

El endemismo en ecología y conservación ha sido usado como distribución restringida (*restricted-range*) y para definir a las especies endémicas se ha empleado un tamaño de área geográfica como límite práctico (Stattersfield *et al.* 1998). Por ejemplo, una especie con un área de distribución menor a 100,584 km^2 (250 millas en cualquier dirección) (Hall & Moreau 1962); 50,000 km^2 (área de distribución sin aumentos desde el año 1,800) (Terborgh & Winter 1983; Stattersfield *et al.* 1998) o 10,000 km^2 (Kier & Barthlott 2001; Bruchmann & Hobohm 2014) tendrá una distribución restringida (Terborgh & Winter 1983; Stattersfield *et al.* 1998) (Fig. 2). De la aplicación del endemismo bajo el criterio de distribución restringida resultan, por ejemplo, lugares de conservación conocidos como Áreas de Aves Endémicas (*Endemic Birds Areas*; EBA). Las Áreas de Aves Endémicas son zonas en las cuales dos o más especies cohabitan y presentan áreas de distribución menores a 50,000 km^2 (Stattersfield *et al.* 1998). Por otra parte la flexibilidad del criterio de restricción ha llevado a que los límites administrativos de un país u otras áreas puedan ser usados para definir taxones endémicos (Ceballos *et al.* 1998; González-García & Gómez de Silva 2003). En el caso de plantas mexicanas, se ha propuesto que especies con áreas de distribución menores, similares o levemente mayores a los límites geopolíticos de México, sean consideradas endémicas (Rzedowski 1991). El endemismo basado en restricción a un país toma un gran valor para los análisis de riqueza de especies y su conservación. De ello resultan otras interpretaciones para definir especies endémicas. Por ejemplo, en México se consideran 157 especies de mamíferos como endémicas (28%, total: 564 especies) (Sánchez-Cordero *et al.* 2014) y en Colombia 42 especies (8.6%, total: 500 especies) (Solari

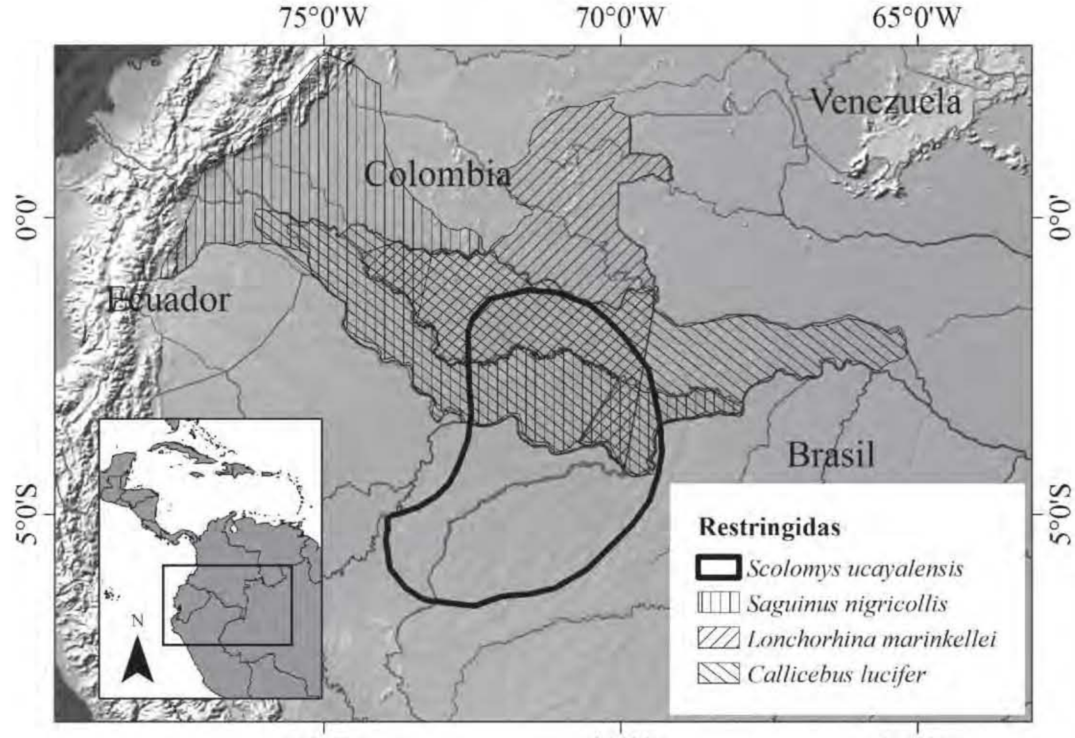

Figura 2. Mapas de distribución de cuatro especies de mamíferos considerados como especies restringidas por tener un área menor a 50,000 km^2. De acuerdo con este criterio, las cuatro especies pueden ser consideradas endémicas. El primate *Callicebus lucifer* Thomas, 1914 cumple con los criterios de endemismo de área restringida y restricción dentro de los límites administrativos de un país (Colombia); por lo tanto, es endémico de la Amazonía colombiana y endémico de Colombia.

et al. 2013). Ambos casos representan especies endémicas usando el criterio de restricción dentro del país. No obstante, en México se consideró una clasificación de los mamíferos endémicos restringidos y ampliamente distribuidos. Los mamíferos endémicos restringidos presentaban áreas menores a 50,000 km^2 y los confinados dentro de México fueron considerados endémicos ampliamente distribuidos (Ceballos *et al.* 1998).

VARIANTES DEL ENDEMISMO

Una interpretación adicional del endemismo fue propuesta por González-García & Gómez de Silva Garza (2003), quienes consideran que las especies endémicas pueden ser categorizadas en cuasiendémicas y semiendémicas. Las especies cuasiendémicas "son aquellas que penetran ligeramente a algún país vecino debido a la continuidad de los hábitat o sistemas orográficos". Por otra parte, las especies semiendémicas se definen como "las especies que son endémicas a un país o a una región durante una época del año" (González-García & Gómez de Silva 2003). Las anteriores variaciones del "endemismo" coinciden con la propuesta de la Unión Internacional para la Conservación de la Naturaleza, con base en la restricción y nativo de una isla pequeña, de un país o de un continente (UICN 2012).

Por otra parte se ha intentado relacionar el endemismo con la historia de los taxones y su distribución. Se ha propuesto el paleoendemismo para definir a los taxones antiguos y restringidos a un área geográfica (Prentice 1976; Major 1988), los cuales inicialmente tuvieron amplias áreas de distribución (Malik 2015). Son taxones sistemáticamente aislados, tales como géneros representados por una única especie. Sus áreas de distribución representan remanentes de áreas de distribución amplias, pero que se han reducido por ejemplo a causa de variaciones climáticas. Desde la perspectiva filogenética los taxones paleoendémicos son taxones que divergieron muy temprano y tienen distribuciones que se superponen con formaciones geológicas antiguas (Ferreira & Boldrini 2011).

En otro lugar está el neoendemismo para los taxones recientes y restringidos (Prentice 1976). Son taxones extremadamente divergentes, con sus distribuciones que se traslapan con formaciones geológicas recientes (Ferreira & Boldrini 2011). Se considera que este tipo de taxones podrían estar listos para expandir sus áreas de distribución y también sus genes (Kruckeberg & Rabinowitz 1985), debido a que en plantas resultan de procesos de hibridación con la consecuente poliploidía. Lo cual les confiere adaptación divergente a diferentes condiciones ambientales (Malik 2015).

La desventaja en la aplicación de los términos paleoendemismo y neoendemismo es que estos son relativos a las edades de los taxones dentro del grupo de comparación. Por ejemplo, según Noguera-Urbano & Escalante (2015) en los Andes del Norte hay cinco especies de mamíferos endémicos (*Thomasomys aureus* [Tomes 1860], *Cuniculus taczanowskii* [Stolzmann 1865], *Didelphis pernigra* J.A. Allen 1900, *Marmosops impavidus* Tschudi 1845 y *Monodelphis adusta* [Thomas 1897]). Los cuales están estrechamente relacionados a la evolución de los Andes. Al comparar las edades de las cinco especies, la zarigüeya *M. impavidus* (2.5 Ma) (Jansa *et al.* 2013) con la menor edad sería neoendémica, mientras que la zarigüeya de cola corta *M. adusta* (20.5 Ma.) (Vilela *et al.* 2015) con la mayor edad podría ser considerada paleoendémica (Fig. 3). Sin embargo, al hacer la comparación entre dos de las cinco especies, el ratón *T. aureus* (3.1 Ma) (Parada *et al.* 2015) sería neoendémica y la paca *C. taczanowskii* (3.8 Ma) (Upham & Patterson 2012) sería paleoendémica.

En botánica se propuso una clasificación que relaciona el endemismo con la edad de los taxones, inferida a partir del conjunto de cromosomas (Contandriopoulos 1962; Major 1988). En dicha clasificación se asume que las plantas endémicas con baja ploidía (conjunto de cromosomas), posiblemente divergieron más tempranamente que los que presentan alta ploidía (Favarger & Contandriopoulos 1961; Bruchmann & Hobohm 2014). Favarger y Contandriopoulos (1961) propusieron que los paleoendémicos y patroendemismos son los grupos antiguos, mientras que los apoendémicos y esquizoendémicos son los jóvenes o recientes. La poliploidía puede provocar la formación de nuevas especies, así el patroendemismo define a las plantas diploides cuyos progenitores son poliploides que presentan distribución amplia (Fig. 4). El apoendemismo define a plantas poliploides derivadas de diplodes ampliamente distribuidos (Fig. 4) y esquizoendemismo para las plantas cuyo número de cromosomas se ha conservado (ploidía) (Fig. 4) (Contandriopoulos 1962; Major 1988).

Aunque la evolución cromosómica es una estrategia evolutiva muy importante en plantas y otros grupos, se poco claro cómo la ploidía aporta en la definición de endemismo (Bruchmann & Hobohm 2014). Por ejemplo las especies de plantas *Allium dirphianum* Brullo & al., *A. calamarophilon* Phitos & Tzanoukadis, *Asperula euboea*, *Campanula constantini* Beauverd & Topali, *C. cymaea*

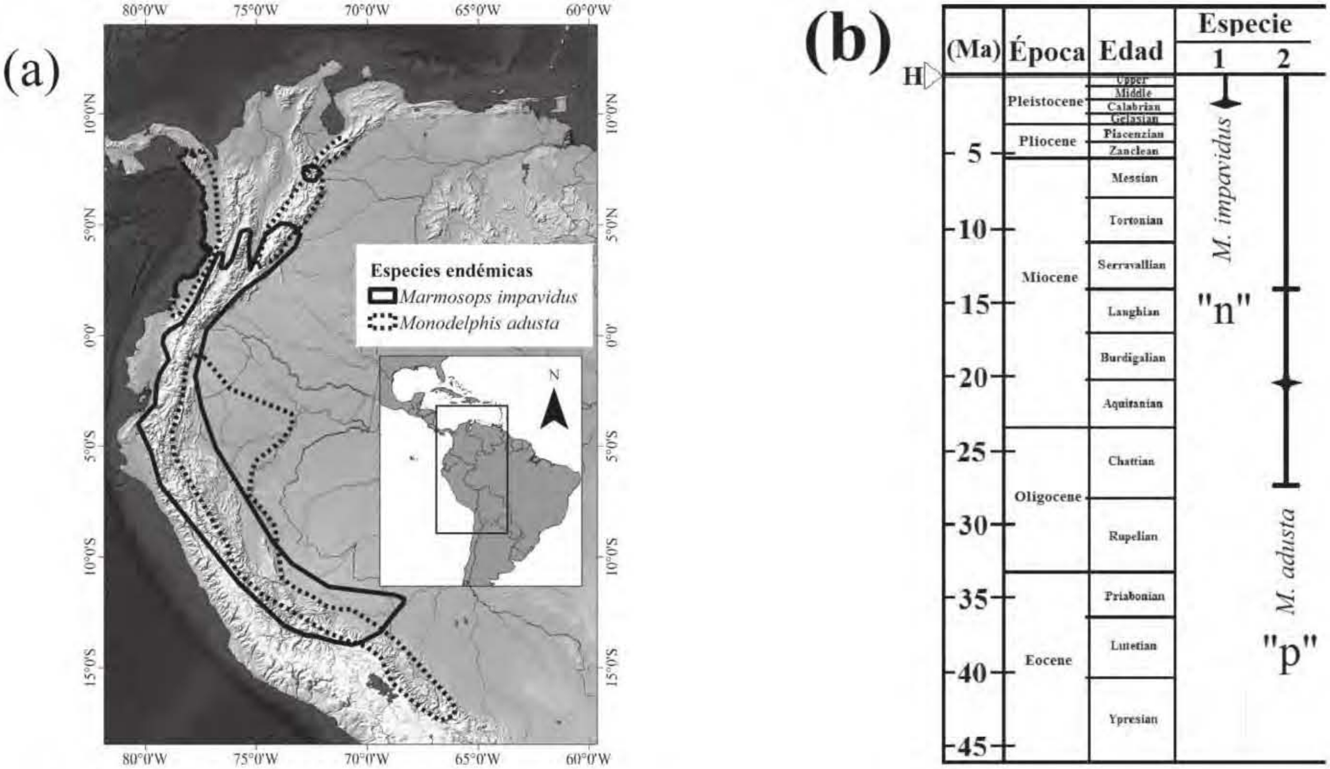

Figura 3. Aplicación del neoendemismo (n) y paleoendemismo (p) a dos especies de mamíferos andinos. (a) Mapas de distribución de las dos especies. (b) Tiempo aproximado de divergencia de las dos especies. H = Holoceno, Modificado de Noguera-Urbano 2016.

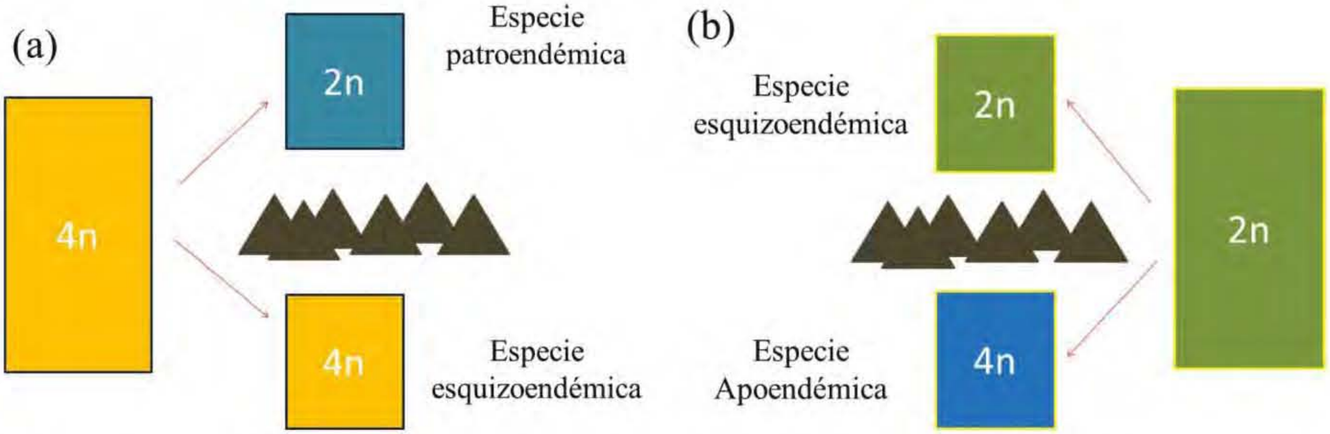

Figura 4. Esquemas que representan los tipos de endemismo de acuerdo con la evolución cromosómica de plantas. (a) Especie poliploide ampliamente distribuida. (b) Especie diploide ampliamente distribuida. Los rectángulos y cuadros representan áreas de distribución hipotéticas, los cuales cambian de tamaño por un evento de vicarianza (triángulos). n= número de cromosomas.

Phitos, *Chaerophyllum euboeum* Halácsy e *Hypericum fragile* Heldr. & Sart son consideradas endémicas de la las Islas del oeste del Egeo (Trigas & Iatrou 2006). A la vez *A. calamarophilon*, *Asperula euboea*, *Campanula constantini* y *C. cymaea* están clasificadas como esquizoendémicas (Trigas & Iatrou 2006).

Al momento la clasificación del endemismo con base en los cromosomas ha sido superada por clasificaciones basadas en el tiempo y el lugar de divergencia. De ello resulta que se haya relacionado el concepto de endemismo con el sitio de evolución de las especies (van Steenis 1964; Merckx *et al.* 2015). Se considera el "endemismo céntrico" para definir a las especies endémicas que han tenido una evolución *in situ* (Fig. 5) (Merckx *et al.* 2015) y el "endemismo excéntrico" es usado para las especies que han migrado de sus sitios de divergencia (Merckx *et al.* 2015) (Fig. 5). En un sentido práctico de los anteriores conceptos, Merck *et al.* (2015) definieron como endémicas a aquellas especies con poblaciones restringidas a su área de muestreo (Parques Kinabalu y Crocker Range en Malasia) y relacionaron el sitio de dispersión tomando como base de comparación el piso altitudinal que ocupan la especie endémica y su congénere cercana (Merckx *et al.* 2015). Los autores concluyeron que las especies endémicas en estudio, pueden evolucionar en el sitio actual de desarrollo o a partir de áreas vecinas (Merckx *et al.* 2015).

Una propuesta que ha sido levemente discutida es la de aplicar el endemismo según el concepto de especie de referencia (González-García & Gómez de Silva 2003); por ejemplo el "endemismo biológico" toma en cuenta el concepto biológico de especie (Dobzhansky 1935; Mayr 1942), en el cual es posible reconocer subespecies endémicas; y el "endemismo filogenético" se basa en el concepto filogenético (Cracraft 1989). Con la aplicación del concepto filogenético de especie muchas subpoblaciones consideradas como subespecies con el concepto biológico de especies, pasan a ser especies. Por lo tanto, con el endemismo filogenético, sólo se reconocen especies endémicas (González-García & Gómez de Silva 2003). Considero que la definición de los taxones con base en linajes, grupos monofiléticos, etc. contribuyen a la cuantificación del endemismo, no obstante, la diferenciación de los dos tipos de endemismo aporta poco a la base conceptual del endemismo, la cual sigue siendo la restricción geográfica a un área. Por otra parte, para las especies extintas la información filogenética puede ser incompleta o ausente. Así el endemismo filogenético de González-García y Gómez de Silva (2003) se vuelve impráctico. Si se toma el endemismo para considerar subespecies, como es el caso de taxones fósiles, el único criterio empleado es la restricción a un área geográfica determinada. Por ejemplo el ciervo siciliano *Cervus elaphus siciliae* es una subespecie endémica de Sicilia, registrada a partir de depósitos del Pleistoceno medio en Sicilia (Mangano 2005).

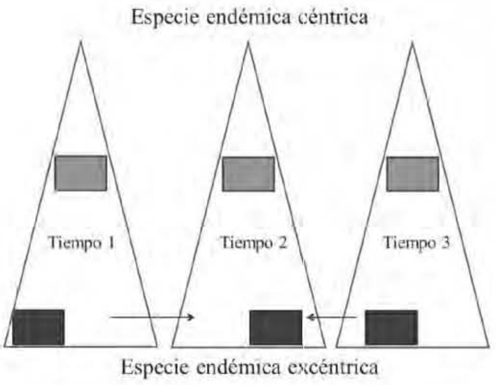

Figura 5. Representación esquemática del endemismo céntrico y excéntrico. El triángulo representa un área geográfica, mientras que los rectángulos indican las áreas de distribución de dos especies. En la especie endémica excéntrica las flechas indican la movilidad de la distribución desde el tiempo de divergencia (Tiempo 1) hasta el Tiempo 3, cuando la especie se acerca parcialmente a su sitio de divergencia.

La necesidad de integrar múltiples dimensiones de la diversidad biológica en la interpretación del endemismo, ha llevado a que se interprete el termino dentro de un contexto filogenético. En este sentido Faith *et al.* (2004) propusieron el endemismo filogenético (EF) con base en la diversidad filogenética (DF), para representar la historia evolutiva singularmente representada por un conjunto de taxones en un área geográfica (Faith *et al.* 2004). Aunque Faith *et al.* (2004) fueron ambiguos en su definición, Rosauer *et al.* (2009) incluyen a la restricción geográfica como determinante del endemismo filogenético, una medida filogenética de endemismo absoluto. Una ventaja del endemismo filogenético es que permite incluir directamente datos filogenéticos para la interpretación de patrones espaciales del endemismo.

ÁREA ENDÉMICA, ÁREA DE ENDEMISMO Y CENTRO DE ENDEMISMO

La aplicación del endemismo ha llevado a crear otros términos relacionados: el área endémica, el centro de endemismo y el área de endemismo. Inicialmente la presencia de un taxón endémico permitió caracterizar a una zona geográfica como área endémica (Polunin 1960; Nelson & Platnick 1981; Rosen 1988; Axelius 1991; Parenti & Ebach 2009). Polunin (1960) (p. 205) afirma que "un área endémica es el área de una especie u otro taxón que, en su distribución, se limita a cierta región natural o hábitat únicos por causas históricas y/o ecológicas". En este contexto un taxón endémico presentaba un área endémica, así que cualquier taxón nativo y restringido podía ser endémico a alguna área (Anderson 1994). El endemismo es relativo al área geográfica que se tome para la comparación (Cracraft 1985), así que un "área endémica" podía ser un concepto equivalente al área de distribución (Polunin 1960).

La puesta en práctica del endemismo en estudios ecológicos y conservación, ha requerido generalizar el área endémica para describir zonas habitadas por varias especies endémicas restringidas. De modo que la superposición, recurrencia o concentración de áreas de distribución de especies endémicas definen a un patrón de endemismo. Por ejemplo un área de aves endémicas será aquella área ocupada por varias especies con distribuciones restringidas (menores a 50,000 km^2) (Stattersfield *et al.* 1998). Desde esta perspectiva el área endémica revisada por Polunin (1960) toma otro sentido en conservación, al representar un patrón de endemismo conformado por varias especies restringidas y que se codistribuyen sólo en esa área.

Por otra parte, un área de endemismo es una zona geográfica definida por la congruencia espacial de las áreas de distribución geográfica de dos o más especies (Platnick 1991; Espinosa *et al.* 2001; Noguera-Urbano 2016). La congruencia espacial es explicada por procesos diferentes al azar (Morrone 1994) y representa la integración de los taxones en el espacio y tiempo en estratos temporales (Fig. 6) (Noguera-Urbano 2016). Tanto las áreas endémicas de Stattersfield *et al.* (1998) como las áreas de endemismo representan patrones de endemismo definidos por límites geográficos, sin embargo las áreas de endemismo pueden presentar cualquier tamaño en su área. De acuerdo a lo anterior se podrían tomar algunos conceptos como equivalentes. Es decir, si el endemismo de Candolle (1820) en el contexto histórico define el "área endémica" como aquella área donde se encuentra un taxón endémico, el "área endémica" (Polunin 1960) estaría representando una unidad geográfica similar a la de Candolle. Para generalizar el uso de los términos y evitar malas interpretaciones sobre el endemismo, considero que se debería homologar los conceptos de Candolle (1820) y Polunin (1960) para área endémica, mientras que se podría generalizar el uso de "áreas de endemismo" para definir los patrones de endemismo.

Otra manera de representar el endemismo son los centros de endemismo (Crisp *et al.* 2001; Linder 2001a). Los centros de endemismo son sitios con alta concentración de especies que presentan áreas de distribución restringida (Williams *et al.* 1996; Crisp *et al.* 2001; Linder 2001b). El supuesto de los centros de endemismo es que las áreas de distribución de los taxones restringidos se superponen unas sobre otras y que los patrones de endemismo que conforman se traslapan unos sobre otros en la naturaleza (Crisp *et al.* 2001). Sin embargo, se ha propuesto que es difícil comprobar que los taxones sean endémicos a los centros de endemismo, o que las distribuciones de las especies tengan congruencia espacial (Linder 2001a).

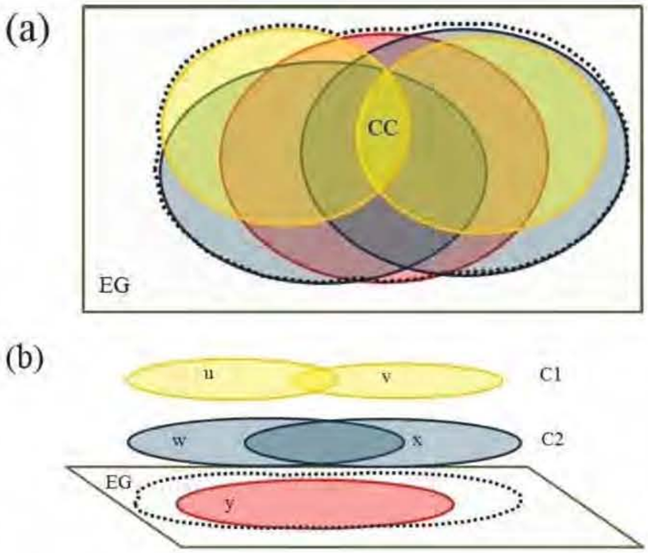

Figura 6. Modelo simplificado de un área de endemismo. (a) Vista actual de las áreas de distribución integradas en el espacio-tiempo. (b) Como se verían las distribuciones separándolas con respecto a la edad de los taxones endémicos. Se indica el espacio geográfico (EG) con el cual se referencia el área de endemismo, un centro de congruencia (CC), especies endémicas (u, v, w, x, y, z) y dos cenocrones o estratos temporales (C1, C2). Modificado a partir de Noguera-Urbano (2016).

Desde mi punto de vista, los tres términos relacionados con endemismo: área endémica (según Stattersfield *et al.* 1998), centro de endemismo y área de endemismo, toman en cuenta que las áreas de distribución de los organismos proveen información sobre la relación compleja entre los ambientes físicos y los atributos biológicos de los organismos. Sin embargo, emplean criterios diferentes para delimitar el endemismo. Las áreas endémicas y los centros de endemismo se basan en la restricción a un área de tamaño y límites arbitrarios, mientras que las áreas de endemismo se basan en la superposición de las áreas de distribución geográfica.

Con respecto a la integración evolutiva de los taxones, Linder (2001a) ha mencionado que en los centros de endemismo los taxones presentan historias múltiples y que las áreas de endemismo contienen biota con historia única. En mi opinión, en las áreas endémicas según Stattersfield *et al.* (1998), los centros de endemismo y las áreas de endemismo, los taxones se encuentran integrados en el espacio, pero tienen múltiples historias. Pero en algunos casos los taxones pueden conformar subgrupos y tener historias compartidas en el tiempo. Por ejemplo en el área de endemismo Andina la integración de los taxones endémicos ha ocurrido en diferentes tiempos en la evolución de América del Sur, pero todos han sido afectados por el levantamiento de los andes y la orogenia de la zona (Fig. 6) (Noguera-Urbano 2016).

Se considera que las áreas de endemismo y los centros de endemismo pueden ser representados valorando tanto la concentración de las áreas de distribución de las especies endémicas (continuidad del patrón de endemismo) como sus límites geográficos (Cracraft 1985; Anderson 1994; Crisp *et al.* 2001; Noguera-Urbano 2016). En una perspectiva integradora de los dos conceptos "centros y áreas de endemismo", se podría considerar que las áreas de endemismo al tener un centro de congruencia con valores máximos de endemismo (Fig. 6) (Noguera-Urbano 2016), podrían contener centros de endemismo. En un área de endemismo los centros de endemismo estarían conformados por la alta congruencia de las especies endémicas. Además, las áreas de endemismo pueden estar superpuestas conformando diferentes estratos de integración temporal, estratos temporales (Fig. 6), y estarían representando historias múltiples como los centros de endemismo.

MÉTODOS DE CUANTIFICACIÓN DEL ENDEMISMO Y PATRONES BASADOS EN RESTRICCIÓN

Una vez definidas las especies distribuidas en algún área geográfica, es posible aplicar diferentes tipos de descriptores para cuantificar el endemismo (Apéndice I) e identificar áreas de endemismo (Apéndice II). La cuantificación del endemismo se relaciona con la estimación de la riqueza de taxones endémicos por unidad de área (país, provincias, celdas) con el objetivo de hacer comparaciones, conocer la distribución del endemismo en un área geográfica, evaluar la correlación del número de especies endémicas con la riqueza de especies o dirigir esfuerzos de conservación. Por otra parte, la identificación de áreas de endemismo se dirige a conocer y describir patrones evolutivos con base en las distribuciones de las especies, en ellas se toma como argumento teórico que la tierra y la biota evolucionaron juntos. Con los métodos de identificación de áreas de endemismo se busca proponer hipótesis biogeográficas que puedan ser interpretadas para explicar la integración espacio-temporal de las especies endémicas.

En los métodos usados para cuantificar el endemismo se aplica el endemismo como "distribución restringida" (Apéndice I). Estos métodos son sencillos en su aplicación, pero pueden ser poco útiles en la comparación entre regiones de diferente tamaño (Major 1988). Por ejemplo la estimación de la Riqueza de endemismo y Proporción de endemismo son medidas directas del número de especies endémicas dentro de un área o con relación a un área respectivamente (Apéndice I). Ambas métricas brindan poca información sobre el área de distribución de las especies y no toman en cuenta el tamaño de las unidades de comparación (Kier & Barthlott 2001).

Otros métodos como el Índice de Bykow (Major 1988; Hobohm & Tucker 2014), la densidad de endemismo (Hobohm & Tucker 2014) y la relación área-endemismo (Major 1988; Harte & Kinzig 1997; Hobohm & Tucker 2014) son empleados para evaluar la concentración de endemismos entre unidades geográficas (continentes, países, celdas, etc.). Los tres índices incluyen en sus ecuaciones el tamaño de las áreas de distribución y el área geográfica analizada (Apéndice I), no obstante, su interpretación se debe realizar con cuidado, ya que el supuesto básico es que las especies están bien muestreadas en el área de estudio (Kier & Barthlott 2001). En el caso de la densidad de endemismo y la relación área-endemismo su aplicación se vuelve poco práctica, cuando las áreas en comparación tienen tamaños diferentes (Hobohm & Tucker 2014).

La selección de taxones endémicos con criterios arbitrarios y basados en un valor absoluto del endemismo, son factores condicionantes al momento de estudiar y comparar sitios de interés. Así que se desarrollaron índices para la evaluación de la distribución espacial del endemismo y la identificación de sitios de alta concentración de endemismos (Apéndice I), los cuales son representados en mapas de endemismo. Los patrones de concentración de especies endémicas fueron denominados como áreas de rareza (Williams *et al.* 1996) o centros de endemismo (Crisp *et al.* 2001; Linder 2001a), los cuales son conceptos equivalentes, si se toma en cuenta que representan concentraciones de sitios con los mayores valores de endemismo (Williams *et al.* 1996; Crisp *et al.* 2001; Linder 2001b).

Para la identificación de centros de endemismo fueron desarrollados los índices de Endemismo Ponderado (WE) y Endemismo Ponderado Corregido (CWE), que toman como unidad de comparación celdas de una gradilla (Apéndice I). El CWE es una modificación del WE, con el cual se busca disminuir la correlación entre la riqueza de especies y el endemismo (Crisp *et al.* 2001; Linder 2001b). El CWE facilita la identificación de centros de endemismo pobres en especies (Crisp *et al.* 2001), pero en sitios con bajo muestreo de especies ampliamente distribuidas el índice puede resultar inflado (Slatyer *et al.* 2007).

Otra modificación al WE, denominada Riqueza de endemismo (Cs), fue propuesta por Kier & Barthlott (2001) con el objetivo de generalizar el índice para cualquier tipo de UGO (gradillas, corotipos, biomas, ecoregiones, etc.). En este índice se considera que cada especie contribuye al inventario general del área, se incluye el tamaño del área de distribución y su valor complementario dentro del área estudiada como factores de la formula (Apéndice I). Los tres métodos coinciden en descartar el uso de un criterio a priori para identificar a las especies endémicas (Williams *et al.* 1996; Lovett *et al.* 2000).

En búsqueda de aumentar el peso de las especies endémicas en los índices, se ha propuesto el uso de ventanas (v.g. 3x3 celdas) para estimar el endemismo. Sobre las ventanas de análisis se calcula el índice WE y su valor se relativiza con la riqueza de especies por ventana (Slatyer *et al.* 2007). Laffan, Lubarsky & Rosauer (2010) propusieron otros cambios a los índices WE y CWE. Algunos índices del endemismo se encuentran disponibles en el programa *Biodiverse* (Laffan *et al.* 2010), incluyendo los WE y CWE normalizados con el número de celdas que componen el área de estudio (Apéndice I). Otras aplicaciones incluyen la identificación de endemismo con el uso de ventanas para diferentes niveles taxonómicos (orden, familia, género) en el llamado Endemismo Completo con Partición Jerárquica (Laffan *et al.* 2013) (Apéndice I), bajo el supuesto que cada nivel taxonómico contribuye al endemismo de un taxón.

A partir del concepto de endemismo filogenético de Rosauer *et al.* (2009), se han propuesto índices que integran la diversidad filogenética y los índices WE y CWE, por ejemplo el Índice de Endemismo Filogenético (EF) (Apéndice I). El EF representa la cantidad de diversidad filogenética de un taxón o clado restringido a un área geográfica con base en dos criterios (Rosauer *et al.* 2009): a) mide la variación del endemismo a través de cada unidad (celdas) dentro del área de estudio; y b) integra todos los niveles filogenéticos representados en la filogenia usados en el análisis. Los dos criterios hacen que el EF pueda ser medido para cualquier área de interés, a diferentes escalas y además que dependa poco de los niveles taxonómicos de los taxones analizados. Cerca de otras 12 modificaciones se han desarrollado al EF para incorporar las correcciones realizadas a los índices WE y CWE (Laffan *et al.* 2010). Dos ejemplos de índices usados para describir el EF son los Rareza Filogenética Corregida-Ponderada y el Endemismo Filogenético Ponderado Corregido (variante central). El primer índice incluye la abundancia de los taxones, buscando dar mayor peso a las especies raras. Mientras que el segundo considera grupos de celdas (ventanas) para estimar la restricción de la DP. Otras modificaciones al EF ingresan como factor la simulación de pérdida de clados en la filogenia, con la intensión de evaluar el efecto de la disminución de taxones superiores sobre la PD y por lo tanto el endemismo. Las anteriores variantes de la DP se encuentran también implementadas en el programa *Biodiverse* (Laffan *et al.* 2010).

MÉTODOS DE IDENTIFICACIÓN DE ÁREAS DE ENDEMISMO

En biogeografía evolutiva se toma al endemismo como restricción a un área sin importar el tamaño. Las áreas de endemismo se identifican a partir de la evaluación de la congruencia espacial de las áreas de distribución de las especies, para retener a aquellas áreas soportadas por las especies con alta congruencia espacial. Sin embargo, la descripción de patrones de endemismo ha sido controversial por la ausencia de un valor cuantificable de la congruencia espacial (Henderson 1991). Esto ha llevado a pensar que el uso de la congruencia espacial como criterio para la identificación de las áreas de endemismo, puede ser poco útil cuando se trata de especies endémicas sin congruencia espacial que habitan islas (Harold & Mooi 1994).

En biogeografía evolutiva de acuerdo con la interpretación de la congruencia espacial y la puesta a prueba de su validez, se han desarrollado aproximadamente 11 métodos para la identificación de patrones de endemismo "áreas de endemismo" (Apéndice II): (a) los que generalizan las presencias a unidades geográfica operativas (celdas, ecosistemas o tipos de vegetación, etc.) y luego las comparan para identificar grupos, medidos a partir de la alta congruencia espacial de los taxones; (b) los que toman como distribuciones a las localidades de presencia y por lo tanto la congruencia se mide a ese nivel; y (c) aquellos métodos que buscan probar la significancia matemática de la congruencia espacial, a partir de la evaluación de la no aleatoriedad de las áreas de endemismo.

En el primer grupo se encuentran el Análisis de Parsimonia de Endemismos (PAE) (Rosen & Smith 1988), el Análisis de Parsimonia de Endemismos para celdas (PAE) (Morrone 1994) y el Análisis de Endemicidad o Criterio de Optimización (AE) (Szumik *et al.* 2002; Szumik & Goloboff 2004). La identificación de áreas de endemismo en el PAE puede incluir localidades, provincias, celdas y otros UGOs, mientras que en el AE las distribuciones son representadas solo por localidades o el uso de matrices de taxones por celdas.

Se ha mencionado que los métodos que jerarquizan UGOs desestiman la representación de los sistemas naturales (Szumik *et al.* 2002; Casagranda *et al.* 2009), así que la diferencia entre el PAE y el AE, se fundamenta en esa filosofía. Con el PAE se identifican sistemas jerarquizados de áreas de endemismo, mientras que con el AE se obtienen áreas de endemismo superpuestas. En cuanto a la aplicación metodológica, el PAE ha sido criticado por la inclusión indirecta del componente espacial. Por esta razón en el AE se comparan celdas y se obtiene un índice de endemismo para cada especie y área de endemismo, esto involucra el componente espacial dentro de la evaluación del endemismo (Szumik *et al.* 2002; Casagranda *et al.* 2009).

El segundo grupo está integrado por el Método de Análisis de Redes (NAM) (Dos Santos *et al.* 2008) y la Interpolación Geográfica del Endemismo (GIE) (Oliveira *et al.* 2015). En el NAM se evalúa la congruencia a nivel de localidades (Dos Santos *et al.* 2008), haciendo implícito el componente espacial para identificar áreas de endemismo. Sin embargo, los patrones con poca congruencia detectadas en el NAM han sido criticados por considerar que cumplen vagamente con el criterio de área de endemismo (alta congruencia espacial) (Casagranda *et al.* 2009). La comparación de las distribuciones en el NAM, se realiza considerando la conexión entre localidades y la posterior identificación de patrones con análisis de redes. El análisis de redes permite incluir a las especies y sus relaciones espaciales (Dos Santos *et al.* 2008), esto lo diferencia del PAE y el AE que son dependientes de celdas de grillas.

El GIE es una adaptación de la interpolación espacial Kernel para la representación del endemismo (Oliveira *et al.* 2015). Este método define áreas circulares de influencia alrededor de los puntos de presencia, las cuales son usadas para evaluar su traslape con una función de densidad Kernel y representar el endemismo como un continuo en el espacio geográfico. Las selecciones de los radios para comparar las distribuciones son definidos por el usuario (Oliveira *et al.* 2015), por lo tanto, la distribución de los valores de endemismo podría depender del radio que se tome.

En cuanto a la implementación de los métodos, el PAE puede ser ejecutado en programas que tengan parsimonia como método filogenético, el AE ha sido desarrollado en el programa NDM/VNDM (Goloboff 2014) y NAM se encuentra en el paquete SyNet del programa R (Dos Santos *et al.* 2008; Dos Santos 2011). Mientras que el GIE se encuentra como extensión de un programa comercial de Sistemas de información geográfica (Oliveira *et al.* 2015).

En el tercer grupo se encuentran el reconocimiento de áreas de endemismo de Harold & Mooi (1994), el criterio de optimización para evaluar métodos de endemismo (Linder 2001a), el Análisis de Co-presencia significante de taxones (Sigcot) (Mast & Nyffeler 2003), el Análisis de Endemismo de Áreas Anidadas (NAEA) (Deo & DeSalle 2006) y Sigcot con PAE (Giokas & Sfenthourakis 2008). Harold & Mooi (1994) criticaron el uso de la congruencia espacial como único criterio para identificar áreas de endemismo y propusieron la inclusión de información filogenética para la identificación de áreas de endemismo (criterio de congruencia espacial y filogenética). El protocolo es teórico y hasta el momento se encuentra sin implementar.

El Sigcot permite filtrar los taxones antes de aplicar cualquier método para la identificación de las áreas de endemismo. Se fundamenta en la evaluación de la congruencia espacial, con modelos nulos. Para ello se aleatoriza las distribuciones y se mide la congruencia entre las distribuciones generadas. Si la congruencia observada se encuentra con frecuencia alta en las comparaciones de las distribuciones generadas, entonces la congruencia podría ser explicada por el azar (Mast & Nyffeler 2003). En el criterio de Sigcot (Linder 2001a) y Sigcot con PAE se busca poner a prueba las áreas de endemismo y la congruencia espacial, y se ejecutan antes o después de identificar las áreas de endemismo. En el Sigcot (Linder 2001a) se desarrolló el índice de congruencia (CON, Apéndice II) el cual pondera el tamaño del área de distribución con el tamaño del área de endemismo. Este índice mide el ajuste de la distribución de las especies endémica al área de endemismo. El Sigcot con PAE, sigue los principios básicos del Sigcot pero en lugar de ejecutar los modelos nulos sobre la matriz completa, la comparación se hace con los taxones en cada área de endemismo (Giokas & Sfenthourakis 2008).

El NAEA es una adaptación del análisis de clados anidados (Deo & DeSalle 2006), empleado en filogeografía para el estudio de flujo de genes y poblaciones (Templeton 1998). Una de las ventajas del NAEA, es la evaluación de la significancia de la congruencia espacial para identificar las áreas de endemismo (Deo & DeSalle 2006). La desventaja general para este y otros métodos que generalizan las distribuciones a celdas, es la dependencia del resultado al tamaño de celda, especies endémicas con un tamaño de celda particular podrían no serlo con otro tamaño de celda (Morrone & Escalante 2002). Con respecto a la implementación del NAEA, este método se puede ejecutar en el programa original para el análisis filogeográfico de clados anidados (Deo & DeSalle 2006).

PROBLEMAS ASOCIADOS A LA CUANTIFICACIÓN DEL ENDEMISMO Y A LA DESCRIPCIÓN DE PATRONES DE ENDEMISMO

Los resultados de los cálculos de los índices para el análisis del endemismo pueden ser afectados por variaciones en las variables de las fórmulas (riqueza de especies, tamaño del área de estudio, tamaño de celdas, sesgos de muestreo, etc.). En el caso de los métodos de cuantificación del endemismo, la evaluación de la concentración del endemismo o la identificación de áreas de endemismo que son dependientes de celdas, el efecto del tamaño y divisiones de la gradilla pueden ocultar los patrones (Linder 2001a; Morrone & Escalante 2002). Para el PAE, NDM, entre otros, la modificación del tamaño de celdas altera la generalización de las distribuciones a las celdas, así que un taxón que es endémico a una escala, podría no serlo en otra (Morrone & Escalante 2002).

La extensión del área de estudio puede condicionar la ubicación de los centros de endemismo o la identificación de las áreas de endemismo. Si se incluyen áreas de distribución incompletas, los índices de cuantificación del endemismo cambian, debido al efecto que tiene el número de celdas sobre la ponderación del endemismo (Lovett *et al.* 2000). En los métodos de identificación de áreas de endemismo este punto ha sido poco explorado, no obstante, se podría esperar que se identifiquen áreas de endemismo falsas al encontrar congruencia espacial alta entre un área de distribución completa y el fragmento de otra (Fig. 7).

En los índices que consideran ventanas o radios para estimar la densidad durante la ponderación, se ha mencionado que el movimiento y tamaño de las ventanas incrementan los valores de endemismo (Laffan *et al.* 2013). Esto se relaciona con el uso de la riqueza para corregir el índice de endemismo, donde la riqueza alrededor de la celda objetivo puede ser variable. Por ejemplo, usar una ventana de cuatro celdas podría involucrar conteos incompletos, en comparación con una ventana de nueve o más celdas. En el caso del GIE, modificaciones en el tamaño del radio de análisis, ocasiona cambios en la densidad del endemismo.

La dependencia de todos los métodos al conjunto de taxones analizados es alta, la adición o sustracción de especies afecta la evaluación del endemismo (Linder 2001b). Los índices de riqueza de endemismo, relación endemismo-riqueza total y densidad, se vuelven incomparables si existen vacíos en información sobre la riqueza total y distribuciones de los taxones. Por ejemplo, si se comparan las riquezas de mamíferos endémicos en el presente y su representatividad en el Cuaternario (Cuadro 1), se observa que los valores más altos de endemismo se encuentran en el presente. Esta es una conclusión poco acertada, considerando que el conocimiento sobre la riqueza de mamíferos endémicos del Cuaternario y otros periodos es incompleto. Por lo tanto, se considera que los patrones de endemismo son hipótesis que deben ser probadas con nuevos datos (Harold & Mooi 1994), analizadas con diferentes enfoques metodológicos y generalizadas a partir de comparaciones con otros patrones (Morrone 1994). El desarrollo de protocolos para la evaluación del endemismo y los patrones que conforma aún es un campo en desarrollo.

PERSPECTIVAS

La mayoría de índices iniciaron con la descripción de patrones espaciales del endemismo, pero se ha progresado en el desarrollo de índices como el endemismo filogenético, con el objeto de darle peso a la historia evolutiva de los taxones. Sin embargo, se considera que la inclusión de las dimensiones espacio-tiempo y forma podría ser un nuevo enfoque para el análisis de los patrones de endemismo (Noguera-Urbano 2016).

En general el término endémico se refiere a la exclusividad de un taxón a un área geográfica. Por ejemplo el

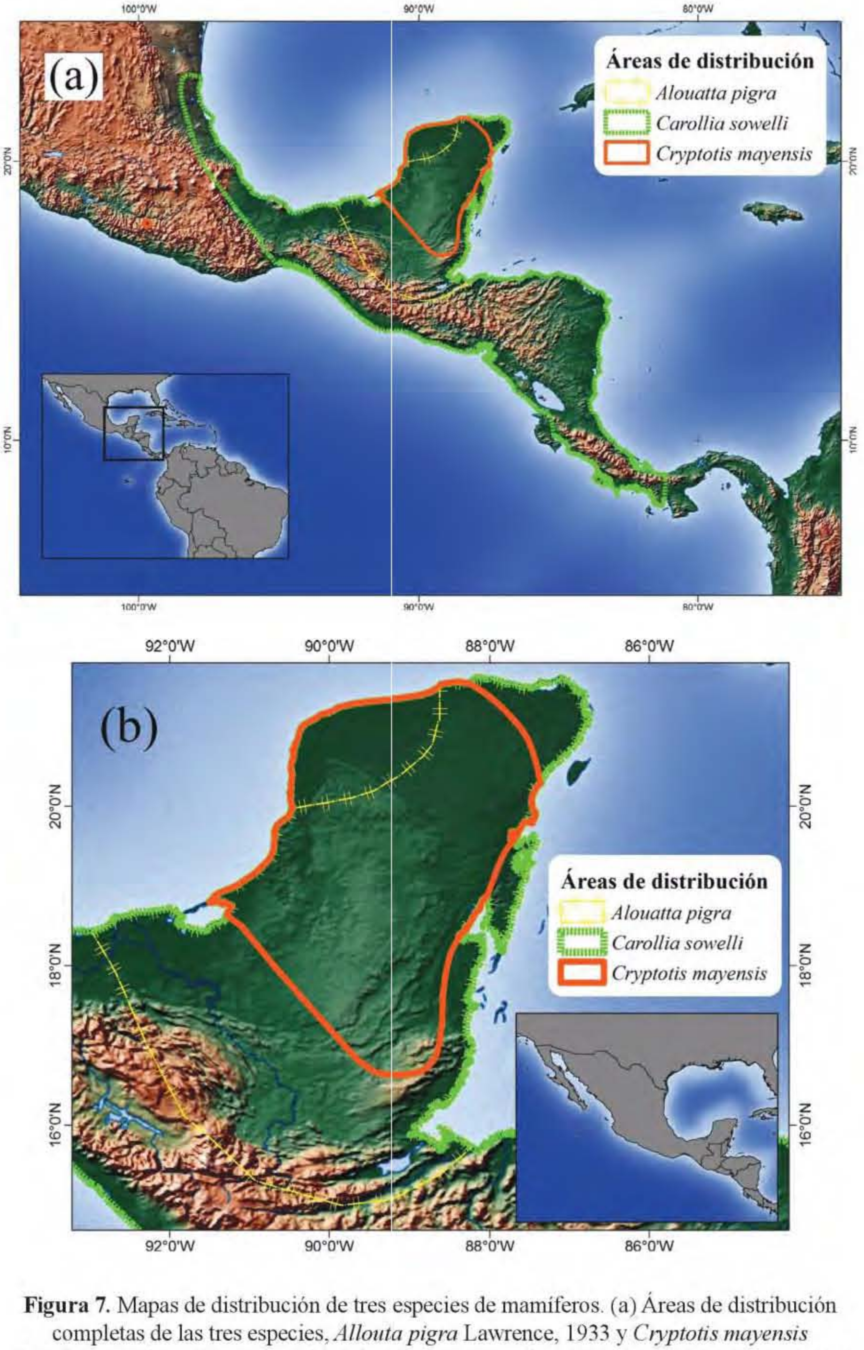

Figura 7. Mapas de distribución de tres especies de mamíferos. (a) Áreas de distribución completas de las tres especies, *Allouta pigra* Lawrence, 1933 y *Cryptotis mayensis* (Merriam 1901) pueden ser consideradas que soportan a la Península de Yucatán como área de endemismo. (b) La distribución de *Carollia sowelli* Baker, Solari & Hoffmann, 2002 está incompleta en el mapa, durante un análisis de endemismo que incluya la panorámica presentada las tres especies podría soportar a la Península de Yucatán como área de endemismo. En este caso *C. sowelli* es un falso endemismo de la Península, resultado de incluir una distribución incompleta.

Cuadro 1. Aplicación del endemismo tomando en cuenta la restricción de mamíferos a un país. Se presentan el número de taxones endémicos de México en el presente y las cifras suponiendo que los mismos taxones fueron endémicos en el pasado (Cuaternario tardío). Endémico es E y riqueza es S.

		Unidad	Orden	Familias	Género	Especie	Referencia
Actual	Riqueza total	#	13	46	202	544	Ceballos, 2014
	Riqueza E	#	0	0	11	170	Ceballos, 2014
	E/S	%	0	0	6	31	Este estudio
	E/A	(SpE/km^2)	0	0	$6*10^{-6}$	$9*10^{-5}$	Este estudio
Holoceno tardío	Riqueza total	#	12	44	146	279	Arroyo-Cabrales *et al.* 2002; Ceballos *et al.* 2010; Ferrusquía-Villafranca *et al.* 2010
	Riqueza E	#	0	0	4	23	Este estudio
	E/S	%	0	0	$3*10^{-2}$	8	Este estudio
	E/A	(SpE/km^2)	0	0	$4*10^{-6}$	$1*10^{-5}$	Este estudio

roedor *Neotoma cinerea* (Ord 1815) es considerado endémico, porque está restringido al norte del Pacífico de América del Norte (Zabel & Anthony 2003). Sin embargo, los registros fósiles del Pleistoceno indican que la especie se encontraba en México (Ferrusquía-Villafranca *et al.* 2010). Este caso refleja el sentido variable de la aplicación del endemismo, al ser tomado como restricción geográfica. Las especies que en la actualidad son consideradas endémicas, pudieron tener mayores o menores distribuciones en el pasado o estar restringidas en zonas geográficas diferentes a las actuales. La identificación de patrones de endemismo requiere un conocimiento aceptable de las distribuciones de los taxones. En el análisis de provincialismo de mamíferos pleistocénicos en México (Ferrusquía-Villafranca *et al.* 2010), los autores integraron la información de mamíferos extintos y existentes para identificar patrones. A partir de ello se propusieron ocho corredores que permitieron el flujo de mamíferos a lo largo y dentro del territorio mexicano. Esto demuestra que los patrones biogeográficos pueden ser recuperados usando distribuciones multitemporales integradas. En la actualidad son pocos los análisis que incluyen fósiles para estudiar patrones de endemismo, este puede ser un nuevo camino a explorar.

Generalmente en los índices de endemismo filogenético se estima la historia evolutiva de los taxones sobre una o más celdas y luego se comparan entre conjuntos de celdas. En este proceso se deja un lado el análisis de la historia independiente de cada taxón endémico. La composición de los taxones en los patrones de endemismo es un punto que empieza a ser explorado. Por ejemplo, para las áreas de endemismo se sabe que su estructura puede ser asincrónica con respecto a la edad de cada taxón (Noguera-Urbano, 2016). Se piensa que en las áreas de endemismo pueden ocurrir múltiples tiempos de integración, dependiendo de la evolución de los taxones endémicos en cada área de endemismo. Por lo tanto, es necesaria su evaluación integral para dejar de percibir al endemismo como restricción, e interpretarlo dentro del contexto evolutivo (unicidad). Además, hace falta explorar e incorporar en los índices la forma de los taxones representada en atributos biológicos. La inclusión de mayor información biológica podría mejorar la interpretación del endemismo en las tres dimensiones (espacio- tiempo-forma).

CONCLUSIONES

En ecología y conservación el endemismo se interpreta con relación a un área geográfica de referencia y dentro un marco temporal determinado. Mientras que en biogeografía evolutiva se considera al endemismo como restricción a un área natural sin importar el tamaño, además permite identificar patrones que han perdurado a través del tiempo.

Tradicionalmente en ecología el endemismo bajo criterios prácticos es relacionado con la restricción de una especie a un área determinada a priori o los límites geopolíticos. Esto permite hacer comparaciones entre áreas o priorizar sitios donde el endemismo toma alto valor. Mientras que en la perspectiva evolutiva generalmente se usan límites naturales para definir taxones endémicos y la congruencia espacial como criterio práctico para la determinación de taxones endémicos.

Las áreas endémicas, áreas de endemismo y centros de endemismo representan unidades geográficas derivados de la aplicación de diferentes criterios de endemismo. En el primero se usa como criterio "distribución restringida", mientras que la presencia de dos o más especies que pueden tener o no congruencia espacial soportan el área endémica. En las áreas de endemismo los taxones endémicos son aquellos que habitan áreas de cualquier tamaño, pero que tienen alta congruencia espacial con al menos otro taxón. En los centros de endemismo los taxones endémicos son identificados con base en el criterio de distribución restringida, y el endemismo es relativizado en el espacio geográfico de acuerdo al tamaño de área de distribución de cada especie endémica.

Todo lo anterior demuestra la necesidad de un concepto unificado del endemismo, es decir, se podría generalizar la aplicación de la definición de Candolle (1820) para referirse a taxones nativos y de distribución única, aplicable a área de endemismo. Y si se toma en cuenta que las áreas endémicas y los centros de endemismo se basan en áreas de distribución restringida, entonces los dos tipos de unidades geográficas se podrían llamar áreas con especies restringidas y centros de distribuciones restringidas respectivamente.

La identificación de las áreas endémicas, áreas de endemismo y centros de endemismo están directamente relacionadas con la estimación y delimitación de las áreas de distribución o con la definición del área de estudio. Por ejemplo, la comparación de áreas de distribución parciales podría resultar en la identificación de áreas de endemismo falsas. Por otra parte, la escala espacial puede tener efecto sobre la caracterización de los patrones. Por ejemplo, en los métodos dependientes de grillas, los índices de endemismo y la forma de los patrones de endemismo puede variar con el cambio en el tamaño de celda. Por ejemplo celdas grandes podrían homogenizar el endemismo dentro del área de estudio, mientras que celdas chicas podrían desagregar el patrón.

Finalmente, la poca inclusión de información de taxones extintos en los análisis biogeográficos de áreas de distribución, puede ocasionar sesgos o pérdida de los patrones de endemismo (Wagner & Marcot 2013). Aunque cuando los patrones son robustos y la calidad de las distribuciones es aceptable, las distribuciones de especies actuales permiten hacer inferencias sobre procesos evolutivos en múltiples marcos temporales (Martínez-Meyer *et al.* 2004; Wagner & Marcot 2013). Por lo tanto, la inclusión de distribuciones de taxones extintos obtenidas de registros fósiles podría mejorar la identificación e interpretación de patrones biogeográficos propuestos para describir el endemismo.

AGRADECIMIENTOS. A Adolfo Navarro, David Espinosa, Fernando A. Cervantes, Joaquín Arroyo-Cabrales y Juan J. Morrone, por incentivar la escritura de este documento. A Tania Escalante por las sugerencias que permitieron mejorar el documento. Al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM) y al Consejo Nacional de Ciencia y Tecnología de México (CONACyT) (Beca Doctoral 262582), por el apoyo brindado para la escritura de este documento. A Alfredo N. y Maria Jesus U. por el apoyo brindado desde la distancia y que ha permitido conceptualizar esta idea. Al editor y revisores del manuscrito por las sugerencias y observaciones que mejoraron substancialmente el documento.

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APÉNDICE I

Métodos ecológicos empleados para la evaluación del índice de endemismo

Nombre	Siglas	Cálculo	Interpretación	Resultado	Autor
Riqueza de endemismo	?	∑Endémicas	Criterio: Distribución restringida. Valor absoluto de endemismo.	Número de especies endémicas.	Sin definir
Proporción de endemismo	E/S	# Taxones endémicos/ riqueza total de especies E/S=(E100)/S	Criterio: Distribución restringida. Valor absoluto de endemismo.	Proporción o porcentaje de endemismos.	Sin definir
Índice de Bykow	i	i = |ef/en|; donde ef: porcentaje de endemismo en la región de estudio con base a la riqueza total. "en" se obtiene de-> log en=0.373 log a - 1.043; donde a: área km^2, en: % endemismo esperado	Criterio: Distribución restringida. Valor absoluto de endemismo.	0<i< 1. Si el índice "i" es cercano a 1, entonces el área tiene el endemismo esperado para el área.	Major 1988; Hobohm & Tucker 2014
Densidad de endemismo	E/A	# Endémicos/ área	Criterio: Distribución restringida. Valor absoluto de endemismo.	Valores que indican concentración de endemismos.	Sin definir
Relación área-endemismo	EAR	logE = z logA + logc; E = cAz ; E= # especies endémicas de un área, A= tamaño del área, z y c= constantes empíricas	Criterio: Distribución restringida. Valor absoluto de endemismo.	Valor que indica la relación entre área y riqueza de endemismos.	Major 1988; Harte & Kinzig 1997
Endemismo ponderado	RSR o WE	RSR o WE=∑(1/Ci) ; donde Ci: número de UGO en las cuales se encuentra el taxón i.	Distribución del endemismo en un espacio geográfico compuesto por celdas u otras unidades de comparación.	Mapas compuestos por celdas. Valores altos del índice indica centros de endemismo; un taxón en una sola celda tendrá valor de 1 para esa celda.	Williams et al. 1996; Linder 2001b
Endemismo ponderado corregido	CWE	CWE=∑(1/Ci)/S; donde Ci: número de UGO en las cuales el taxón i se encuentra. Se: número total de especies en cada celda	Distribución del endemismo en un espacio geográfico compuesto por celdas u otras unidades de comparación.	Mapas compuestos por celdas. Promedio del endemismo por celda o porcentaje de especies restringidas a un grupo de celdas.	Linder 2001b; Crisp et al. 2001
Riqueza de endemismo	Cs	Cs = (∑Ii/Gi)/A ; donde Cs: riqueza de endemismo; n: número de especies en cada unidad de muestreo; Ii: tamaño de la área de distribución dentro de la unidad de muestreo (# celdas); Gi: tamaño de la área de distribución fuera de la unidad de muestreo; A: tamaño total del área	Distribución del endemismo en un espacio geográfico compuesto por celdas u otras unidades de comparación.	Mapas compuestos por celdas. Mayor riqueza de endemismo mayor valor del índice.	Kier & Barthlott 2001

Nombre	Siglas	Cálculo	Interpretación	Resultado	Autor
Endemismo filogenético	EF	EF= ∑ Lc/Rc ; Lc: longitud del brazo con relación a una filogenia; Rc: área de distribución para cada clado	Diversidad filogenética de linajes o taxones endémicos.	Mapas compuestos por celdas. Valor de 1 expresa el valor máximo del endemismo filogenético.	Rosauer et al. 2009
Endemismo completo	EW	EW=PE/S; EF ponderado con la riqueza total o con un grupo de celdas (ventana).	Riqueza de taxones endémicos con respecto al área total en estudio.	Mapas compuestos por celdas. Los valores indican el promedio del endemismo por celda o porcentaje de especies restringidas a un grupo de celdas.	Laffan et al. 2010
Endemismo completo con partición jerárquica	WEP	Múltiples formulas.	Endemismo medido dentro de niveles jerárquicos en la filogenia.	Mapas compuestos por celdas. Los valores altos indican mayor endemismo de múltiples taxones.	Laffan et al. 2013

APÉNDICE II

Métodos biogeográficos evolutivos empleados para la evaluación del endemismo

Método	Siglas	Unidad de comparación	Criterio	Resultado	Autor
Análisis de Parsimonia de Endemicidad	PAE	Áreas o localidades de distribución	Conteo de especies	Grupos de áreas o localidades	Rosen & Smith 1988
Análisis de Parsimonia de Endemicidad	PAE	Celdas de gradilla	Conteo de especies	Grupos de celdas	Morrone 1994, 2014
Criterio para el reconocimiento de áreas de endemismo	-	Áreas de distribución y filogenias	Relación entre áreas de distribución	Grupos de áreas	Harold & Mooi 1994
Criterio de optimización para evaluar métodos de endemismo	-	Celdas de gradilla	Índice de congruencia de al menos dos especies (con) y congruencia de sus áreas de distribución (CON)	Grupos de celdas asociadas con parsimonia o similitud	Linder 2001a
Análisis de endemicidad o criterio de optimización	AE	Celdas de gradilla o localidades de presencia	Índice de endemicidad	Grupos de celdas soportadas por al menos dos especies.	Szumik et al. 2002; Szumik & Goloboff 2004
Co-Presencia SIGnificante de taxones	Sigcot	Celdas de gradilla	Evaluación de la significancia de la congruencia espacial usando modelos nulos	Grupos de celdas y su significancia estadística.	Mast & Nyffeler 2003
Combinación de Sigcot y PAE	-	Celdas de gradilla	Evaluación de la significancia de la congruencia espacial usando modelos nulos y agrupamientos resultado de un PAE	Grupos de celdas y su significancia estadística	Giokas & Sfenthourakis 2008
Análisis de endemismo de áreas anidadas	NAEA	Cladograma de PAE, red de árboles de tendido mínimo, áreas de distribución, celdas de una gradilla	Valores de distancia dentro de grupos de celdas (DC) y el anidamiento de grupos (DN)	Grupos de celdas o áreas con significancia estadística	Deo & DeSalle 2006
Método de análisis de redes	NAM	Localidades de presencia	Identificación y remoción de especies intermedias para segregar unidades de copresencia, usando "medidas de interconexión" y coeficientes de agrupamiento	Grupos de localidades y unidades de copresencia	Dos Santos et al. 2008
Interpolación geográfica de endemismo	GIE	Localidades de presencia	Índice de Kernel para representar el grado de superposición de las distribuciones de las especies	Mapas de intensidad del Índice de Kernel.	Oliveira et al. 2015

Abridged title: DYNAMISM OF AREAS OF ENDEMISM (Enviado *Journal of Biogeography*)

DYNAMISM OF THE AREAS OF ENDEMISM IN NEOTROPICAL MAMMALS: DIFFERENTIAL EFFECTS OF EVOLUTIONARY AND ECOLOGICAL FACTORS

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Aim: To describe the changes or *dynamism* of the potential spatial congruence in the areas of endemism of Neotropical mammals in three geological timespans (Current, Mid Holocene and Last Interglacial), and to assess if historical and ecological factors could be associated with these changes.

Location: Neotropical region.

Methods: Using Maxent, we modelled current potential distributions for 74 endemic species that support 18 Neotropical areas of endemism of mammals, and we selected the most accurate models. Niches were transferred back to 6 ka (Mid–Holocene, MH) and 120-140 ka (Last interglacial, LIG) to retrieve their ancient potential geographic distribution. We quantified the size of the areas of endemism (area occupied by at least two species), and calculated their geographical dinamysm (i.e. stability, contraction and expansion of the areas of endemism) over the three periods. Then, we tested the effect of some ecological and historical factors on the dynamism of the areas of endemism, using a Canonical Correspondence Analysis (CCA). We also evaluated whether the endemic species exhibited significant phylogenetic structure in each area of endemism.

Results: Our analysis reveled that the size of the potential areas of endemism changed over time. The CCA showed a strong influence of historical and ecological factors on the dynamism of the areas of endemism, explaining 70% of the variation. The most important explanatory variables were the number of taxonomic orders, with a positive trend in a set of 11 areas of endemism, and phylogenetic diversity (PD), which showed a positive trend in a set of ten areas of endemism. The nearest taxa index (NTI) showed that two areas of endemism have phylogenetic clustering: the Magellanic forest province and the Southern Puna province.

Main conclusions: The individual response of the species to climatic variation probably modifies the areas of endemism over ecological time; however, the results support the hypothesis that most of them are true historical units that have persisted throughout MH and LIG. It is possible that the PD and the number of orders represent the diversty of lineages with multiple biological traits (size, form, dispersion form) that may be important determinants of dynamism of the areas of endemism.

KEYWORDS

Climatic change, evolutionary biogeography, endemism, species distribution modelling, sympatry, South America.

INTRODUCTION

An important aim of evolutionary biogeography is to identify areas of endemism to explain the evolutionary history of endemic taxa and their geographic areas (Morrone & Crisci, 1995; Nelson & Platnick, 1981). Areas of endemism are historical units (Morrone, 1994, 2009; Nelson & Platnick, 1981; Parenti & Ebach, 2009), defined as a geographic zone where there is spatial congruence of the distributional areas of two or more endemic species (Espinosa, Aguilar, & Escalante, 2001; Morrone, 1994; Platnick, 1991). Spatial congruence is a result of the interactions between historical and ecological processes that define the boundaries of species' geographic distributions (Morrone & Crisci, 1995; Noguera-Urbano, 2016; Szumik, Cuezzo, Goloboff, & Chalup, 2002). Accordingly, the congruence of distributional areas in an area of endemism represents common history, similar evolutionary processes, and probably ecological similarities between two or more species.

It has been proposed that an area of endemism represents a biotic component (Gámez, Escalante, Espinosa, Eguiarte, & Morrone, 2014; Morrone, 2014a). Crother and Murray (2011) and Noguera-Urbano (2016) mention that areas of endemism are individual entities defined by many features. First, they are identified by the presence of their congruent endemic taxa (Morrone, 1994; Platnick, 1991), which explain their historical and ecological dynamics (e.g., Escalante, Rodríguez-Tapia, Linaje, Morrone, & Noguera-Urbano, 2014). Second, areas of endemism are characterized by their boundaries, which can represent snapshots in time and may change over time and space (e.g., Gámez et al., 2014). Thus, areas of endemism are more than simple sums of species, they represent historical and ecological entities related to historical and ecological processes (Anderson, 1994; Murray & Crother, 2016; Pinilla-Buitrago et al., 2018) because they are bound temporally by speciation, increase or contraction of the distributional areas, geologic vicariance, dispersal and extinction (Anderson, 1994; Crother & Murray 2011; Murray & Crother, 2016). Therefore, areas of endemism may even disappear due to the extinction of one or more endemic species (Anderson, 1994). The modification and even the disappearance of the areas of endemism can occur on short time scales too due to population dynamics; some populations of the endemic species persist, while others migrate and others go extinct, modifying their distributional areas (Murray & Crother, 2016). Thus, areas of endemism exist and change on ecological time scales as a function of metapopulational processes (Murray & Crother, 2016).

Areas of endemism persist as interactors, they arise or extinguish from the processes, alterations and biological dynamics of their congruent endemic taxa and their geographical and ecological space (Anderson, 1994; Murray & Crother, 2016, Noguera-Urbano 2016). Studies about the changes in areas of endemism have shown that some endemic species and areas of endemism in Mexico persist through time (Gámez et al., 2014; Pinilla-Buitrago et al., 2018). The endemic species compose multitemporal strata in areas of endemism because of their asynchronous and synchronous divergence times (Noguera-Urbano, 2016). Moreover, the number and composition of areas of endemism in Mexico change due to climatic variations (Aguado-Bautista & Escalante, 2015; Gámez et al., 2014; Pinilla-Buitrago et al., 2018).

Analyses that have been previously employed to test for the persistance of areas of endemism (Gámez et al., 2014; Aguado-Bautista and Escalante, 2015) have not been fully applied to other portions of the Neotropical region. Furthermore, these authors focused in the identification of areas of endemism in the past, current and future, to compare and describe their persistence, leaving aside explanations about the general evolution of areas of endemism. Therefore, the dynamics and temporal persistence of areas of endemism have been based on the evaluation of spatial congruence changes over time, and the factors which explain the integration of the endemic species have been only slightly explored.

Current and paleontological occurrence data are incomplete or remain inadequate for most species (Lomolino, 2004; Whittaker et al. 2005). Ecological niche modelling (ENM) relates complete or incomplete occurrence data to abiotic factors to estimate areas with suitable environmental conditions for the species (Pearson, Raxworthy, Nakamura, & Townsend, 2007; Shcheglovitova & Anderson, 2013). Thus, ENM can be used to identify zones that have similar environmental conditions to where the species currently maintain populations, and therefore estimate their potential distribution (Guisan & Thuiller, 2005; Pearson et al., 2007; Peterson et al., 2011). Moreover, ecological niche models can be transferred onto modelled past climates to postdict hypothetical past distributional areas (Hijmans & Graham, 2006; Martínez-Meyer, Peterson & Hargrove, 2004). As such, the transfer assumes that the occurrence data–climate association does not change radically over evolutionary time periods (Peterson, 2011; Peterson, Soberón, & Sánchez-Cordero, 1999).

Using ENM and their transference onto several climate scenarios (past and current) have lead to the analysis of changes in areas of endemism over time, and as a consequence, to the integration of historical and ecological biogeography (Gámez et al., 2014). Noguera-Urbano and Escalante (2015) used areas of endemism defined by Neotropical mammals to analyze and describe their temporal dynamics. They identified 101 areas of endemism (Ae) based on 454 Neotropical species of mammals, using the Endemicity Analysis (EA, Szumik et al., 2002; Szumik & Goloboff, 2004), with special focus on the description of the areas at regional and local scales. They concluded that the identified areas of endemism of Neotropical mammals agree with previous biogeographical units (e.g. Morrone 2014b;

Sclater & Sclater 1899; Wallace 1876). The Neotropical areas of endemism identified by Noguera-Urbano and Escalante (2015) have potential to be used as empirical samples to analyze their temporal dynamics. Taking into account the Neotropical areas of endemism of Noguera-Urbano and Escalante (2015), some endemic species were selected to apply ENM and predict current (C) and past at Mid–Holocene (MH) and Last interglacial (LIG) potential distributional areas. Past conditions are represented by simulations of the MH (ca. 6,000 years ago), and the LIG (ca. 120,000 - 140,000 years ago), which had profound changes and were generally warmer or cooler than today respectively (Otto-Bliesner, Marshall, Overpeck, Miller & Hu, 2006; Steig, 1999), so they may be used to model the potential distributional areas of endemic mammals and explain dynamics of the spatial congruence in the areas of endemism.

Hence, considering that the spatial congruence of the distributional areas of two or more species define an area of endemism, and that their congruent endemic taxa and their geographical or ecological space is affected by multiple historical and ecological factors, we hypothesize that (1) if areas of endemism are historical units, they have persisted over time, or (2) if the distributional areas of the endemic species can be affected by climatic variations, areas of endemism change on short time scales (Murray & Crother, 2016). Therefore, the main goal of this study was to describe the changes or *dynamism* of the potential spatial congruence in the areas of endemism of Neotropical mammals in three geological time spans (Current, Mid Holocene, Last Interglaciation), and to assess if historical and ecological predictors could be associated with these changes. The predictors selected were the number of endemic species and the number of taxonomical orders as proxies of biological predictors; the size of the area of endemism as a proxy of geographical factors; and two indices of phylogenetic diversity (Phylogenetic diversity, Faith, 1992; and the nearest taxa index NTI; Webb, 2000) as proxies of historical predictors.

MATERIALS AND METHODS

Areas of endemism and endemic species

We used the areas of endemism of Neotropical mammals described by Noguera-Urbano and Escalante (2015). These authors identified 210 areas of endemism, but we selected only 18 of them which have all data available for the entire analyses. We compiled the phylogenetic and geographic information available that also had high quality and certainty in the online databases and literature for the endemic species. The occurrence data (i.e., presence only) of the endemic species were obtained from diverse data sources including: (1) Global Biodiversity Information Facility (GBIF) database available online (https://www.gbif.org/); (2) "SpeciesLink" (CRIA) database available online (http://www.splink.org.br/); (3) books about Neotropical mammals (Gardner, 2008; Patton, Pardinas & D'Elía, 2016); and (4) systematic surveys in scientific articles (e.g. individual species accounts, lists of species and notes on geographic distributions). Only occurrence data identified at the species level and with longitude-latitude data were retrieved from online databases. Records with the same collector name, collector number, or reported in both online databases and books were considered as duplicates, which was used once in the final selection based on its location quality (prioritizing records with no data conflicts and with the lowest uncertainty). All occurrence data were verified geographically and taxonomically following the suggestions of Chapman (2005). To avoid issues associated with geographic sampling bias and spatial autocorrelation, occurrence data were thinned with a 10 km radius rule using the R package spThin (Aiello-Lammens, Boria, Radosavljevic, Vilela & Anderson, 2015).

Ecological niche modelling (ENM)

The bioclimatic variables with spatial resolution of 30 arc-seconds (~1 km) were used as predictors. As current climatic conditions (C), we used 19 global bioclimatic layers (temperature and precipitation information) downloaded from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Past conditions were characterized using paleoclimate simulations for the Last Interglacial (LIG, ca. 120,000 - 140,000 years ago) and the Mid Holocene (MH, ca. 6000 years ago). LIG is represented by climate data derived from the coupled ocean–atmosphere–land–sea–ice general circulation model ENCAR Community Climate System Model (CCSM; Otto-Bliesner et al., 2006), while the MH is represented by downscaled climate data from simulations with Global Climate Models (GCMs) based on the CMIP5 model. Both past scenarios were downloaded from WorldClim (available at http://www.worldclim.org/past).

Species distribution models (SDM) were built using Maxent (Phillips & Dudik, 2008, Phillips, Anderson, & Schapire, 2006) as implemented by the 'dismo' package (Hijmans et al., 2017; R version 3.3.2; R Core Team 2016) using random seed. Logistic output format was used to describe the probability of presence (Phillips & Dudík, 2008), which is a continuous habitat suitability range between 0 (unsuitable) and 1 (the most suitable). SDM were calculated, tuned and evaluated following the procedure described in Appendix S1. We made the transfer of a single ecological niche model per species tuned onto current climate and they were transferred back to MH (6 ka) and LIG (120-140 ka). The parameters, variables and results of the metrics of evaluation of the SDM are described in Appendix S2 (Supporting Information).

Potential areas of endemism (current and past)

We summed binary maps of the endemic species to obtain dynamic structure for each area of endemism for the three periods (C, MH, LIG; Gámez et al., 2014). We selected only the pixels where two or more species coincided. The size of each potential area of endemism was calculated for the three periods considering the spatial resolution of the bioclimatic variables (1 pixel ~1 km). Because we were interested in analyzing the dynamism of the potential areas of endemism, we represented the tendencies of the sizes in barplots. Then, we evaluated the relationships among the current size and the past sizes of the potential areas of endemism, applying a Kendall's rank correlation (tau; p-value <0.5) to the log-transformed sizes of the potential areas of endemism.

Later, the potential areas of endemism of different periods were summed to obtain hypothetical multitemporal areas of endemism (HAE). We obtained seven different possible values based on the current period: Gain current (G-C); Loss (L-MH); Conserved (C+MH); Loss (L-LIG); Conserved (C+LIG); Loss (L-MH+LIG); and Conserved (C+HM+LIG). For example, if a C potential area of endemism is added to its equivalent in the MH, the resulting HAE correspondes to C+MH, which represents potential persistence of the area of endemism in both periods. We calculated the percentage of change in the sizes of areas of endemism relative to the current, and they were represented in a barplot to describe the dynamism of the areas of endemism.

Spatial dynamism of the areas of endemism and associated historical and ecological factors

We used two set of variables: one describing the dynamism (change) in the size of the areas of endemism (GC, L-MH, C+MH, L-LIG, C+LIG, L-MH+LIG and C+HM+LIG), quantified in number of pixels by the pixel size (~ $1 km^2$). The other set was used to describe the historical and ecological factors that can modify the areas of endemism: (1) number of endemic species of the current areas of endemism (C-sps); (2) size of the area composed by the maximum number of species into the current areas of endemism (C-Size-MaxSp); (3) number of species in the MH areas of endemism (MH-sp); (4) size of the area composed by the maximum number of species into the MH areas of endemism (MH-SizeMaxSp); (5) number of species in the LIG areas of endemism (LIG-sp); (6) size of the area composed by the maximum number of species into the LIG areas of endemism (LIG-SizeMaxSp); (7) number of orders in the current areas of endemism (Order-C); (8) Faith's index of phylogenetic diversity (Faith, 1992) of the current areas of endemism (PD); (9) minimal age of the endemic species in the current area of endemism (MinAge); and (10) maximal age of the endemic species in the current area of endemism (MaxAge). We evaluated normality of the two sets of variables using density plots. Some variables were not normal; therefore, we applied the square root transformation to the full set of variables (Sokal & Rohlf, 1981). Then, we tested the relationship between a linear combination of the dynamism of the size and a linear combination of historical and ecological factors using a Canonical Correlation Analysis (CCoAr; 999 permutations; Hotelling, 1936; Legendre & Legendre, 1998).

Canonical Correspondence Analysis (CCA) integrates ordination and multiple regression techniques (Legendre & Legendre, 1998). CCA explains variation in a set of variables by detecting a linear combination in a second set of environmental variables (ter Braak, 1986), without considering *a priori* knowledge about potential predictor variables (Boren, Engle, Palmer, Masters & Criner, 1999). We evaluated the relationship between dynamism in the areas of endemism and size of the current areas of endemism, due to the variation of the historical and ecological factors using a CCA (Borcard, Gillet & Legendre, 2011; Legendre & Legendre, 1998; ter Braak, 1986), and calculated a forward selection of explanatory variables (p-value<0.5). Previously, we tested the multicollinearity (VIF<10; Zuur, Leno & Elphick, 2010) in both set of variables. The descriptors of size had low collinearity, but C-sps (r=1) and LIG-sp (r=0.98; second set) were excluded because they are correlated with MH-sp. Finally, we explored the tendencies of the phylogenetic structure of the endemic species in the areas of endemism to evaluate phylogenetic associations among their endemic mammals, estimating the nearest taxon index (NTI; Webb, 2000). NTI considers the branch length separating each species from its nearest relative (Swenson, 2014; Webb, Ackerly, McPeek & Donoghue, 2002) and reflects structure at the tips of the phylogeny (Webb *et al.*, 2002; Cardillo, 2011). Positive values of NTI (*p*-value <0.05) indicate increase of clustering and become negative (*p*-value >0.95) with overdispersion (Cardillo, 2011; Swenson, 2014; Webb, 2000; Webb *et al.*, 2002). PD and NTI (null model: taxa labels; runs: 999) were performed in the Picante library (Kembel *et al.*, 2010) for R (R Core Team, 2016), using the entire phylogeny of mammals by Fritz, Bininda-Emonds, & Purvis (2009). All statistics and geographic analyses were performed in QGIS (QGIS Development Team, 2016.) and R Cran (R Core Team, 2016) using basic functions, the Dismo (Hijmans et al., 2016), Picante (Kembel et al., 2010), rgdal (Bivand, Keitt & Rowlingson, 2016) and vegan (Oksanen et al., 2016) packages.

RESULTS

Areas of endemism, endemic species and ecological niche modelling

We obtained distributional records from 116 endemic species of mammals, 42 of which were rejected because of the bad performance of their ENM (jackknife test p-value>0.05; or ROC Partial p>0.05). The list of species, records, number of replicates, variables, and parameters used to build ENMs, as well the results of modelling performance, are given in Appendix S2 (Supporting Information). After the evaluation process, we retained 74 endemic species that supported 18 areas of endemism (Table1, Appendix S3: Figures S1–S18) representing eight orders (Carnivora=1 species; Cetartiodactyla=1; Chiroptera=8; Didelphimorphia=4; Lagomorpha=1; Paucituberculata=1; Primates=7; Rodentia=51). Most endemic especies were bats and rodents. We obtained 222 maps that represent the potential areas of endemism in the current and past (MH, LIG) scenarios and 18 maps that represent the hypothetical dynamism of the areas of endemism (Appendix S4 Figures S1–S18).

Potential areas of endemism (current and past)

We found that the size of the potential areas of endemism changed over time (Fig. 1; Appendix S4 Figures S1–S18), with the smallest areas of endemism from the present and the MH. Additionally, there was a significant positive relationship among the sizes of the current and past areas of endemism (C/MH, tau=0.6, T= 125, p-value= 0.0001048; C/LIG, tau=0.4, T= 110, p-value= 0.01087; MH/LIG, tau=0.5, T= 116, p-value= 0.002244; Fig. 2). The dynamism of the hypothetical areas of endemism showed that nine of them had a major loss of area from the LIG to present (Fig. 1); while the remaing areas (nine) showed their main loss of area from the HM to present (Fig. 3). The persistence of conserved areas was variable among the areas of endemism (Media=50%), ranging from 0.14% (Madeira and Rondônia provinces) to 90% (Southern Puna province; Fig. 3). The Madeira and Rondônia provinces lost the majority of their areas (382%), but gained 58%; the mean gain was 14.8%. The complete sets of factors included are in Appendix S5 (Supporting Information).

Spatial dynamism of the areas of endemism and historical and ecological factors associated

The canonical correlations were high on the first two axes (CanAxis1=0.99; CanAxis2=0.98; RDA R^2=0.64; RDA R^2=0.56), and showed that there were positive tendencies in the relationship between the dynamism of the areas of endemism and the historical and ecological factors (permutational probability = 0.001). The correlations between each of the variables and their respective canonical variates showed that the minimal age of the areas of endemism and the number of species in the MH were positively correlated with three types of changes in the size of the areas of endemism: loss of area since the MH and LIG, area conserved since the MH and the size of the current area (Fig. 4). Additionally, the area occupied by the maximum number of species in the three periods and the phylogenetic diversity were positively correlated with the size of area conserved since the HM and LIG and the area conserved since the LIG. Individually, minimal age of the endemic species in the current area of endemism was negatively correlated with the number of orders in the current areas of endemism. These results are congruent with a general positive relationship, except for the negative correlation of maximal age of the endemic species in the current area of endemism.

The CCA showed a strong influence of historical and ecological factors on the dynamism of the areas of endemism (Total inertia=4.151), explaining 70% of the variation (Table 2). The first two canonical axis were significant (CCA1 *pseudo-F*= 11.82, p-value= 0.002; CCA2 *pseudo-F*= 6.71; p-value=0.01), and they explained 73% of the variation (Table 2). There were three well-defined groups of areas of endemism; one of them linked to high Order-C, PD and MH-sp and included the Magellanic forest province, Parana dominion and Northern Mexican transition zone). The second group was linked to MH-SizeMaxSp and LIG-SizeMaxSp and contained the Southern Puna province, Northwestern Chacoan subregion, Madeira and Rondônia provinces. Finally, the third was related to

MaxAge and included Central Chilean subregion, North Andes, Western Brazilian subregion, Western Mexican transition zone, Pacific Lowlands and Balsas Basin provinces and Northern Mexico (Fig. 5a); indicating distinctiveness of the areas of endemism due to their size, age and number of species. The remaining areas of endemism were distributed among undefined factors (Fig. 5a).

The most important explanatory variables in the CCA were two: the number of orders and phylogenetic diversity. The number of orders (Order-C, *pseudo-F*= 3.89, p-value= 0.02; Fig. 5b) had a positive tendency in a set of 11 areas of endemism (Northwestern Chacoan subregion, Central Chilean subregion and Maule province, Puna province, Atacama Desert, Puna and Yungas provinces, Madeira and Rondônia provinces, Magellanic forest province, Parana dominion, Pacific Lowlands and Balsas Basin provinces, Northern Mexican transition zone, Central Mexico, Western Mexican transition zone). Phylogenetic diversity (PD; *pseudo-F*= 3.36, p-value= 0.02; Fig. 5) had a positive tendency in a set of ten areas of endemism (Atacama, Desert, Puna and Yungas provinces, Central Chilean subregion, Southern Puna province, Magellanic forest province, Northwestern Chacoan subregion, Parana dominion, Western Brazilian subregion, Northern Mesoamerican dominion, Western Mexican transition zone and Mexican transition zone; Fig. 5b; Table 3). A stronger relationship beetwen PD and number of orders and loss of area since the MH was detected (Fig. 5b). In addition, NTI showed two areas of endemism with phylogenetic clustering: the Magellanic forest province (Magellanic forest province; $NTI_{calculated}$= -0.27; p-value=0.428) and the Southern Puna province (Southern Puna province; $NTI_{calculated}$= -3.08; p-value=0.006; Table 4). The other areas of endemism did not show any phylogenetic pattern.

DISCUSSION

The projection of the current ENM onto past climate indicated that the shape and composition of the areas of endemism are affected by changes to climatic regimes. The observed dynamism of the areas of endemism is a consequence of the modifications of the distributional areas, since climatic regimes influence the species' distributions and population dynamics (Walther et al., 2002). It has been suggested that communities of mammals vary in species composition over time (Pleistocene and Holocene), but they remain organized into similar biogeographic patterns (faunal provinces, Graham et al., 1996). Our results support the observations made by Anderson (1994) that the number of endemic species and shape of areas of endemism may change due to the expansion and contraction of the distributional area of one or more endemic species. In other cases, the area of endemism may disappear due to the extinction of one or more endemic species. Therefore, the variation in size of areas of endemism suggests that the contractions and expansions of the distributional areas have played a predominant role in their structure (Murray & Crother, 2016).

During MH and LIG, landscapes and climates were different from the present day. MH climatic conditions in tropical South America were considerably warmer and probably wetter than today (De Vivo & Carmignotto, 2004), causing reduction, expansion and fragmentation of distributional areas of some Neotropical mammals. For example, some species of rodents that had a wider distribution in open habitats and which survived in savanna are currently present as disjunct populations that inhabit the northern and central South American savannas (Nuñez, Grosjean, & Cartajena, 2001). Another case is the rodent *Scapteromys aquaticus* Thomas 1920, which at present inhabits drainage basins in the Chaco province, but their past distribution included the fluvial beds between the Guerrero and Río Salado in the central Buenos Aires Province (Tonni, Cione, & Figini, 1999). On the other hand, four areas endemism of Neotropical region (Madeira and Rondônia provinces, Northwestern Chacoan subregion, Southern Puna province, Puna province) and two areas of the Andean region (Magellanic forest province, Central Chilean subregion) expanded their size in the LIG, and therefore their endemic mammals expanded their distributional areas. This result partially agrees with the expansion of tropical forest in South America during the LIG (Leite et al., 2016).

We found that the size of the current areas of endemism is positively correlated with the size of the areas of endemism in the past (Fig. 2). This tendency may indicate that the climatic regimes and physical geography have periods of stability, that contribute to maintaining the size of the areas of endemism at several biogeographical scales. However, small distributional areas indicate habitat specificity (Purvis, Gittleman, Cowlishaw & Mace, 2000) that affect the ability of the endemic species to disperse over environmental heterogeneous areas. Consequently, small areas of endemism have remained small, while the currently large areas of endemism were large too in the past. Even when each species seems to be differentially influenced by climatic variations (Gilman, Urban, Tewksbury, Gilchrist & Holt, 2010; Graham et al., 1996), the endemic species appear to be affected as a group in each area of endemism. As has been suggested (Pinilla-Buitrago et al., 2018), our results demonstrated that areas of endemism persist over time, but their persistence varies substantially from area to area (Fig. 3) because climatic regimes induce modifications in the species distributional areas (Gaston, 2003). Changes in distribution are often asymmetrical among lineages, with some species spreading faster than others (Walther et al., 2002), affecting the species composition of the areas of endemism (Aguado-Bautista & Escalante, 2015; Gámez et al., 2014).

The relationship between dynamism of the areas of endemism and historical and ecological factors does not appear to be a simple one. The younger areas of endemism with lower number of species have lost less area since the MH, and are smaller in the present (Fig. 4); while the older ones, with a higher number of species in the MH, showed an increase in the two variables. Willis (1922) proposed a positive relationship between evolutionary age and the size of distributional areas of the species to explain the temporal dynamics of the distributional areas. The existence of a correlation between age and size in the areas of endemism suggests that they maintain a signal that at least partly reflects the transformation of the distributional areas of the endemic species. One explanation is that in the case of Neotropical mammals, younger species tend to have small areas of endemism with minor changes in the size because of their habitat specificity (Purvis et al., 2000). By contrast, older species that have defined to large areas of endemism for a long time may be able to overcome geographical and ecological barriers, thus extending and contracting their distributional area in a cycle as suggested by Ricklefs & Cox (1972).

The positive relationship among maximum number of species, phylogenetic diversity and the size of area conserved since the past (LIG and HM, Fig.4), could indicate that the number of endemic species constrains the changes in the size of the areas of endemism. Thus, larger areas of endemism resulted from the integration of a large number of endemic species, and consequently, they are more susceptible to decrease in the size by the effects of the climatic changes than smaller ones. Groups of areas of endemism do not show any clear geographical organization in relation to the explanatory variables in the CCA (Fig. 5). However, the distinctiveness of the areas of endemism due to their size, age and number of species, could indicate that each one is affected by different factors, no matter its geographical position.

The PD and the number of orders affect the size of the areas of endemism. This is consistent with the dependence of the size of the areas of endemism on the number of species that comprise them (Fig. 4). Our results suggest that the species composition, the age of the endemic species condensed in the PD and the number of orders have a strong signal in the assemblages of the endemic species. For example, the PD of the Parana dominion shows a strong relationship with the number of species and the number of orders (Fig. 5), while the Central Chilean subregion and Maule province show the lowest values in number of orders and species. This pattern can be attributed to a general relationship between PD and number of species (Swenson, 2014). Orders, families and genera suggest common ancestry and therefore phylogenetic relationships, which are supported by intrinsic traits inherited by each species (Davidson et al., 2012). Therefore, the relationship among the size of the areas of endemism and the number of orders may reflect the contrasting traits among endemic species groups, different adaptations to dispersal and climatic conditions. Moreover, the range in the number of orders in the areas of endemism (1 to 3 orders) offers evidence that the endemic species have several evolutionary histories as suggested by Noguera-Urbano (2016), who mentioned that some areas of endemism are integrated by endemic species that speciated in different time spans.

Cracraft (1985) suggested that the species that integrate areas of endemism possess distant phylogenetic relationships; this idea applies to most of the areas of endemism here analyzed, because 16 of them are not covered by any phylogenetic pattern. Two areas of endemism were an exception to that idea, however. First, we have a strong pattern describing the Southern Puna province supported by 12 rodent species (*Abrocoma cinerea*, *Akodon albiventer*, *Akodon lutescens*, *Andinomys edax*, *Auliscomys sublimis*, *Calomys boliviae*, *Ctenomys opimus*, *Eligmodontia puerulus*, *Octodontomys gliroides*, *Oxymycterus* *paramensis*, *Phyllotis osilae* and *Rhipidomys austrinus*), which have evolved in the tropics of South America (Schenk, Rowe & Steppan, 2013). Second, there is a weak pattern describing the Magellanic forest province, because it is supported by only three species, two of which are bats (*Lasiurus varius* and *Myotis chiloensis*), while the other species is a rodent (*Abrothrix longipilis*). This shows that the phylogenetic pattern of the Magellanic forest province is supported by bats. The ages of the clades and their relationship with other sister groups determine the phylogenetic structure of the assemblages (Cardillo, 2011; Procheş, Wilson & Cowling, 2006; Rabosky, 2009). Moreover, some similar biological traits related to species' habitat use, mobility or diet are associated with the phylogenetic structure of species (Barnagaud et al., 2014). Therefore, the phylogenetic clustering showed by the Magellanic forest province and the Southern Puna province indicate that their endemic species are highly related and share some biological traits.

Concluding remarks

Similar responses by each of the endemic species to climatic variations could promote the apareance of areas of endemism over ecological time. However, our results support the first hypothesis that the areas of endemism are historical units which have persisted since the LIG and MH. Our analyses could not distinguish whether current species distribution models reflect the past distribution of the endemic species or not; however, fossil evidence support the idea that biogeographic patterns persist over time (Graham et al., 1996). Further evidence is needed from other biological groups to determine the proposed dynamism of areas of endemism here described and to generalize the relationships among dynamism and historical-ecological factors. In addition to the interest in historical and ecological drivers of areas of endemism in Neotropical region given their status as biodiversity hotspots, our analyses offer potential insights into the persistence and dynamism of the areas of endemism in a general context. It is possible that populations of the endemic species persist, migrate and other go extinct, modifying the areas of endemism over time; as a consequence, areas of endemism may be governed by population dynamics (Murray & Crother, 2016). This supports our second hypothesis, that spatial congruence of the endemic species can be affected by climatic variations, and although they change on short time scales (i.e. ecological time scale), areas of endemism are biogeographical units that have evolved because of the evolution of their endemic species (geological time scale). Changes in mammal areas of endemism were tested against the direct effects of climate. However, other factors like biological interactions, geographic dispersion and population dynamism could also have played an important role. Thus, future analyses could give some insights on the potential relationships among endemic species and their requirements, in addition to individual ENMs. It is possible that the PD and the number of orders represents biological differences among endemic species that may be important determinants of dynamism of the areas of endemism, although this needs to be tested, given the absence of functional variables in our analysis. The absence of phylogenetic patterns in most of them indicate that the endemic species compose multitemporal strata and multiple histories of integration (lineages) in the areas of endemism (Noguera-Urbano, 2016).

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Figures

Figure 1. Variation of the size of the potential areas of endemism (Ae) in three temporal sceneries of climatic variation in order by size. Northern Mesoamerican dominion (Ae10); Pacific Lowlands and Balsas Basin provinces (Ae84); Madeira and Rondônia provinces (Ae91); Northern Andes (AET125); Atacama, Desert, Puna and Yungas provinces (Ae93); Northern Mexican transition zone (Ae14); Western Brazilian subregion (Ae19); Northwestern Chacoan subregion (Ae32); Parana dominion (Ae34); Magellanic forest province (Ae97); Central Chilean subregion (Ae98); Central Chilean subregion and Maule province (Ae99); Mesoamerican dominion (Ae20); Western Mexican transition zone (Ae22); Northern Mexico (AET41); Central Mexico (AET43); Southern Puna province (Ae59); and Puna province (Ae60).

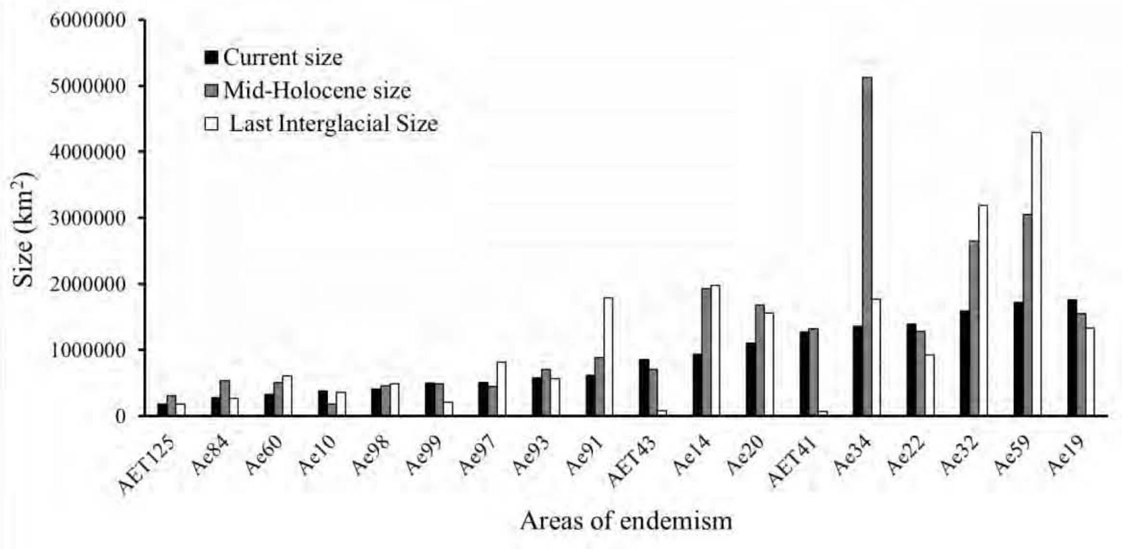
Figure 2. Tendencies of the changes in size of the potential areas of endemism (Ae) in three temporal sceneries of climatic variation. C= current, MH= Mid Holocene, LIG= Last interglacial. Northern Mesoamerican dominion (Ae10); Pacific Lowlands and Balsas Basin provinces (Ae84); Madeira and Rondônia provinces (Ae91); North Andes (AET125); Atacama, Desert, Puna and Yungas provinces (Ae93); Northern Mexican transition zone (Ae14); Western Brazilian subregion (Ae19); Northwestern Chacoan subregion (Ae32); Parana dominion (Ae34); Magellanic forest province (Ae97); Central Chilean subregion (Ae98); Central Chilean subregion and Maule province (Ae99); Mesoamerican dominion (Ae20); Western Mexican transition zone (Ae22); Northern Mexico (AET41); Central Mexico (AET43); Southern Puna province (Ae59); and Puna province (Ae60).

Figure 3. Changes in size of the potential areas of endemism (Ae) in three temporal sceneries of climatic variation. C= current, MH= Mid Holocene, LIG= Last interglacial. Northern Mesoamerican dominion (Ae10); Pacific Lowlands and Balsas Basin provinces (Ae84); Madeira and Rondônia provinces (Ae91); Northern Andes (AET125); Atacama, Desert, Puna and Yungas provinces (Ae93); Northern Mexican transition zone (Ae14); Western Brazilian subregion (Ae19); Northwestern Chacoan subregion (Ae32); Parana dominion (Ae34); Magellanic forest province (Ae97); Central Chilean subregion (Ae98); Central Chilean subregion and Maule province (Ae99); Mesoamerican dominion (Ae20); Western Mexican transition zone (Ae22); Northern Mexico (AET41); Central Mexico (AET43); Southern Puna province (Ae59); Puna province (Ae60).

Figure 4. Biplots of a canonical correlation analysis (CCorA) of the dynamism (a) and evolutionary and ecological factors (b) of the areas of endemism of Neotropical mammals. Size of the area composed by the maximum number of species into the current areas of endemism (C-Size-MaxSp); size of the area composed by the maximum number of species into the MH areas of endemism (MH-SizeMaxSp); size of the area composed by the maximum number of species into the LIG areas of endemism (LIG-SizeMaxSp); number of orders in the current areas of endemism (Order-C); Faith's index of phylogenetic diversity of the current areas of endemism (PD); minimal age of the endemic species in the current area of endemism (MinAge); and maximal age of the endemic species in the current area of endemism (MaxAge).

Figure 5. Biplot of CCA. (a) Plot with fitted areas of endemism scores, the numbers represent the areas of endemism. (b) Plot with fitted variable scores of dynamisms. Size of

the area composed by the maximum number of species into the current areas of endemism (C-Size-MaxSp); size of the area composed by the maximum number of species into the MH areas of endemism (MH-SizeMaxSp); size of the area composed by the maximum number of species into the LIG areas of endemism (LIG-SizeMaxSp); number of orders in the current areas of endemism (Order-C); Faith's index of phylogenetic diversity (Faith, 1992) of the current areas of endemism (PD); minimal age of the endemic species in the current area of endemism (MinAge); and maximal age of the endemic species in the current area of endemism (MaxAge).


6000000
5000000
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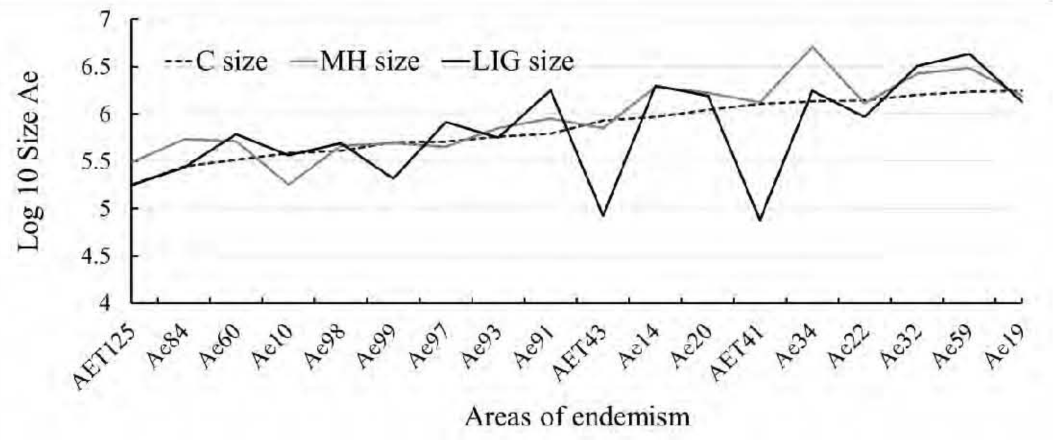
Size (km^2)
■ Current size
▨ Mid-Holocene size
☐ Last Interglacial Size
AET125
Ae84
Ae60
Ae10
Ae98
Ae99
Ae97
Ae93
Ae91
AET43
Ae14
Ae20
AET41
Ae34
Ae22
Ae32
Ae59
Ae19
Areas of endemism


7
6.5
6
5.5
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4.5
4
Log 10 Size Ae
C size
MH size
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AET125
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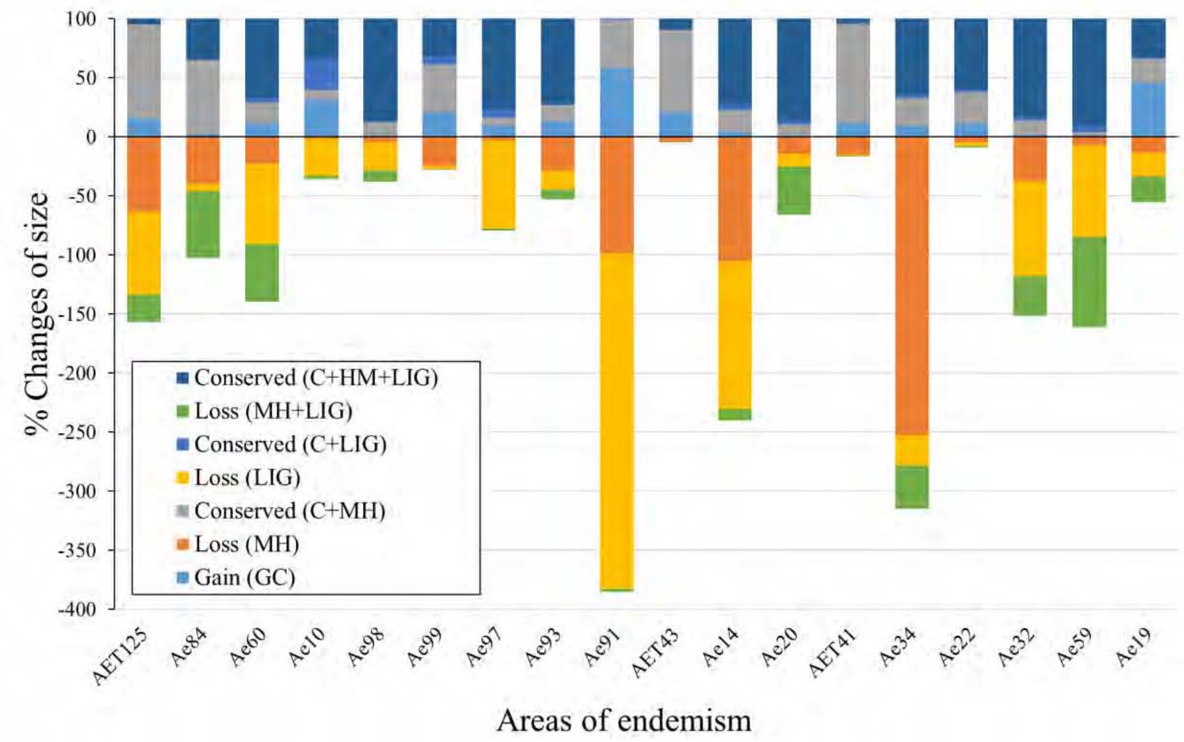
Areas of endemism


% Changes of size
100
50
0
-50
-100
-150
-200
-250
-300
-350
-400
Conserved (C+HM+LIG)
Loss (MH+LIG)
Conserved (C+LIG)
Loss (LIG)
Conserved (C+MH)
Loss (MH)
Gain (GC)
AET125
Ae84
Ae60
Ae10
Ae98
Ae99
Ae97
Ae93
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AET41
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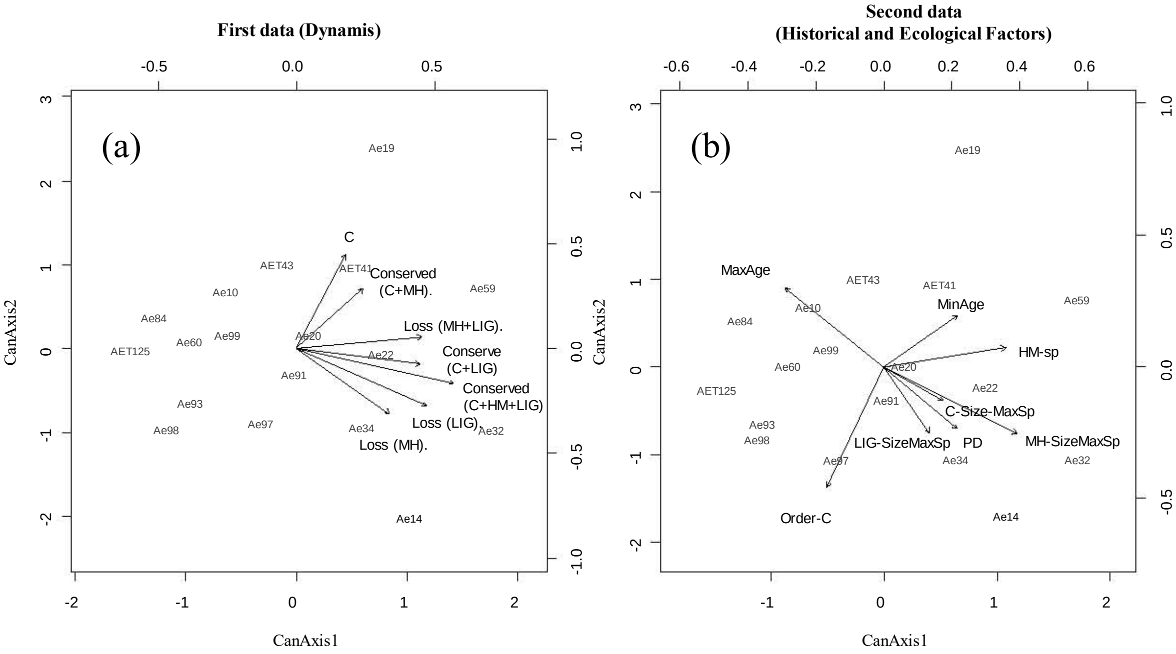
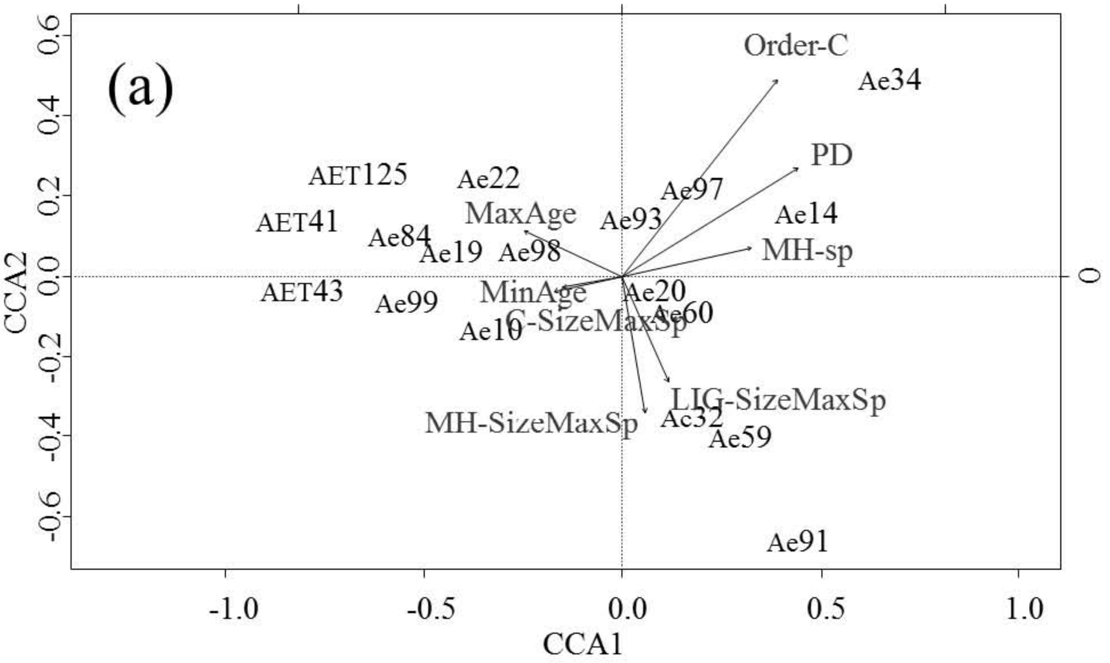
Ae59
Ae19
Areas of endemism


First data (Dynamis)
(a)
-0.5
0.0
0.5
3
2
1
0
-1
-2
1.0
0.5
0.0
-0.5
-1.0
CanAxis2
CanAxis1
-2
-1
0
1
2
Ae19
C
AET43
AET41
Conserved
(C+MH).
Ae59
Ae10
Ae84
Loss (MH+LIG).
Ae99
Ae20
AET125
Ae60
Conserve
(C+LIG)
Ae22
Ae91
Conserved
(C+HM+LIG)
Ae93
Loss (LIG)
Ae98
Ae97
Ae34
Ae32
Loss (MH).
Ae14
Second data
(Historical and Ecological Factors)
(b)
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
3
2
1
0
-1
-2
1.0
0.5
0.0
-0.5
CanAxis2
CanAxis1
-1
0
1
2
Ae19
MaxAge
AET43
AET41
Ae59
Ae10
MinAge
Ae84
Ae99
HM-sp
Ae60
Ae20
AET125
Ae22
Ae91
C-Size-MaxSp
Ae93
Ae98
LIG-SizeMaxSp
PD
MH-SizeMaxSp
Ae97
Ae34
Ae32
Order-C
Ae14


(a)
Order-C
Ae34
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AET125
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MaxAge
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Ae84
Ae19
Ae98
MH-sp
AET43
Ae99
MinAge
Ae20
Ae60
C-SizeMaxSp
Ae10
LIG-SizeMaxSp
MH-SizeMaxSp
Ae32
Ae59
Ae91
CCA1
CCA2
-1.0
-0.5
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0.5
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-0.6
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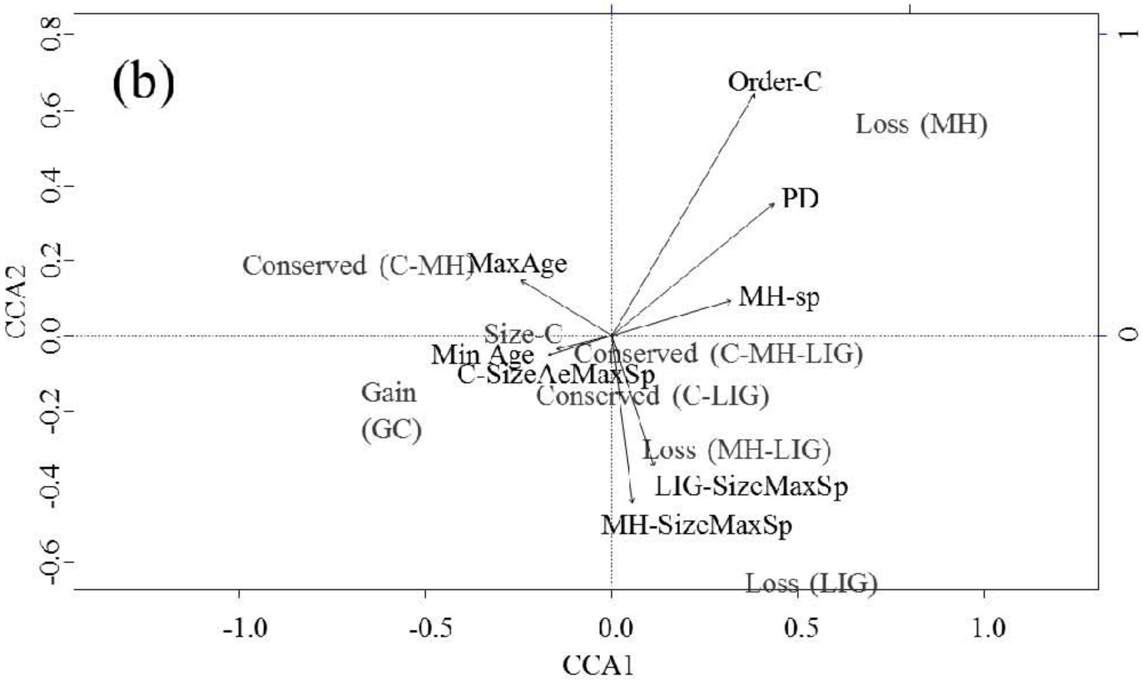
(b)
Order-C
Loss (MH)
PD
Conserved (C-MH)
MaxAge
MH-sp
Size-C
Min Age
Conserved (C-MH-LIG)
C-SizeAeMaxSp
Gain
(GC)
Conserved (C-LIG)
Loss (MH-LIG)
LIG-SizeMaxSp
MH-SizeMaxSp
Loss (LIG)
CCA1
CCA2
-1.0
-0.5
0.0
0.5
1.0
-0.6
-0.4
-0.2
0.0
0.2
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0.8
1
0

Tables

Table 1. Neotropical areas of endemism (Ae) analyzed. AET= Area of endemism in transitional zones. Codes and names after Noguera-Urbano and Escalante (2015). Nes= Number of endemic especies.

Code	Ae	Nes
Ae10	Northern Mesoamerican dominion	2
Ae91	Madeira and Rondônia provinces	2
Ae98	Central Chilean subregion	2
Ae99	Central Chilean subregion and Maule province	2
Ae22	Western Mexican transition zone	2
Ae93	Atacama, Desert, Puna and Yungas provinces	3
Ae32	Northwestern Chacoan subregion	3
Ae97	Magellanic forest province	3
Ae84	Pacific Lowlands and Balsas Basin provinces	4
AET125	North Andes	4
Ae19	Western Brazilian subregion	4
AET41	Northern Mexico	4
AET43	Central Mexico	4
Ae60	Puna province	4
Ae14	Northern Mexican transition zone	5
Ae20	Mesoamerican dominion	6
Ae34	Parana dominion	8
Ae59	Southern Puna province	12

Table 2. Summary of statistics for canonical correspondence analysis of dynamism and evolutionary and ecological factors of the areas of endemism of Neotropical mammals. CCA= Canonical Component Axis.

	CCA1	CCA2
Eigenvalue	0.21	0.12
% Proportion Explained	47	27
% Cumulative Proportion	47	74
Site constraints (linear combinations of constraining variables)		
Northern Mesoamerican dominion (Ae10)	-1.03	-0.31
Pacific Lowlands and Balsas Basin provinces (Ae84)	-1.32	0.41
Madeira and Rondônia provinces (Ae91)	0.91	-1.96
North Andes (AET125)	-1.40	0.75
Atacama, Desert, Puna and Yungas provinces (Ae93)	-0.04	0.54
Northern Mexican transition zone (Ae14)	0.91	0.57
Western Brazilian subregion (Ae19)	-1.07	0.16
Northwestern Chacoan subregion (Ae32)	0.25	-1.06
Parana dominion (Ae34)	1.37	1.54
Magellanic forest province (Ae97)	0.24	0.61
Central Chilean subregion (Ae98)	-0.57	0.14
Central Chilean subregion and Maule province (Ae99)	-1.27	-0.06
Mesoamerican dominion (Ae20)	0.00	0.05
Western Mexican transition zone (Ae22)	-0.89	0.78
Northern Mexico (AET41)	-1.98	0.54
Central Mexico (AET43)	-1.68	-0.01
Southern Puna province (Ae59)	0.36	-1.09
Puna province (Ae60)	0.16	-0.12
Scores for constraining variables		
C-Size-MaxSp	-0.21	-0.06
MH-sp	0.40	0.12
MH-SizeMaxSp	0.07	-0.55
LIG-SizeMaxSp	0.14	-0.43
Order-C	0.48	0.80
PD	0.54	0.44
MinAge	-0.18	-0.04
MaxAge	-0.30	0.18

Table 3. Summary of statistics of a forward selection of explanatory variables. AIC= Akaike criterion. *Significant explanatory variables in the Canonical Correspondence Analysis. Number of orders in the current areas of endemism (Order-C); Faith's index of phylogenetic diversity (Faith, 1992) of the current areas of endemism (PD); number of species in the MH areas of endemism (MH-sp); size of the area composed by the maximum number of species into the LIG areas of endemism (LIG-SizeMaxSp); size of the area composed by the maximum number of species into the MH areas of endemism (MH-SizeMaxSp); maximal age of the endemic species in the current area of endemism (MaxAge); size of the area composed by the maximum number of species into the current areas of endemism (C-Size-MaxSp) and minimal age of the endemic species in the current area of endemism (MinAge).

Variable	Df	AIC	*False-F*	p-value
Order-C	1	259.16	3.8957	0.02*
PD	1	259.65	3.3645	0.025*
MH-sp	1	260.8	2.1631	0.245
LIG-SizeMaxSp	1	261.51	1.4649	0.455
MH-SizeMaxSp	1	261.69	1.2925	0.555
MaxAge	1	261.75	1.2316	0.555
C-Size-MaxSp	1	261.88	1.1056	0.595
MinAge	1	262.81	0.2488	0.970

Table 4. The nearest taxon index (NTI) values of the 18 Neotropical areas of endemism of mammals. Phylogenetic clustering is indicated with an asterisk (*).

Names	Observed	Calculated	p-value
North Andes (AET125)	209.63	1.01	0.80
Pacific Lowlands and Balsas Basin provinces (Ae84)	123.17	-0.90	0.19
Puna province (Ae60)	95.13	-1.56	0.06
Northern Mesoamerican dominion (Ae10)	120.80	-0.53	0.26
Central Chilean subregion (Ae98)	192.40	0.41	0.79
Central Chilean subregion and Maule province (Ae99)	32.60	-1.69	0.09
Magellanic forest province (Ae97)	145.53	-0.27	0.428*
Atacama, Desert, Puna and Yungas provinces (Ae93)	139.13	-0.38	0.37
Madeira and Rondônia provinces (Ae91)	47.20	-1.53	0.15
Central Mexico (AET43)	137.07	-0.52	0.26
Northern Mexican transition zone (Ae14)	222.80	1.46	0.93
Mesoamerican dominion (Ae20)	171.48	0.21	0.61
Northern Mexico (AET41)	118.47	-0.98	0.17
Parana dominion (Ae34)	167.54	0.14	0.56
Western Mexican transition zone (Ae22)	171.20	0.09	0.49
Northwestern Chacoan subregion (Ae32)	140.07	-0.42	0.36
Southern Puna province (Ae59)	88.89	-3.08	0.006*
Western Brazilian subregion (Ae19)	45.07	-2.62	0.02

SUPPORTING INFORMATION

Dynamism of the areas of endemism of Neotropical mammals: differential effects of evolutionary and ecological factors

Appendix S1 Methods used to estimate the species distribution models (SDM) of each endemic species assessed

Supplementary Information

MATERIALS AND METHODS

The study region (M) or area of accessibility has important implications for all aspects of species distribution modelling (e.g. model training, model validation and model comparisons; Soberón, 2010; Barve et al., 2011). The boundaries of M must be carefully assessed, since it represents the geographic area that species have been able to reach during a relevant period of time (Soberón, 2010; Barve et al., 2011), and must be informative about the dispersal barriers that have constrained the species' distribution (Barve et al., 2011). Therefore, we estimated current M for each species following an operational approach (Soberón, 2010; Tocchio et al., 2015), which involved first selecting the watersheds that overlap with at least one record of the species, and then broaden its size with the addition of adjoining river basins. We think that this procedure enables including landscape that has been "tested" by the species, but has not been occupied (Barve et al., 2011). Occurrence records of the species were thus overlapped in a watersheds shapefile (HydroSHEDS database lev 5; Lehner & Grill, 2013; available at http://www.hydrosheds.org/) to produce an M for each species, using QGIS (QGIS Development Team, 2015). The Neotropical watersheds represent current distributional barriers, and they are implicated in speciation and vicariant events of mammals (e.g. Patterson et al., 2012; Giarla & Jansa, 2014; Kay, 2015). We defined five large zones to allow model back-projection (MH and LIG) using target-groups of species with close M. They represent potential back conditions and reflect the dispersal ability of the grouping species. For each species, we calculated the variance inflation factor (VIF) in the R package HH (Richard, 2016), to identify multicollinearity of the original 19 variables, and exclude correlated variables from the model formulation considering the "rule of thumb" of VIF > 10 (Zuur et al., 2010).

Species distribution models were built using Maxent (Phillips et al. 2006, 2008) as implemented by the 'dismo' package (Hijmans et al., 2017; R version 3.3.2; R Core Team 2016) using random seed. Logistic output format was used to describe the probability of presence (Phillips & Dudík, 2008), which is a continuous habitat suitability range between 0 (unsuitable) and 1 (the most suitable). The performance of SDM is affected when using datasets with few occurrence records (Pearson et al., 2007; Shcheglovitova & Anderson, 2013); the model accuracy decreases, and model variability increases with decreasing occurrence records (Wisz et al., 2008). Hence, we followed two approaches to produce models that maximize the utility of the information available:

(1) The delete-one jackknife approach by Pearson et al. (2007; called "n − 1 jackknife") was applied to species with few records (9 to 25). We made multiple predictions per species with one of the records excluded in each case, and then assessed the model's performance testing the ability of the model to predict the excluded locality under a statistical significance (Pearson et al., 2007). We applied the other Maxent settings by default and chose the lowest predicted value (lowest presence threshold, LPT) associated with any one of the observed presence records to test the models (Pearson et al., 2007; $P < 0.05$). We made the

transfer of a single ecological niche model per species onto current climate and past climate conditions, using its complete records and reporting its statistical significance.

(2) For species with large number of records (26 or more) we retained 75% of the records to train the model and 25% to evaluate the predictive power of the model. We used a model selection procedure to tune the β multiplier (regularization parameter) and features selection to reduce the complexity of the models (Anderson & González, 2011; Warren & Seifert, 2011; Shcheglovitova & Anderson, 2013) using the the 'ENMeval' package (Muscarella et al., 2014; R version 3.3.2; R Core Team 2016). The regularization multiplier varied from 0.5 to 4.0 in increments of 0.5, and the following four feature classes (or their combinations) were tested: (1) linear; (2) linear and quadratic; (3) hinge; and (4) linear, quadratic, and hinge. Model performance was assessed using the Akaike Information Criterion corrected for small sample sizes (AICc; Warren & Seifert 2011). The result of this process was a single ecological niche model for each species with its own β value and features.

We tested the predictive power of the models using partial Receiver Operator Characteristic (partial ROC) approaches, which avoids at least some of the failings associated with traditional ROC analyses (Peterson et al., 2008). We used an acceptable omission error threshold of E = 10 (Peterson et al., 2008), and 1000 replicate with 50% bootstrap resampling to establish whether the ROC AUC (area under the curve) ratio was above 1.0. These tests were run using online tools available at Conabio (year; http://shiny.conabio.gob.mx:3838/nichetoolb2/). Significance of partial ROCs was assessed by direct count of the proportion of replicate analyses with an AUC ratio ≤1.0. We transferred the current ecological niche model for each species onto past climate conditions using the β multiplier (regularization parameter) and features tuned.

Threshold is an important step to obtain SDM since a fixed threshold to transform model output (logistic values to binary) will exaggerate prediction errors (Fielding & Bell, 1997). Therefore, we applied two thresholds:

(1) Lowest presence threshold (LPT) was applied to species with few records (< 25). It represents the lowest value of the prediction for any of the pixels that correspond to the localities used in calibrating the model (Pearson et al., 2007); this case excluded the consideration of mistakes in the records.

(2) Omission error threshold of E = 10 (Peterson et al., 2008) was applied to species with a large number of records (26 or more). E = 10, represents 10% of the records that can be misleading. When the number of records increases, the error in the available data may also increase, thus the E= 10 is useful to reduce error acceptable in the model (Peterson et al., 2008).

When transferring models, some zones of extrapolation may be encountered. To identify these regions, we used multivariate environmental similarity surfaces (MESS) and the most dissimilar variable (MoD; Elith et al., 2010) outputs generated by Maxent software. Areas identified as extrapolative were removed from analyses to avoid interpreting results outside of known climatic response conditions for the endemic species.

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Appendix S2. Summary of the data and parameters used in the ecological niche modelling process. Code= number of the area of endemism by Noguera-Urbano and Escalante (2015), Name= name of the area of endemism by Noguera-Urbano and Escalante (2015); Endemic species= species for which the ENM was obtained; TR= number of total records; N° RT10= number of records after filter the records at 10km (Thin10 km); Bio= number (code following Worldclim) of the bioclimatic variables selected after running the Variance Inflation Factor (VIF<10); Evaluation= type of metric used to evaluate the models; P-value= probability for the metrics used in the evaluation of the models; Concl= Conclusion (p>0.05) about the ENM, Accepted= accepted and analyzed species; and TH=Threshold used to reclassify the logistic models to binary maps.

Code	Name	Endemic species	TR	N° RT10	Bio	Evaluation	*P-value*	Concl	TH
Ae10	Northern Mesoamerican dominion	*Artibeus hirsutus*	121	68	12, 14, 15, 18, 19, 2, 3, 9	Partial ROC	0	Accepted	0.278586
		Natalus lanatus	22	21	10, 14, 15, 16, 18, 19, 2, 3	n − 1 jackknife	0.000001	Accepted	0.232
Ae14	Northern South American transition zone	*Cuniculus taczanowskii*	39	33	15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.413781
		Didelphis pernigra	66	63	13, 14, 15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.234624
		Marmosops impavidus	55	50	15, 16, 18, 19, 2, 3, 4, 8	Partial ROC	0.008	Accepted	0.266968
		Monodelphis adusta	32	28	13, 15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.365916
		Thomasomys aureus	82	57	13, 15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.400916
Ae19	Western Brazilian subregion	*Aotus nancymaae*	5	5	13, 19, 3, 4, 7, 8, 9	n − 1 jackknife	0.075605	Excluded	
		Cacajao calvus	25	20	13, 14, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.03414	Accepted	0.066
		Callicebus cupreus	41	29	13, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.42349

		Callicebus regulus	9	9	13, 14, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.008842	Excluded by overprediction	
		Lagothrix poeppigii	20	17	13, 15, 18, 2, 4, 8, 9	n − 1 jackknife	0.047879	Accepted	0.338
		Neacomys minutus	10	10	10, 13, 18, 19, 2, 3, 8	n − 1 jackknife	0.677937	Excluded	
		Philander mcilhennyi	12	10	13, 15, 18, 2, 3, 8	n − 1 jackknife	0.096089	Excluded	
		Saguinus mystax	28	15	13, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.023133	Accepted	0.284
Ae31	Brazilian Boreal Dominion	*Lophostoma schulzi*	7	7	14, 16, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.498377	Excluded	
		Marmosops parvidens	44	37	13, 14, 15, 18, 19, 2, 3, 4, 8	Partial ROC	0.23	Excluded	
		Myoprocta acouchy	25	25	13, 14, 15, 16, 18, 19, 2, 3, 4, 8	Partial ROC	0	Excluded by overprediction	
		Neacomys paracou	29	23	13, 14, 15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.085014	Excluded	
		Oecomys auyantepui	24	19	15, 16, 18, 19, 3, 4, 7, 8	n − 1 jackknife	0	Excluded by overprediction	
		Oecomys rutilus	13	12	13, 15, 16, 18, 19, 2, 3, 4, 9	n − 1 jackknife	0.520861	Excluded	
		Pithecia pithecia	30	28	13, 14, 15, 18, 19, 3, 4, 7, 8	Partial ROC	0.024	Excluded by overprediction	

		Saccopteryx gymnura	11	10	13, 14, 15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.049503	Excluded	
		Saguinus midas	32	31	13, 14, 15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Excluded by overprediction	
Ae32	Northwestern Chacoan subregion	*Calomys expulsus*	26	23	13, 14, 15, 18, 19, 3, 4, 7, 8, 9	n − 1 jackknife	0.050418	Excluded	
		Kerodon rupestris	14	14	12, 14, 15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.046601	Accepted	0.344
		Thrichomys apereoides	30	27	12, 14, 15, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.473395
		Wiedomys pyrrhorhinos	21	19	12, 14, 15, 18, 3, 4, 7, 8, 9	n − 1 jackknife	0.000003	Accepted	0.234
Ae34	Parana dominion	*Akodon montensis*	149	86	13, 18, 19, 3, 6, 7	Partial ROC	0	Accepted	0.326859
		Akodon serrensis	42	35	10, 12, 13, 18, 3, 7, 8, 9	Partial ROC	0.012	Accepted	0.240841
		Bibimys labiosus	13	11	14, 18, 3, 7, 8, 9	n − 1 jackknife	0.000173	Accepted	0.214
		Cebus nigritus	51	44	12, 13, 18, 2, 3, 8, 9	Partial ROC	0	Accepted	0.472156
		Delomys dorsalis	15	14	10, 12, 13, 3, 7, 8, 9	n − 1 jackknife	0.207728	Excluded	
		Euryzygomatomys spinosus	28	27	10, 12, 13, 18, 3, 7, 8, 9	Partial ROC	0	Accepted	0.455627
		Gracilinanus microtarsus	135	60	13, 18, 19, 3, 4, 7, 8	Partial ROC	0	Accepted	0.337332
		Juliomys pictipes	37	23	1, 12, 13, 18, 2, 3, 8, 9	Partial ROC	0	Accepted	0.405698
		Kannabateomys amblyonyx	37	29	1, 12, 13, 2, 3, 8, 9	Partial ROC	0	Accepted	0.427581

		Monodelphis scalops	25	13	1, 12, 13, 18, 2, 3, 8, 9	n − 1 jackknife	0.457515	Excluded	
		Phyllomys medius	9	7	10, 13, 18, 19, 3, 7, 8, 9	n − 1 jackknife	0.953927	Excluded	
		Vampyressa pusilla	13	11	12, 13, 18, 3, 6, 7, 8, 9	n − 1 jackknife	0.241259	Excluded	
Ae97	Magellanic forest province	*Abrothrix longipilis*	565	260	13, 14, 15, 3, 4, 6, 8, 9	Partial ROC	0	Accepted	0.253791
		Lasiurus varius	15	13	14, 15, 16, 3, 4, 6, 8, 9	n − 1 jackknife	0.002858	Accepted	0.206
		Myotis chiloensis	51	34	1, 13, 14, 15, 3, 4, 8, 9	Partial ROC	0.008	Accepted	0.37749
Ae98	Central Chilean subregion	*Geoxus valdivianus*	131	78	14, 15, 3, 4, 8, 9	Partial ROC	0	Accepted	0.284367
		Hippocamelus bisulcus	11	9	14, 15, 3, 4, 8, 9	n − 1 jackknife	0.073839	Excluded	
		Histiotus magellanicus	35	25	1, 14, 15, 3, 4, 8, 9	Partial ROC	0	Accepted	0.280755
		Loxodontomys micropus	27	27	14, 15, 19, 3, 4, 6, 8, 9	Partial ROC	0.096	Excluded	
Ae99	Central Chilean subregion and Maule province	*Chelemys macronyx*	118	81	14, 15, 3, 4, 6, 8, 9	Partial ROC	0	Accepted	0.19252
		Eligmodontia morgani	92	58	14, 15, 19, 3, 4, 6, 8, 9	Partial ROC	0.012	Accepted	0.147444
Ae20	Mesoamerican dominion	*Carollia sowelli*	52	28	14, 15, 16, 18, 19, 2, 3, 8	Partial ROC	0.064	Excluded	
		Handleyomys rostratus	121	38	13, 14, 15, 18, 19, 2, 4, 8	Partial ROC	0.062	Excluded	
		Myotis elegans	47	34	14, 15, 16, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.385416
		Orthogeomys hispidus	248	129	13, 14, 15, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.332301
		Rhogeessa tumida	105	71	13, 14, 15, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.275038

		Sciurus deppei	379	209	13, 14, 15, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.342757
		Sphiggurus mexicanus	32	25	14, 15, 16, 18, 19, 3, 7, 8	n − 1 jackknife	0.012765	Accepted	0.154
		Tylomys nudicaudus	133	70	14, 15, 16, 18, 19, 3, 7, 8	Partial ROC	0	Accepted	0.300086
Ae22	Western Mexican transition zone	*Choeronycteris mexicana*	319	207	1, 14, 15, 16, 18, 19, 2, 3, 8, 9	Partial ROC	0.558	Excluded	
		Leptonycteris yerbabuenae	440	237	1, 13, 14, 15, 18, 19, 2, 3, 9	Partial ROC	0	Accepted	0.210882
		Mephitis macroura	356	232	13, 14, 15, 18, 19, 2, 3, 8, 9	Partial ROC	0	Accepted	0.308863
AET41	Northern Mexico	*Cratogeomys castanops*	586	284	13, 15, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.271448
		Neotoma leucodon	73	51	13, 14, 15, 18, 19, 2, 3, 8, 9	Partial ROC	0	Accepted	0.285562
		Neotoma micropus	1055	566	13, 14, 15, 18, 2, 3, 8, 9	Partial ROC	0	Accepted	0.304637
		Perognathus merriam	178	143	13, 14, 15, 18, 2, 3, 8, 9	Partial ROC	0	Accepted	0.300986
AET43	Central Mexico	*Ammospermophilus interpres*	140	72	13, 14, 15, 18, 19, 2, 3, 8, 9	Partial ROC	0	Accepted	0.289994
		Chaetodipus eremicus	185	128	11, 14, 15, 18, 19, 2, 8, 9	Partial ROC	0	Accepted	0.299334
		Chaetodipus nelsoni	506	278	13, 14, 18, 19, 2, 6, 8, 9	Partial ROC	0	Accepted	0.339048
		Onychomys arenicola	323	171	11, 12, 14, 15, 18, 19, 2, 8, 9	Partial ROC	0	Accepted	0.223042
Ae48	Pantepui province	*Platyrrhinus aurarius*	19	15	13, 14, 15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.076848	Excluded	
		Proechimys hoplomyoides	12	6	13, 15, 18, 19, 3, 4, 7, 8	n − 1 jackknife	0.141626	Excluded	

		Rhipidomys macconnelli	16	16	13, 14, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0	Excluded by overprediction	
		Rhipidomys wetzeli	11	7	13, 15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.000002	Excluded by overprediction	
Ae59	Southern Puna province	*Abrocoma cinerea*	25	22	14, 15, 18, 2, 3, 9	n − 1 jackknife	0	Accepted	0.049
		Akodon albiventer	91	71	14, 15, 18, 2, 3, 9	Partial ROC	0	Accepted	0.390042
		Akodon lutescens	61	52	14, 15, 18, 2, 3, 9	Partial ROC	0	Accepted	0.386966
		Andinomys edax	36	30	14, 15, 18, 3, 7, 9	Partial ROC	0	Accepted	0.422758
		Auliscomys sublimis	55	40	13, 14, 15, 18, 2, 3, 8	Partial ROC	0	Accepted	0.314054
		Calomys boliviae	30	22	13, 14, 15, 18, 3, 7, 9	n − 1 jackknife	0	Accepted	0.146
		Chaetophractus nationi	13	11	14, 15, 18, 19, 3, 4, 9	n − 1 jackknife	0.121701	Excluded	
		Ctenomys opimus	63	43	14, 15, 18, 2, 4, 9	Partial ROC	0	Accepted	0.38117
		Eligmodontia puerulus	30	26	11, 12, 14, 15, 3	Partial ROC	0	Accepted	0.394825
		Octodontomys gliroides	27	24	14, 15, 17, 18, 2, 4, 9	n − 1 jackknife	0	Accepted	0.084
		Oxymycterus paramensis	64	48	13, 14, 15, 18, 2, 3, 9	Partial ROC	0	Accepted	0.342169
		Phyllotis osilae	90	71	13, 14, 15, 18, 2, 3, 9	Partial ROC	0	Accepted	0.291989
		Rhipidomys austrinus	19	18	13, 14, 15, 2, 3, 8	n − 1 jackknife	0.000004	Accepted	0.193
Ae60	Puna province	*Akodon boliviensis*	82	53	13, 14, 15, 18, 2, 3, 8	Partial ROC	0	Accepted	0.325869
		Akodon fumeus	41	30	13, 14, 15, 2, 3, 8	Partial ROC	0	Accepted	0.422342

		Microcavia niata	12	12	14, 15, 16, 19, 3, 4, 7, 9	n − 1 jackknife	0	Accepted	0.365
		Necromys amoenus	22	20	13, 14, 15, 18, 2, 3, 9	n − 1 jackknife	0	Accepted	0.23
Ae84 Ae84 Ae84	Pacific Lowlands and Balsas Basin provinces	*Cratogeomys fumosus*	32	23	12, 14, 15, 17, 18, 19, 2, 3, 8	Partial ROC	0.218	Excluded	
		Hodomys alleni	53	36	12, 14, 15, 17, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.354232
		Osgoodomys banderanus	182	89	14, 15, 16, 17, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.329177
		Sigmodon allenii	46	29	12, 14, 15, 17, 18, 19, 2, 3, 8	Partial ROC	0	Accepted	0.270224
		Sylvilagus cunicularius	135	71	12, 14, 15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.357027
Ae91	Madeira and Rondônia provinces	*Aotus nigriceps*	36	30	13, 14, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.403763
		Lagothrix cana	22	22	13, 14, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.000013	Accepted	0.116
		Pithecia irrorata	47	37	10, 13, 14, 18, 19, 2, 3, 4	Partial ROC	0	Excluded by overprediction	
AET125	Northern Andes	*Akodon affinis*	40	32	15, 18, 19, 2, 3, 4, 6	Partial ROC	0.092	Excluded	
		Artibeus rosenbergii	17	16	15, 18, 19, 2, 3, 4, 9	n − 1 jackknife	0.000767	Excluded by overprediction	
		Caenolestes convelatus	17	15	15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.000003	Accepted	0.252

		Choeroniscus periosus	9	8	15, 18, 19, 2, 3, 4, 9	n − 1 jackknife	0.052025	Excluded	
		Coendou rufescens	48	37	15, 18, 19, 2, 3, 4, 8	Partial ROC	0	Accepted	0.238934
		Neusticomys monticolus	22	17	15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0	Accepted	0.258
		Platyrrhinus chocoensis	17	15	15, 18, 19, 3, 4, 7, 9	n − 1 jackknife	0.395343	Excluded	
		Rhinophylla alethina	11	11	18, 19, 2, 3, 4, 8	n − 1 jackknife	0.107902	Excluded	
		Rhipidomys caucensis	10	8	15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.051515	Excluded	
		Sturnira aratathomasi	5	5	14, 15, 18, 19, 3, 4, 7, 8	n − 1 jackknife	0.006253	Excluded by overprediction	
		Thomasomys cinereiventer	27	21	15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0	Excluded by overprediction	
		Thomasomys popayanus	9	6	13, 15, 2, 3, 4, 8	n − 1 jackknife	0.0078016	Accepted	0.504
		Tylomys mirae	25	21	15, 18, 19, 2, 3, 4, 8	n − 1 jackknife	0.010259	Excluded by overprediction	
		Zygodontomys brunneus	16	14	14, 15, 18, 19, 2, 3, 4, 6	n − 1 jackknife	0.001047	Excluded by overprediction	
Ae93	Atacama, Desert, Puna	*Abrothrix jelskii*	85	70	13, 14, 15, 18, 2, 3, 8	Partial ROC	0	Accepted	0.254799
		Calomys lepidus	94	73	13, 14, 15, 18, 2, 3, 8	Partial ROC	0	Accepted	0.358175
		Cavia tschudii	40	31	14, 15, 18, 2, 3, 8	Partial ROC	0.078	Excluded	

	and Yungas provinces	*Hippocamelus antisensis*	13	13	14, 15, 18, 2, 3, 8, 9	n − 1 jackknife	0.006426	Accepted	0.26
		Mormopterus kalinowskii	11	9	13, 14, 15, 3, 4, 7, 8	n − 1 jackknife	0.000012	Excluded by overprediction	

References

Noguera-Urbano, E. A., & Escalante T. (2015) Áreas de endemismo de los mamíferos (Mammalia) neotropicales. *Acta Biológica Colombiana, 20*, 47–65.

Appendix S3. Current areas of mammal endemism analyzed in this study, obtained summing the endemic potential distribution of mammals for each area of endemism.

Figure S1. Northern Mesoamerican dominion (Ae10)

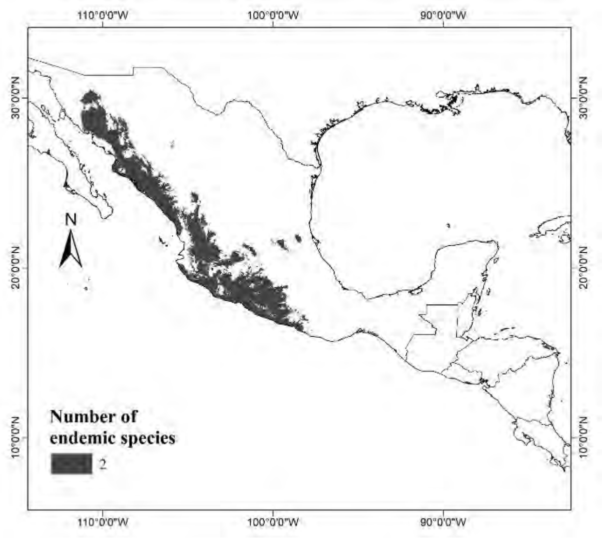


Figure S2. Northern South American transition zone (Ae14)

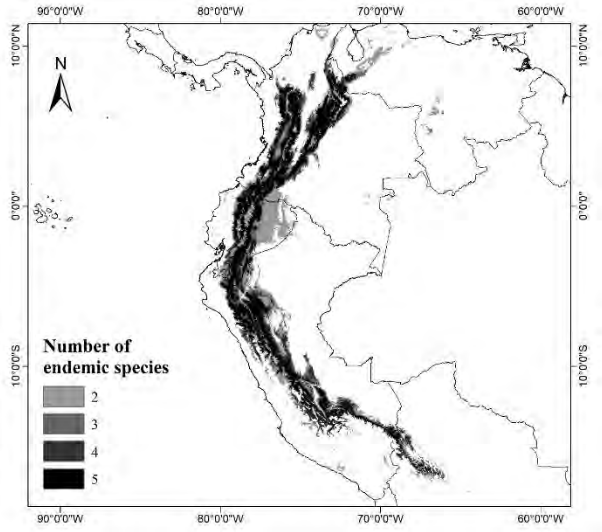


Figure S3. Western Brazilian subregion (Ae19)

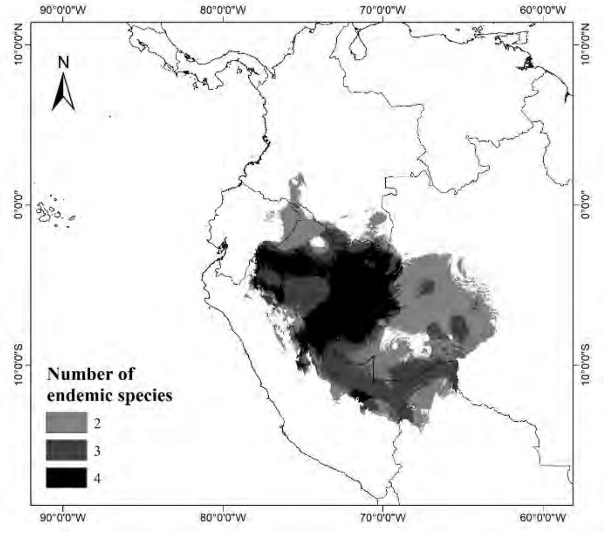


Figure S4. Mesoamerican dominion (Ae20)

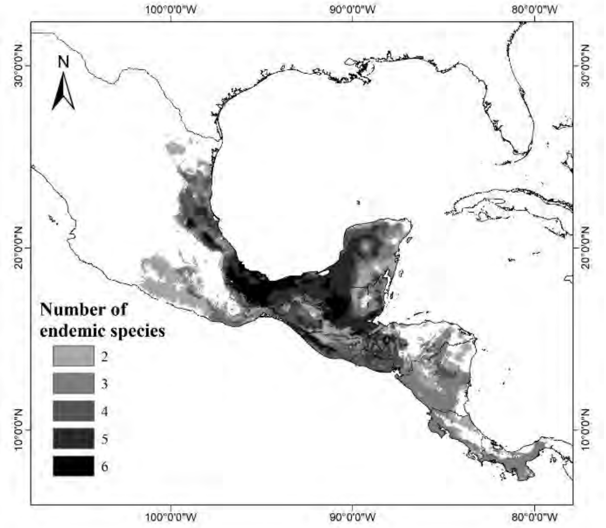


Figure S5. Western Mexican transition zone (Ae22)

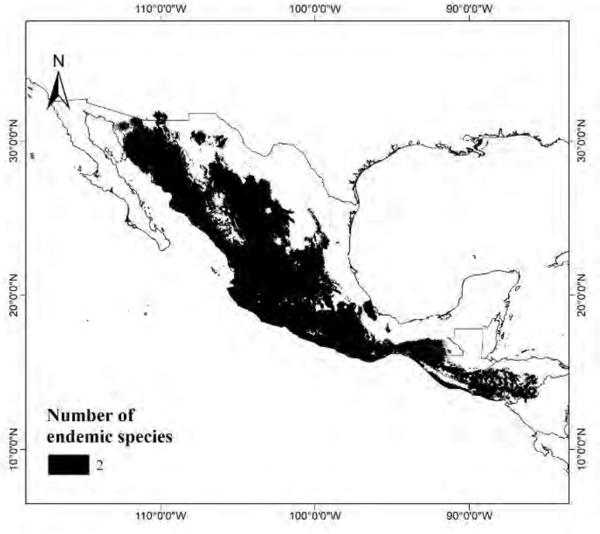


Figure S6. Northwestern Chacoan subregion (Ae32)

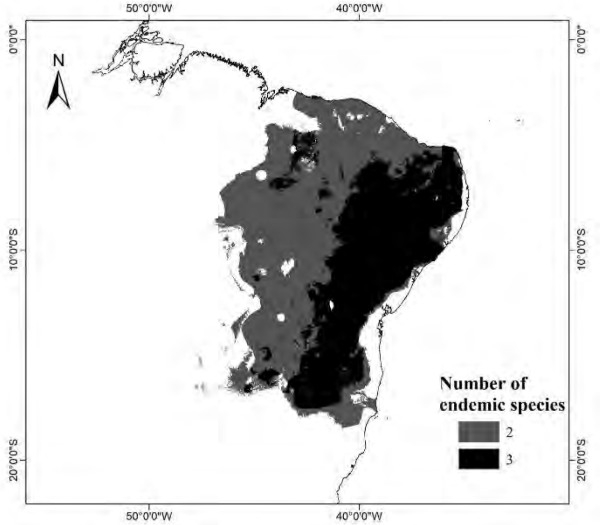


Figure S7. Parana dominion (Ae34)

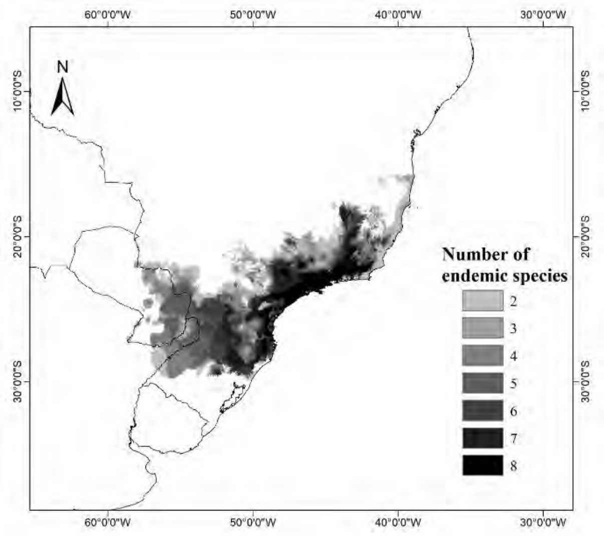


Figure S8. Northern Mexico (AET41)

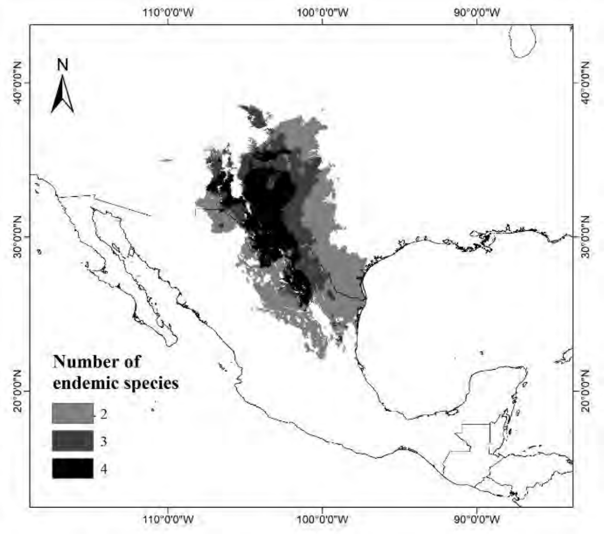


Figure S9. Central Mexico (AET43)

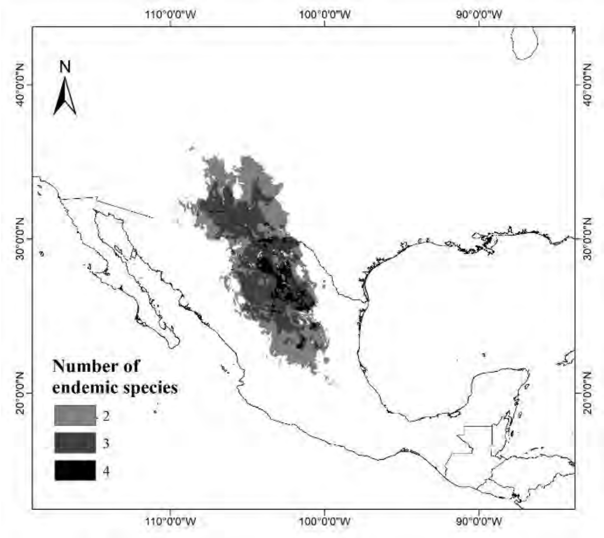


Figure S10. Southern Puna province (Ae59)

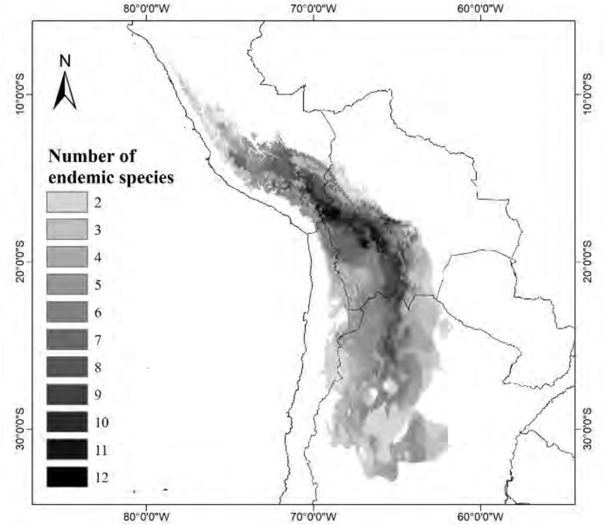


Figure S11. Puna province (Ae60)

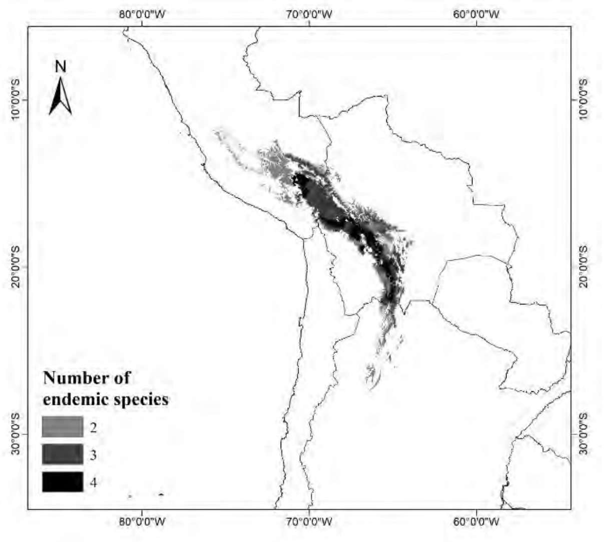


Figure S12. Pacific Lowlands and Balsas Basin provinces (Ae84)

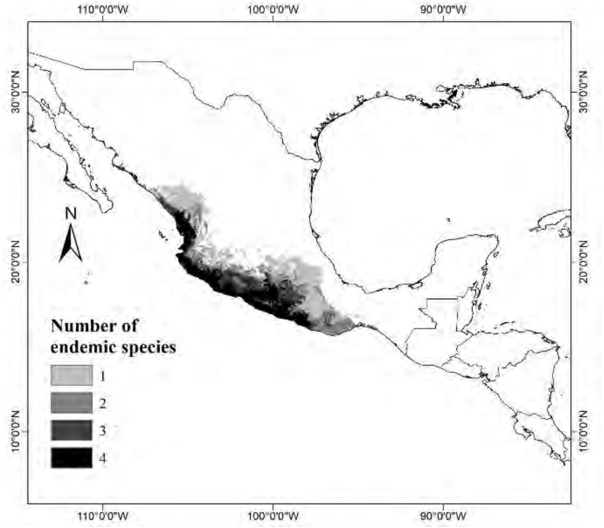


Figure S13. Madeira and Rondônia provinces (Ae91)

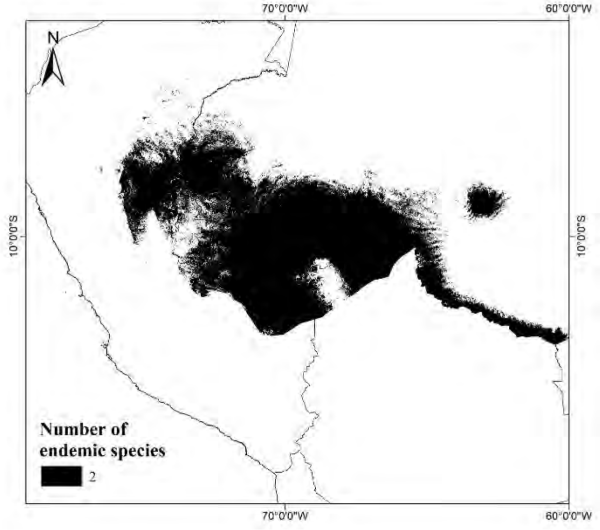


Figure S14. Atacama Desert, Puna and Yungas provinces (Ae93)

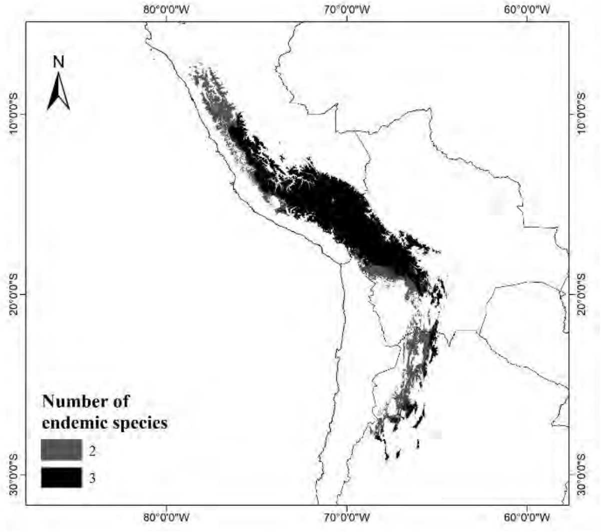


Figure S15. Magellanic forest province (Ae97)

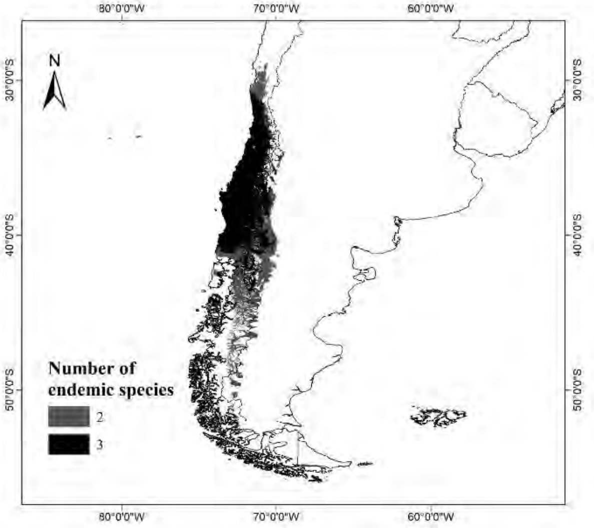


Figure S16. Central Chilean subregion (Ae98)

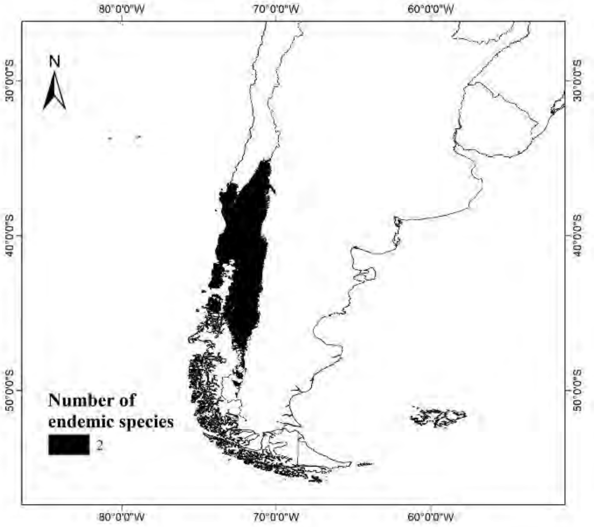


Figure S17. Central Chilean subregion and Maule province (Ae99)

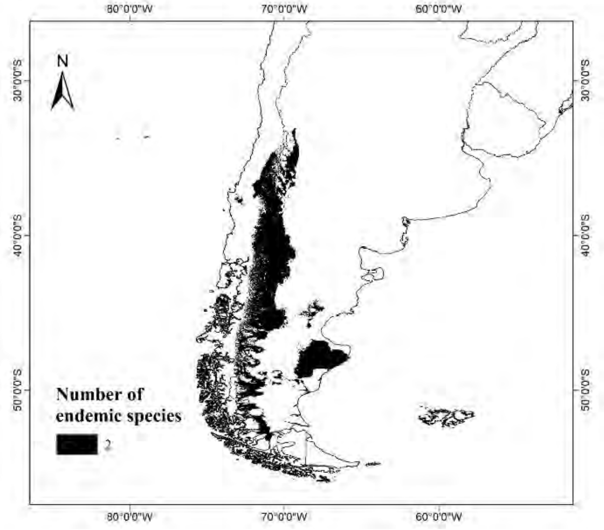
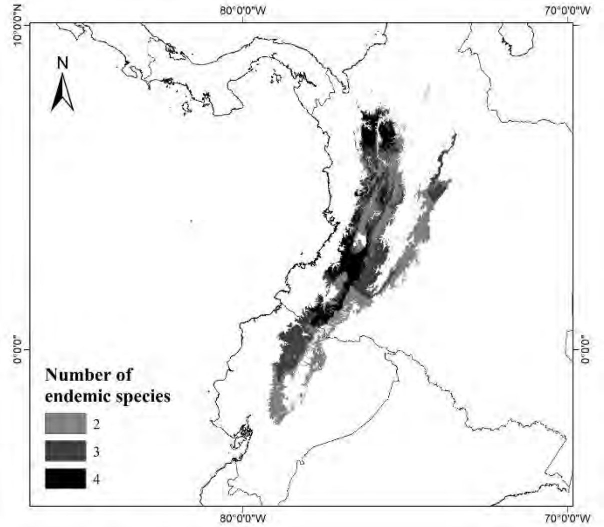


Figure S18. Northern Andes (AET125)



Appendix S4. Dynamism of the Neotropical areas of endemism based on distribution of mammal species from the sum of the areas of endemism from three time spans (C=Current, MH=Mid Holocene, LIG= Last Interglaciation).

Figure S1. Northern Mesoamerican dominion (Ae10)

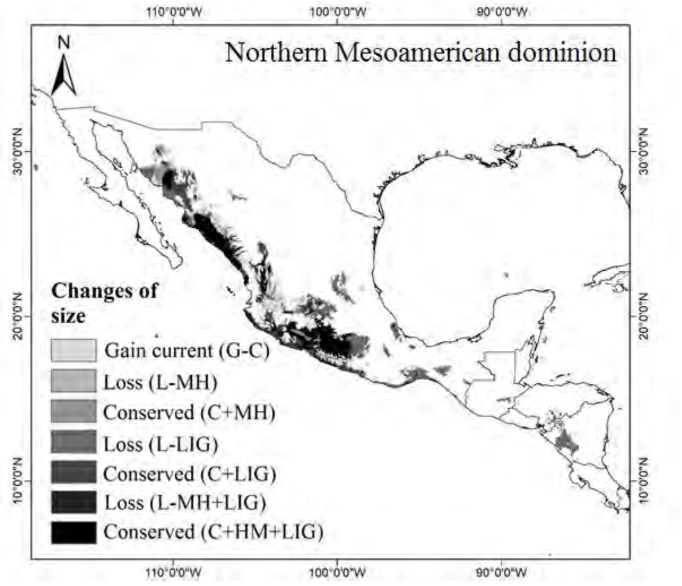


Figure S2. Northern South American transition zone (Ae14)

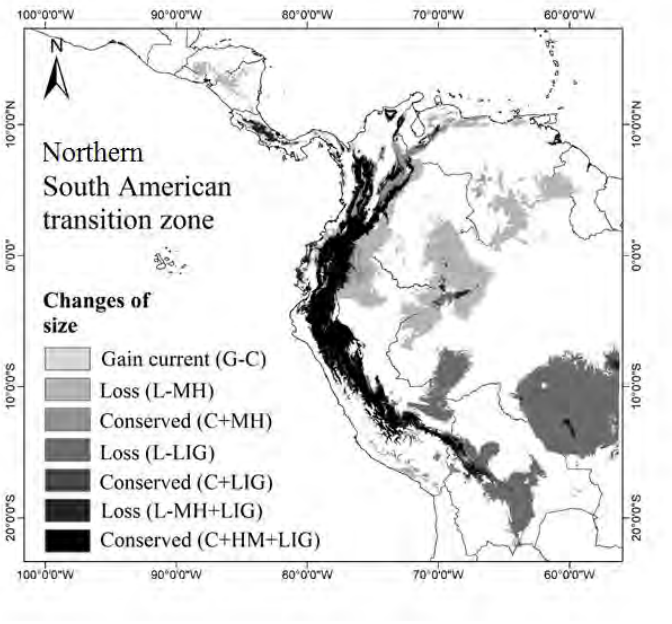


Figure S3. Western Brazilian subregion (Ae19)

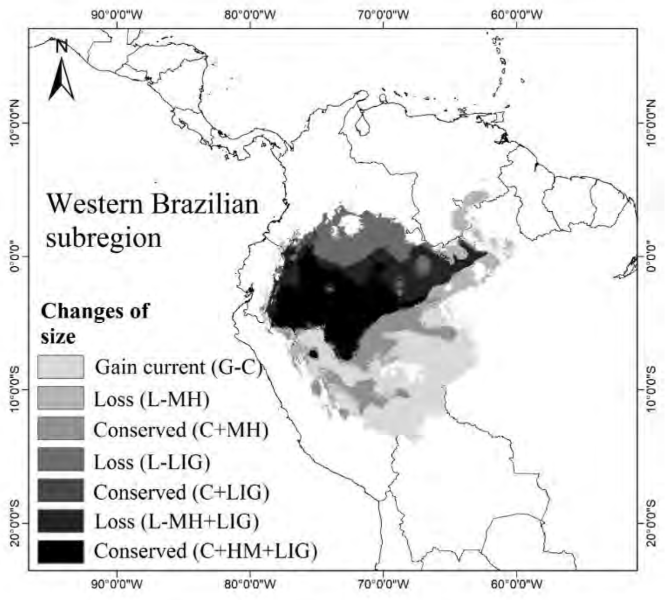


Figure S4. Mesoamerican dominion (Ae20)

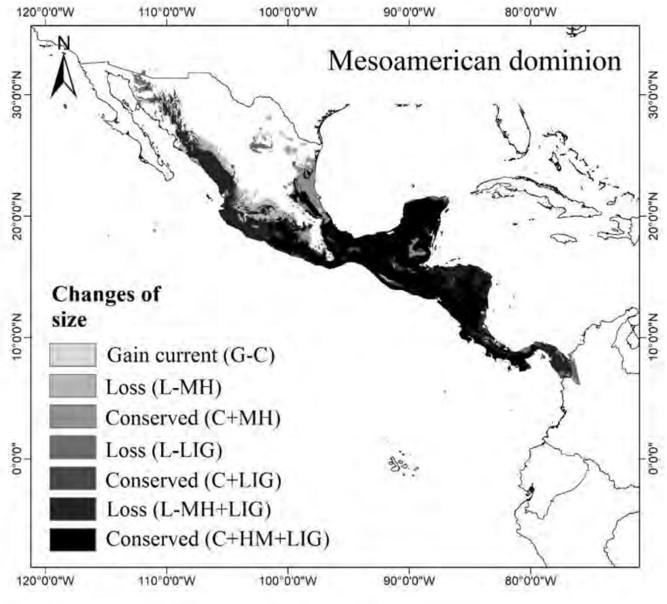


Figure S5. Western Mexican transition zone (Ae22)

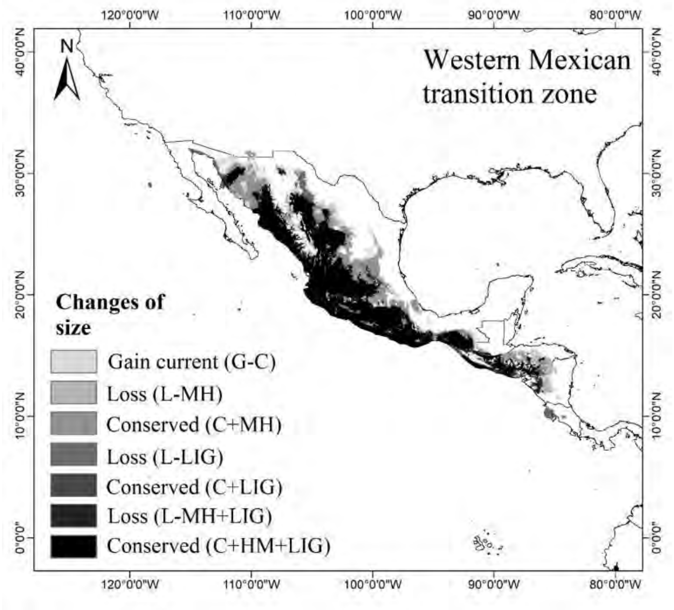


Figure S6. Northwestern Chacoan subregion (Ae32)

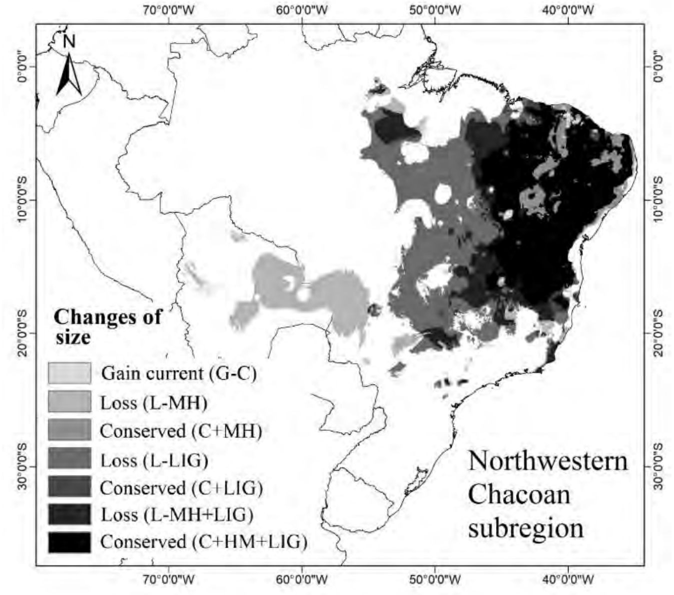


Figure S7. Parana dominion (Ae34)

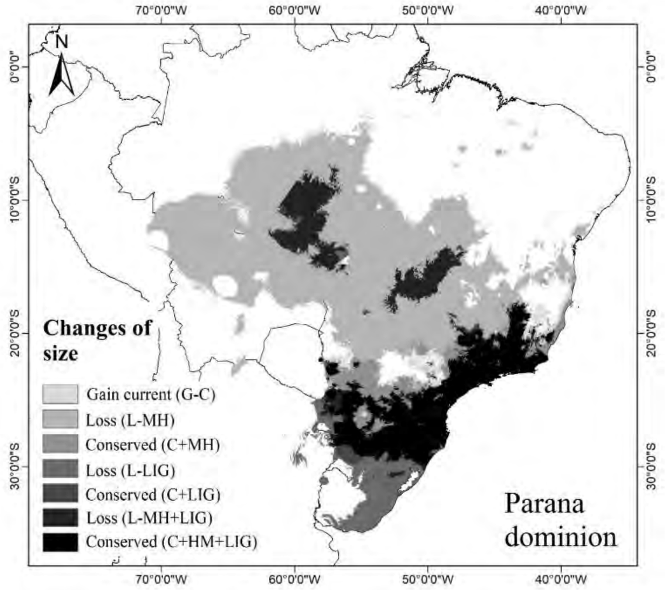


Figure S8. Northern Mexico (AET41)

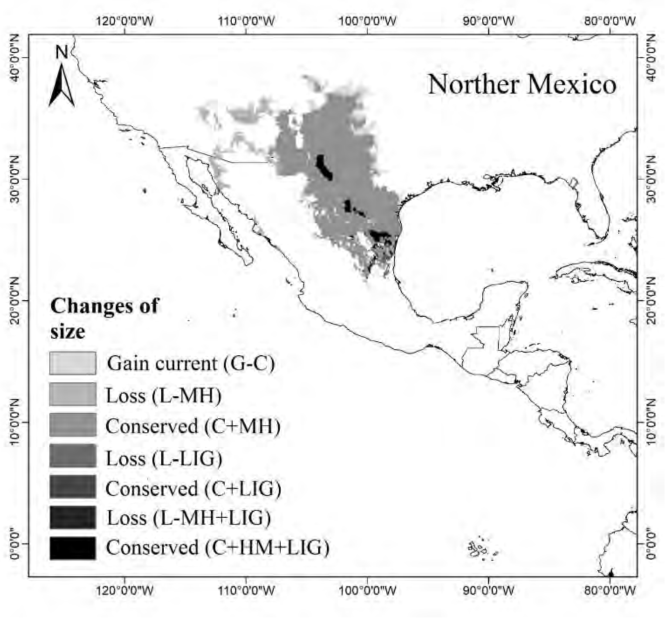


Figure S9. Central Mexico (AET43)

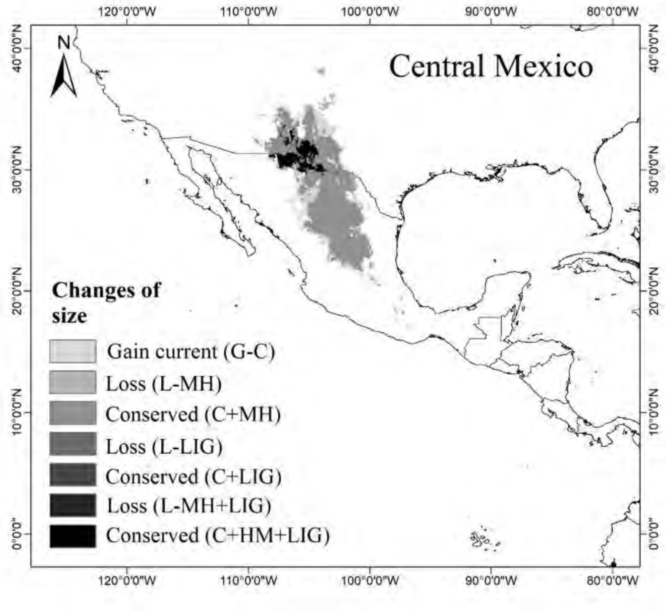


Figure S10. Southern Puna province (Ae59)

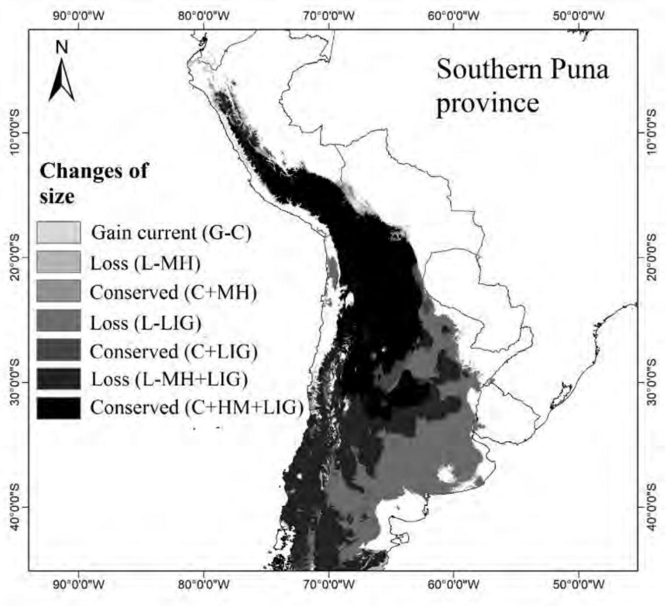


Figure S11. Puna province (Ae60)

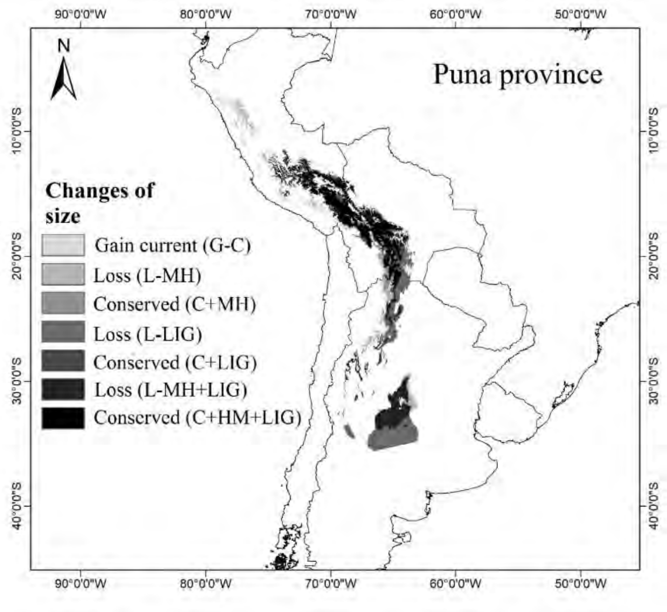


Figure S12. Pacific Lowlands and Balsas Basin provinces (Ae84)

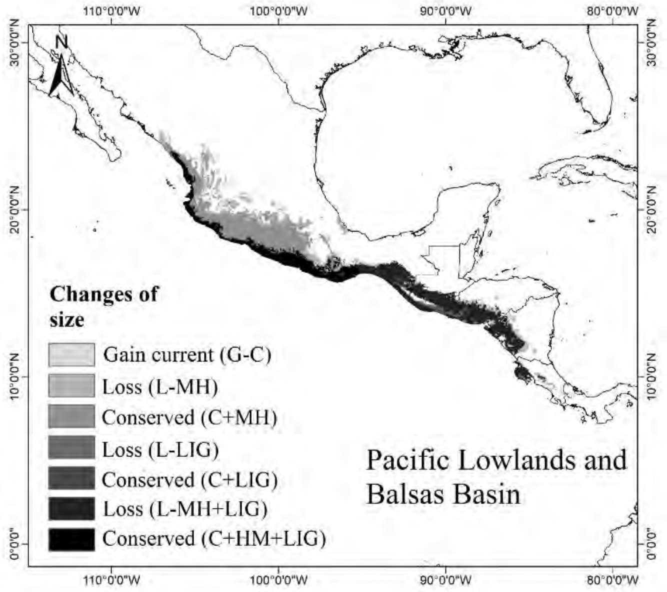


Figure S13. Madeira and Rondônia provinces (Ae91)

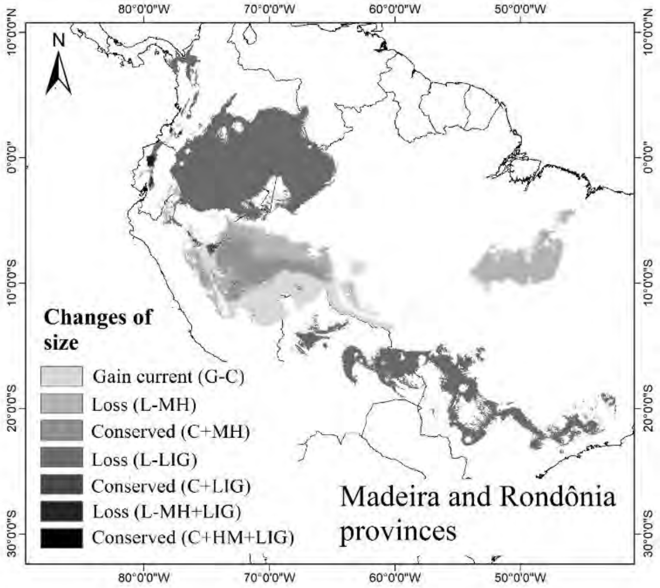


Figure S14. Atacama Desert, Puna and Yungas provinces (Ae93)

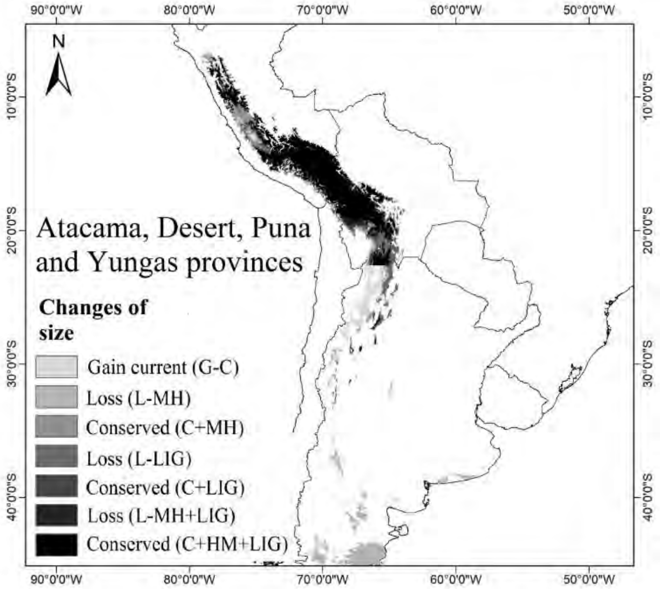


Figure S15. Magellanic forest province (Ae97)

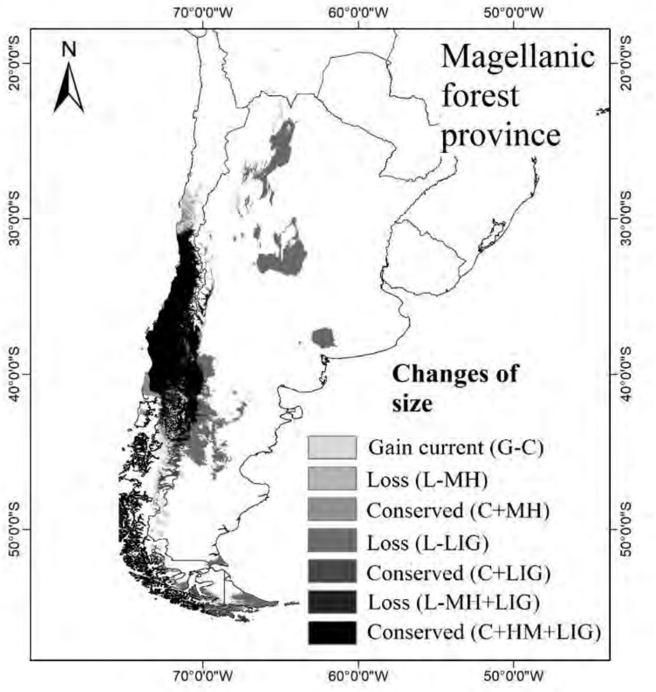


Figure S16. Central Chilean subregion (Ae98)

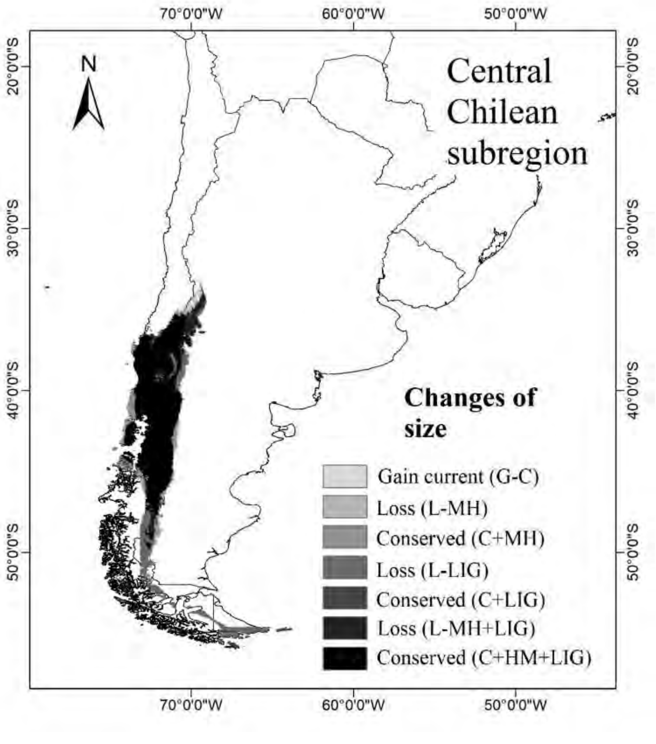


Figure S17. Central Chilean subregion and Maule province (Ae99)

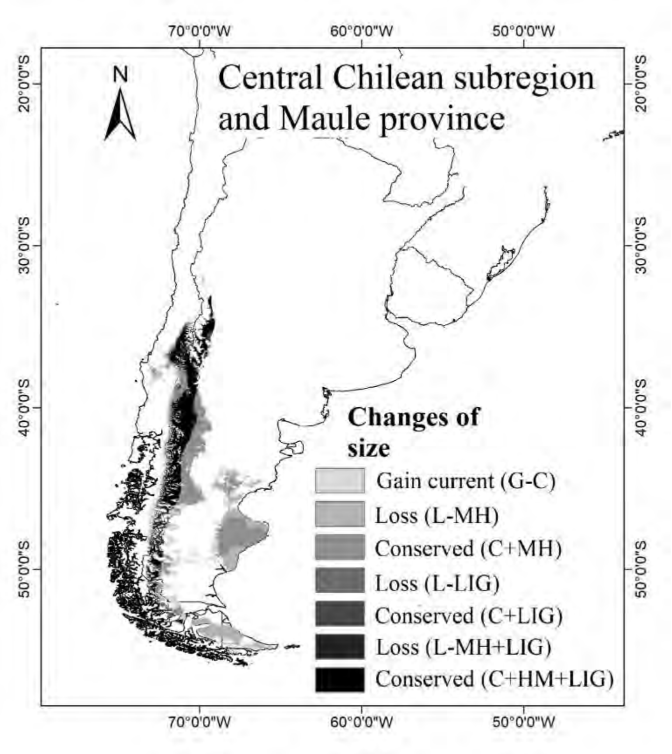
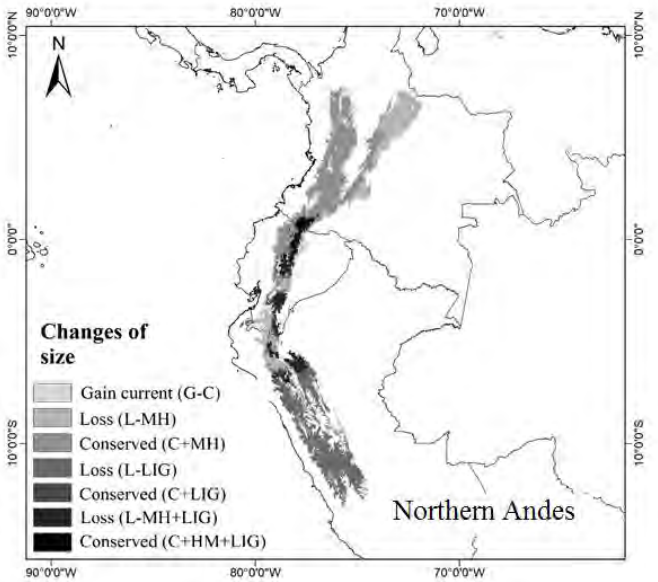


Figure S18. Northern Andes (AET125)



Appendix S5. Set of variables used to analyze of dynamism of the areas of endemism of Neotropical mammals. C total size= Size of the area of endemism in the current (km^2); MH total size= Size of the area of endemism in the Mid Holocene (km^2); LIG total size= Size of the area of endemism in the Last Interglacial (km^2); G-C= Gain current; L-MH= Mid Holocene area loss in the current; C+MH= Mid Holocene area conserved in the present; L-LIG= Last Interglacial area loss in the current; C+LIG= Last Interglacial area conserved in the current; L-MH+LIG= Mid Holocene and Last Interglacial areas loss in the current; C+HM+LIG= Mid Holocene and Last Interglacial areas conserved in the current. C-sps= Number of endemic species in the current; C-Size-MaxSp= Size of the area composed by the maximum number of species within the current areas of endemism; MH-sp= Number of species in the Mid Holocene areas of endemism; MH-SizeMaxSp= Size of the area composed by the maximum number of species into the Mid Holocene areas of endemism; LIG-sp= Number of species in the Last Interglacial areas of endemism; LIG-SizeMaxSp= Size of the area composed by the maximum number of species within the Last Interglacial areas of endemism; Order-C= Number of orders in the current areas of endemism; PD= Faith's Index of phylogenetic diversity (Faith, 1992) of the current areas of endemism; MinAge= Minimal age of the endemic species in the current areas of endemism; and MaxAge= Maximal age of the endemic species in the current areas of endemism.

Ae	Ae10	Ae84	Ae91	AET125	Ae93	Ae14	Ae19	Ae32	Ae34
C total size	383511	278827	621917	179341	574807	931483	1763501	1595445	1360246
MH total size	178675	538188	889339	307242	710336	1925925	1552731	2657719	5131227
LIG total size	363053	271999	1784586	176339	563574	1978776	1334001	3185755	1764479

G-C	119164	6056	360405	27113	75064	34909	806832	25287	127945
L-MH	6200	110208	615789	113701	164230	979149	237771	600653	3436957
C+MH	32754	176106	256281	143324	78289	178009	359953	198985	316965
L-LIG	121099	19076	1763007	126088	91476	1167124	360071	1282592	346424
C+LIG	102233	1049	4310	34	4281	42885	18923	45082	40750
L-MH+LIG	10361	156258	16348	41347	50644	93087	377214	531990	502719
C+HM+LIG	129360	95616	921	8870	417173	675680	577793	1326091	874586
C-sps	2	4	2	4	3	5	4	3	8
C-Size-MaxSp	383511	118534	621917	31488	379160	314368	475105	686871	120222
MH-sp	2	4	2	4	3	5	4	3	8
MH-SizeMaxSp	178675	223168	889339	51550	355046	379895	161072	1178135	128255
LIG-sp	2	4	2	4	3	5	4	3	8
LIG-SizeMaxSp	363053	64628	1784586	20	321146	239766	249729	823356	43318
Order-C	1	2	1	2	2	2	1	1	3
PD	207.5	300.4	170.7	399.4	259.6	474	212.8	274.8	524.9
MinAge	2.3	3.2	2.2	3.7	0.2	3.4	4.9	4.5	3.1
MaxAge	19.9	30.1	8.7	35.6	18.2	10.8	16.3	4.9	13.3

Ae	Ae97	Ae98	Ae99	Ae20	Ae22	AET41	AET43	Ae59	Ae60
C total size	509587	406038	499146	1105835	1390830	1276486	850808	1718483	326898
MH total size	451157	457975	492742	1675954	1284400	1326244	704456	3047251	512083
LIG total size	816565	491190	206225	1559145	925141	75500	83453	4294487	612031
G-C	45724	4481	101620	11699	161395	142999	179458	16372	37414
L-MH	15646	19654	123029	161922	66533	189154	36136	128457	75045
C+MH	37155	44926	205822	103589	364365	1080009	589373	51089	58225
L-LIG	380568	94807	12650	114572	45872	18097	1390	1327812	222035
C+LIG	37641	2988	29684	34130	25767	322	3116	98970	11183
L-MH+LIG	9289	39752	1871	454026	14199	3925	86	1315653	158737
C+HM+LIG	389067	353643	162020	956417	839303	53156	78861	1552052	220076
C-sps	3	2	2	6	2	4	4	12	4
C-Size-MaxSp	306879	406038	499146	93688	1390830	308813	60021	4052	49836

MH-sp	3	2	2	6	2	4	4	12	4
MH-SizeMaxSp	313338	457975	492742	123730	1284400	320392	53387	500792	22533
LIG-sp	3	2	2	6	2	3	3	11	4
LIG-SizeMaxSp	194521	491190	206225	234802	925141	1657	13	990	11178
Order-C	2	2	1	2	2	1	1	1	1
PD	269.2	243.3	163.4	512.2	232.7	268.5	315.1	434.7	251.4
MinAge	4.5	3.2	1.4	4.5	2.4	2.8	8.7	3.2	2.3
MaxAge	4.6	15.7	9.8	40.8	10.4	17.8	20.5	18.7	8.5

CAPÍTULO II. ESTRUCTURA FILOGENÉTICA DE LAS ESPECIES ENDEMICAS DE MAMÍFEROS NEOTROPICALES

II.I Boundaries of the Neotropical region based on areas of endemism of mammals.

II.II Phylogenetical and ecological relationships into the Neotropical areas of endemism (Enviado *Journal of Natural History*).

CSIRO PUBLISHING

Australian Systematic Botany, 2017, **30**, 470–484
https://doi.org/10.1071/SB16053

The Neotropical region *sensu* the areas of endemism of terrestrial mammals

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Abstract. The mammals are the biological group initially analysed by Wallace to define the Neotropical region (NR). Their areas of endemism (Ae) are considered historical patterns, which have been used to describe biogeographic schemes. However, the Ae at regional scale are currently unclear. In the present study, we analyse Ae of mammals at the regional scale and compare them with previous biogeographic schemes of the NR. The Ae of Neotropical terrestrial mammals were identified using the endemicity analysis (software NDM/VNDM). Our results showed that the NR is composed of 10 Ae, supported by 82 endemic taxa (6 families, 29 genera, and 47 species). The Ae showed a NR with multiple boundaries and with a core of higher overlap of the areas of endemism (OAE) from Veracruz and the Pacific coasts of Mexico to the southern limit of Amazonia in Brazil. The NR boundaries vary strikingly with latitude, with substantially more overlapping areas of endemism in the tropical biomes than in the temperate biomes of America. This pattern of OAE is consistent with the higher mammal-species richness zone within the tropical biomes and other biogeographic patterns such as higher productivity and spatial heterogeneity.

Received 19 November 2016, accepted 27 October 2017, published online 31 January 2018

Introduction

The biogeographic regionalisation of the world proposed by Wallace (1876) has been re-analysed several times (Udvardy 1975; Cox 2001; Procheş 2005; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt *et al.* 2013; Rueda *et al.* 2013; Escalante *et al.* 2014; Morrone 2014*a*, 2015). These re-analyses have resulted in biogeographic regions that exhibit some similarities, but also differ from Wallace's classification. In particular, the Neotropic is a biogeographical area that has been classified as a kingdom, subkingdom, region, subregion, or domain depending on the approach and taxa used to define it (Morrone 2014*a*, 2015, and references therein), with each category involving changes in its geographical size and boundaries.

The Neotropical region (NR) recognised by Sclater (1858, 1895) and Wallace (1876) comprises areas in America, from central Mexico to Patagonia. Udvardy (1975) considered a different northern boundary for the NR, namely Baja California and Sinaloa Coast, Mexico. Some studies agree that the NR extends from northern Mexico to central Argentina (Cabrera and Willink 1973; Smith 1983; Morrone 2001*b*; Kreft and Jetz 2010; Holt *et al.* 2013; Rueda *et al.* 2013). It has been proposed that the NR excludes the Andean region (Morrone 2004, 2014*a*, 2015; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Noguera-Urbano 2013; Noguera-Urbano and Escalante 2015), and that it includes the Mexican transition zone (North) and the South American transition zone (South; Morrone 2004, 2014*a*, 2015; Noguera-Urbano 2013; Noguera-Urbano and Escalante 2015).

In contrast, areas of endemism (Ae) are the basic units of historical biogeographic analysis, and their conceptual and methodological definitions are a central issue in evolutionary biogeography (Platnick 1991; Morrone 1994; Linder 2001). An Ae can be identified by spatial congruence of two or more species (Platnick 1991; Morrone 1994; Noguera-Urbano 2016), which is the result of interactions between ecological and historical factors that limit species' geographic distributions (Müller 1973; Harold and Mooi 1994; Szumik *et al.* 2002; Noguera-Urbano 2016). The search for Ae is the first step in identifying groupings of taxa defined in space and time (Morrone 2001*a*, 2009). Areas of endemism are biogeographic hypotheses that can be tested with the addition of new data (Harold and Mooi 1994) or analysed with different methods (Szumik *et al.* 2002), to propose schemes of biogeographic regionalisation (Escalante *et al.* 2010, 2013).

Many protocols and algorithms have been described for the analysis of biogeographic areas (regions, subregions, provinces, ecoregions; Rosen 1988*a*, 1988*b*; Rosen and Smith 1988; Harold and Mooi 1994; Morrone 1994; Hausdorf and Hennig 2003; Kreft and Jetz 2010; Holt *et al.* 2013; Rueda *et al.* 2013), but few of them explicitly consider the spatial component in their analysis (Szumik *et al.* 2002; Echeverry and Morrone 2010). Szumik *et al.* (2002) and Szumik and Goloboff (2004) proposed and applied an optimality criterion (endemicity analysis; EA) to the delimitation of Ae, which is defined as follows: 'a species could be counted as endemic in an Area A when it satisfies the requirement (evenness rule) that it is present in at least two cells of A, and in each cell C of the area the species is either present, or absent in no more than Q (where $0 < Q < 8$) of the cells around C that belong to A' (Szumik and Goloboff 2004). The EA is implemented in the software NDM/VNDM (P. Goloboff, see http://www.lillo.org.ar/phylogeny/endemism/, accessed November 2017). This method assigns an endemicity score to each species depending on how well it fits the set of cells (species endemicity index, *e*; Szumik *et al.* 2002, Szumik and Goloboff 2004). The *e* can take values from 0 to 1, where 1 indicates a perfect fit. In addition, the values of *e* are summed to obtain a score of endemicity for a set of cells (set endemicity index, *E*) for each preliminary area. Sets of cells with more than two species (e.g. if Sp1 $e = 1$ and Sp2 $e = 1$, then $e + e = 2$, thus $E = 2$) are proposed to be recognised as Ae ($E > 2.0$; Szumik *et al.* 2002; Szumik and Goloboff 2004; Escalante *et al.* 2010, 2013).

Noguera-Urbano and Escalante (2015) identified 101 Ae based on Neotropical mammals, using the EA (NDM/VNDM), with special focus on the description of Ae types with a smaller size (provinces) than the region level. They briefly mentioned that the NR is defined by nine large Ae at a regional scale and 28 endemic taxa, but no conclusions were reached about its boundaries and biogeographic implications. Although the NR is considered a biogeographic pattern or a general distribution pattern delimited by both ecological and historical criteria, descriptions of its boundaries lack consensus and Ae of mammals at the regional scale remain unclear. In addition, it is thought that different analytic methods or taxonomic groups produce different biogeographic schemes (e.g. Cox 2001; Procheş 2005; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt *et al.* 2013; Rueda *et al.* 2013; Escalante *et al.* 2014; Noguera-Urbano and Escalante 2015). The goal of the present study was, therefore, to analyse Ae of mammals at the regional scale and compare them with previous biogeographic schemes of the NR. We defined Ae using the EA at a grid of 4° latitude–longitude and demonstrated that this approach can yield results that show multiple Ae at a regional scale in the NR.

Materials and methods

Areas of endemism and endemic taxa

We included the distributional maps of 1605 species of the Neotropical mammals proposed by the International Union for Conservation of Nature, ver. 2014.1 (IUCN, see www.iucnredlist.org/, accessed 12 October 2014), representing 20 families and 179 genera. IUCN maps follow the nomenclature proposed by Wilson and Reeder (2005). Some families and genera may not be fully represented in the IUCN maps because of taxonomic and nomenclatural changes. Distributional maps were cut with a rectangular mask that extends from the United States of America (USA) to Patagonia (38°N to 56°S and 122°W to 34°W). Even though southern USA does not belong to the NR (Escalante *et al.* 2010; Morrone 2014*a*; Noguera-Urbano and Escalante 2015), it was included for practical reasons because there is no clear demarcation between the Neotropical and Nearctic regions in Mexico (including the Mexican transition zone; Escalante *et al.* 2010; Morrone 2014*a*, 2015). The distribution maps of families, genera and species were combined to identify the endemic taxa of the NR (Escalante *et al.* 2010). Families with a single genus and monospecific genera were represented by the distributional maps of the species to avoid over-representing those taxa (Escalante *et al.* 2010). The distributional maps of the families and genera were stacked with distributional maps of the species in a single file. This stack was overlapped in a 4 × 4° latitude–longitude grid to produce a presence or absence matrix following the nomenclature convention of the software NDM/VNDM (names of taxa as columns and grid cells as rows). This grid size was chosen on the basis of the recommendations of Escalante *et al.* (2010, 2013) to identify regional Ae and species with wide distribution, considering that the use of large cells is convenient for the identification of broad and unfragmented Ae (Casagranda *et al.* 2009). The matrix of 20 families, 179 genera and 1605 species included 1804 taxa (Table S1 of the Supplementary material) in 210 grid cells.

The matrix was analysed using the software NDM/VNDM, ver. 3.0 (P. Goloboff, see http://www.lillo.org.ar/phylogeny/endemism/, accessed November 2016), for the identification of Ae (Szumik *et al.* 2002; Szumik and Goloboff 2004). We performed a heuristic search, keeping areas with at least two endemic species and $E > 2.0$. The option of permutation of one grid cell at a time was used. We retained suboptimal sets below 0.90 worst fit, because accepting those suboptimal solutions is a way to resolve hard optimisation problems, and, therefore, this procedure gives a certain probability to improve the effectiveness of the search (Szumik and Goloboff 2004). The option of 'use edge proportions' was not used. That option considers the cells outside the area of study, but adjacent to it,

Table 1. Neotropical areas of endemism (Ae) obtained with the software NDM/VNDM

E, endemicity index for each Ae; *e*, interval of taxon endemicity index (minimum–maximum); and ETR, endemic-taxon richness. Ae9 is the only one consensus composed of two areas of endemism; therefore, their *E* and *e* ranges are shown

Ae	*E*	*e*	#ETR
1	2.84	0.94–0.95	3
2	2.87	0.93–0.98	3
3	2.64	0.79–0.93	4
4	3.71	0.84–0.88	4
5	4.16	0.75–0.89	4
6	6.92	0.75–0.88	5
7	9.24	0.81–0.91	6
8	9.09	0.81–0.90	8
9	27.3–29.5	(0.000–0.858)–(0.939–0.956)	36

Table 2. Neotropical areas of endemism (Ae) obtained with the software NDM/VNDM

Number in parentheses after each taxon name is its endemicity index (*e*). Size expresses the surface of the Ae resulting from joining the distributional areas of its endemic taxa

Ae	Taxa	Size (km^2)
1	Tayassuidae (0.95), *Nyctinomops* (0.95), *Pecari tajacu* (0.94)	27 682 876
2	Mormoopidae (0.98), *Pteronotus* (0.96), *Pteronotus parnellii* (0.93)	17 880 434
3	*Philander* (0.93), *Vampyressa* (0.92), *Chironectes minimus* (0.79)	14 587 649
4	*Promops* (0.88), *Eira barbara* (0.96), *Leopardus wiedii* (0.95), *Lontra longicaudis* (0.92)	20 531 064
5	*Ateles* (0.88), *Chiroderma villosum* (0.82), *Didelphis marsupialis* (0.89), *Eumops hansae* (0.82), *Philander opossum* (0.75)	14 934 443
6	*Galictis vittata* (0.89), *Lichonycteris obscura* (0.86), *Lophostoma brasiliense* (0.86), *Mimon crenulatum* (0.88), *Peropteryx kappleri* (0.86), *Potos flavus* (0.81), *Rhynchonycteris naso* (0.90), *Uroderma magnirostrum* (0.86)	16 924 974
7	*Cabassous* (0.93), *Eumops bonariensis* (0.98), *Lasiurus ega* (0.89), *Leopardus pardalis* (0.87), *Mazama* (0.96), *Myotis albescens* (0.93), *Myotis nigricans* (0.92), *Myrmecophaga tridactyla* (0.91), *Sylvilagus brasiliensis* (0.90), *Tayassu pecari* (0.95)	20 968 317
8	*Anoura* (0.89), *Artibeus lituratus* (1), *Cynomops* (0.91), *Diclidurus* (0.91), *Diclidurus albus* (0.91), *Chiroderma* (0.93), *Glossophaga* (0.89), *Glossophaga soricina* (0.88), *Saccopteryx* (0.95), *Sturnira* (0.82)	20 923 213
9	*Alouatta* (0.849–0.895), Atelidae (0.000–0.858), *Caluromys* (0.915–0.943), *Carollia* (0.895–0.964), *Carollia perspicillata* (0.895–0.964), Cebidae (0.000–0.929), *Cebus* (0.000–0.925), *Chrotopterus auritus* (0.847–0.892), *Cuniculus paca* (0.000–0.897), *Dasyprocta* (0.841–0.886), Dasyproctidae (0.849–0.895), *Diaemus youngi* (0.000–0.875), *Eptesicus brasiliensis* (0.905–0.911), Erethizontidae (0.000–0.877), *Eumops auripendulus* (0.842–0.886), *Lonchorhina* (0.915–0.943), *Lonchorhina aurita* (0.915–0.943), *Lophostoma* (0.952–0.958), *Macrophyllum macrophyllum* (0.954–0.971), *Marmosa* (0.000–0.917), *Metachirus nudicaudatus* (0.920–0.936), *Micronycteris minuta* (0.000–0.941), *Mimon* (0.907–0.958), *Noctilio albiventris* (0.897–0.912), *Peropteryx* (0.926–0.976), *Peropteryx macrotis* (0.912–0.962), *Phylloderma stenops* (0.934–0.951), *Phyllostomus* (0.947–0.953), *Phyllostomus discolor* (0.942–0.948), *Phyllostomus hastatus* (0.000–0.956), *Platyrrhinus* (0.846–0.852), *Saccopteryx leptura* (0.939–0.956), *Tonatia* (0.851–0.864), *Trachops cirrhosus* (0.934–0.962), *Uroderma* (0.000–0.918), *Uroderma bilobatum* (0.947–0.953)	19 230 005

in the NDM/VNDM mathematical formulations (see Szumik and Goloboff 2004). In our case, those cells did not represent numerical values, because we expected Ae with a size close to that of the study region. We performed 100 analyses in NDM/VNDM. Areas of endemism identified by NDM/VNMD can share a percentage of endemic taxa (Szumik *et al.* 2002, Szumik and Goloboff 2004). Therefore, we retained sets with different scores if >98% of the defining species were exclusive, using the option 'keep overlapping subsets >98%'. A high value of 'keep overlapping subsets' represents a higher percentage of unique species and, thus, leads to maximising the number of unique areas composed by unique taxa (Noguera-Urbano and Escalante 2015). We applied a 'loose' consensus rule to summarise preliminary Ae that shared 50% or more of their defining taxa, because some areas had a similar species composition. This consensus is agglomerative and results in fewer consensus areas, because it combines areas when overlapping distributional patterns exist (Aagesen *et al.* 2013).

The different NR schemes differ in size, as follows: (1) the NR *sensu lato*, which comprises South America, Central America and northern Mexico (e.g. Wallace 1876; Udvardy 1975; Procheş and Ramdhani 2012), and (2) the NR *sensu stricto*, which excludes the Andean region of South America (e.g. Morrone 2014*a*, 2015). We, therefore, retained Ae at the NR *sensu lato* and the NR at the *sensu stricto* scales to describe the multiple shapes and sizes of the NR. For each Ae, we reported the number of endemic mammal taxa, set endemicity indexes (*E*), size (km^2) and geographical boundaries for each area of endemism. In addition, we included the endemic taxa with their species endemicity indexes (*e*).

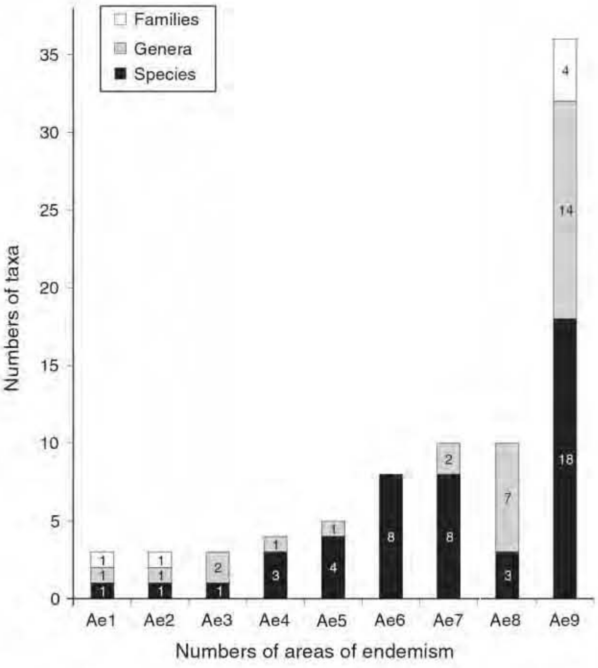

Fig. 1. Composition of endemic taxa for each area of endemism (Ae).

Overlap of the areas of endemism (OAE) in the NR

We mapped each Ae, merging the distributional maps of endemic mammal taxa. Then the Ae maps were coded using a binary code (1: presence in endemism, 0: absence) and transformed to rasters (cell raster 0.25°). The rasters of the Ae were summed to obtain a single NR, which represented the OAE in the NR. We explored the effect of latitude on the OAE map by executing a Spearman correlation test between values of endemism and latitude ($P < 0.05$, reject Ho: there is no relationship). These values were extracted from 300 random points on the OAE map in R (ver. 3.3.1, R Foundation for Statistical Computing, Vienna, Austria, see http://www.r-project.org/, accessed July 2016).

Results

Areas of endemism and endemic taxa

The matrix produced 109 Ae with several extends. But only 10 Ae were close in size to the NR. The consensus analysis resulted in eight single areas and one consensus; they defined nine Neotropical Ae. We reported 82 taxa endemic to the NR (6 families, 29 genera and 47 species, Tables 1, 2). The Ae showed variation in the endemicity index (Table 1), size (Table 2) and richness of endemic taxa, (Fig. 1, Tables 1, 2). The Neotropical Ae9 was the richest, concerning endemic taxa (36 taxa), whereas the Neotropical Ae1 and Neotropical Ae2 had three taxa and showed the lowest endemicity indexes (E = 2.84 and E = 2.87 respectively). Finally, the Neotropical Ae1 was the largest in size (27 682 876 km^2), whereas the Neotropical Ae3 was the smallest (14 587 649 km^2).

Neotropical Ae1

This area extended from southern United States to southern Brazil and central Argentina. But, it excluded Uruguay, the Atacama Desert and Puna in Bolivia, and some Andean zones in Peru, Argentina and Chile (Fig. 2). This pattern included the Caribbean

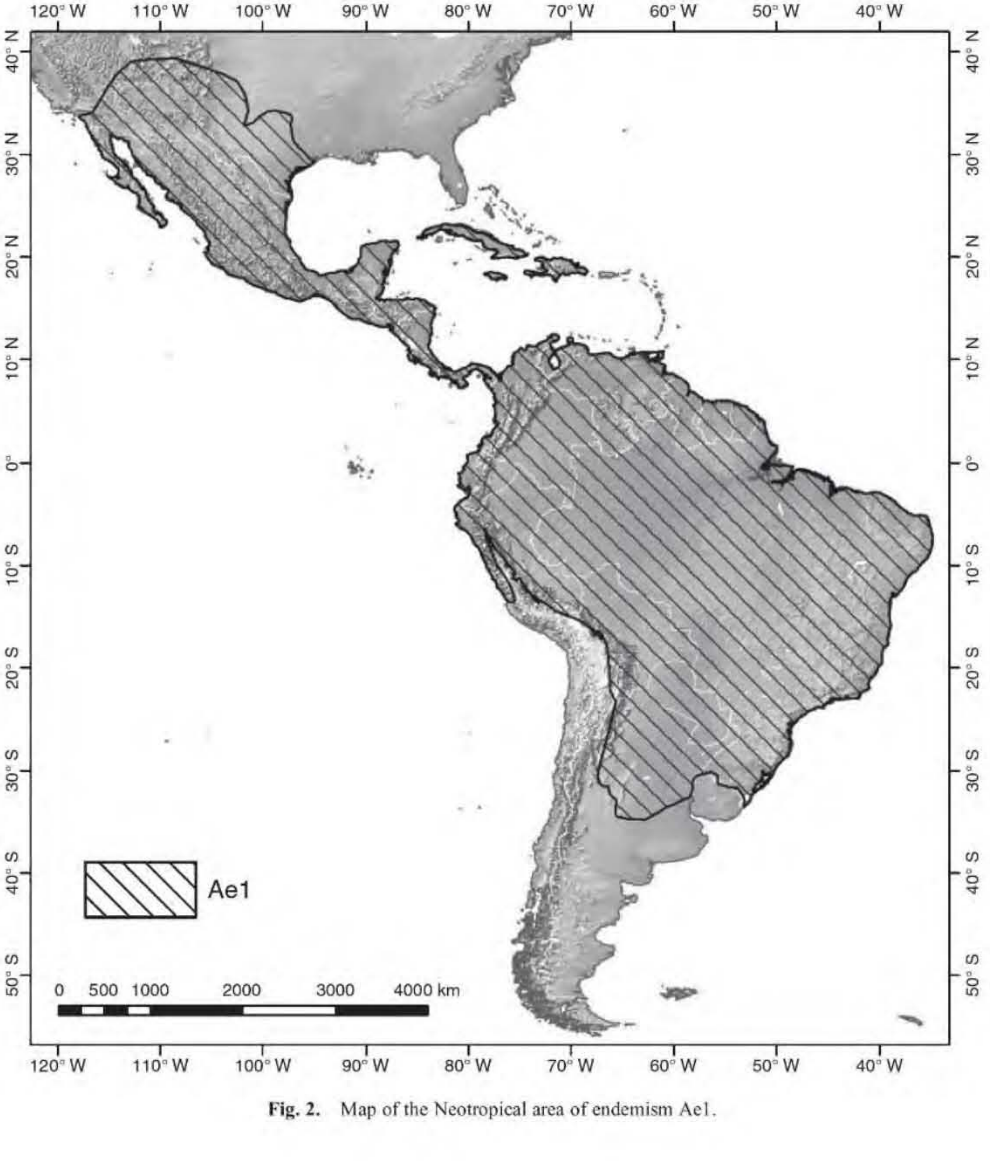

Fig. 2. Map of the Neotropical area of endemism Ae1.

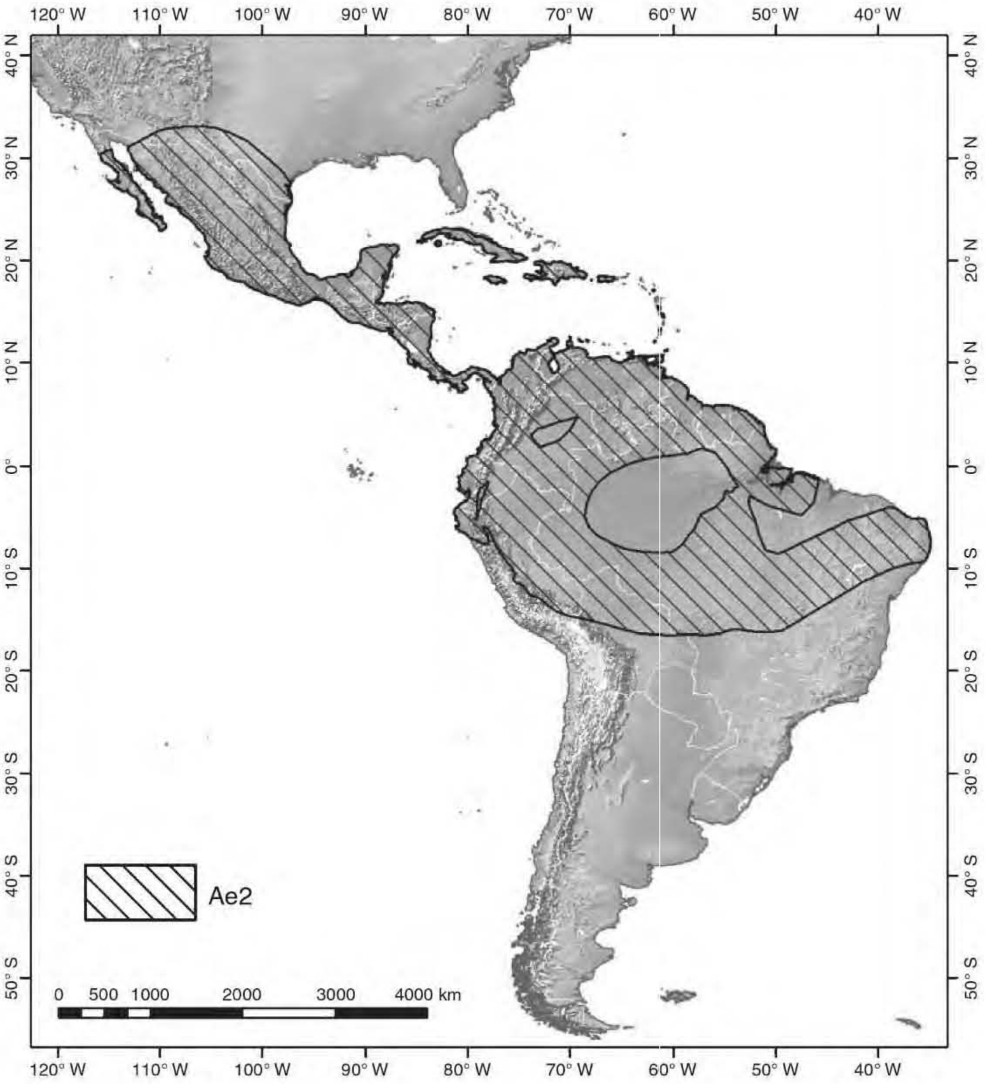

Fig. 3. Map of the Neotropical area of endemism Ae2.

Islands and the Baja California Peninsula. Three taxa defined this area (Table 2).

Neotropical Ae2

This area reached from southern United States to Peru, Bolivia and central Brazil, excluding south-eastern Amazonia and Madeira basin in Brazil, the Andean lands of Peru, and southern Bolivia (Fig. 3). In addition, this pattern included the Caribbean Islands and the Baja California Peninsula. Three taxa defined this area (Table 2).

Neotropical Ae3

This area included from the coast of Veracruz and half of the Sierra Madre del Sur (Mexico) to southern Brazil and northern Argentina. It included northern Bolivia and western Paraguay (Fig. 4). This area excluded Yucatan in Mexico, the Atacama Desert, Puna in Bolivia–Peru, almost all Argentina, Uruguay, and the Caatinga and Cerrado in Brazil. This area was supported by three taxa (Table 2).

Neotropical Ae4

This area extended from the coast of Veracruz and the central Sierra Madre Occidental (Mexico) to central Argentina. However, it excluded the southern portion of the Sierra Madre Oriental and the Trans-Mexican Volcanic Belt in Mexico. It also excluded southern Peru and western Bolivia (Fig. 5), as well as the Caatinga in Brazil. This area was supported by four taxa (Table 2).

Neotropical Ae5

This area extended from the coast of Veracruz, the Sierra Madre Oriental and southern Sierra Madre del Sur in Mexico to southern Brazil, Peru and Bolivia (Fig. 6). Zones such as the Chaco

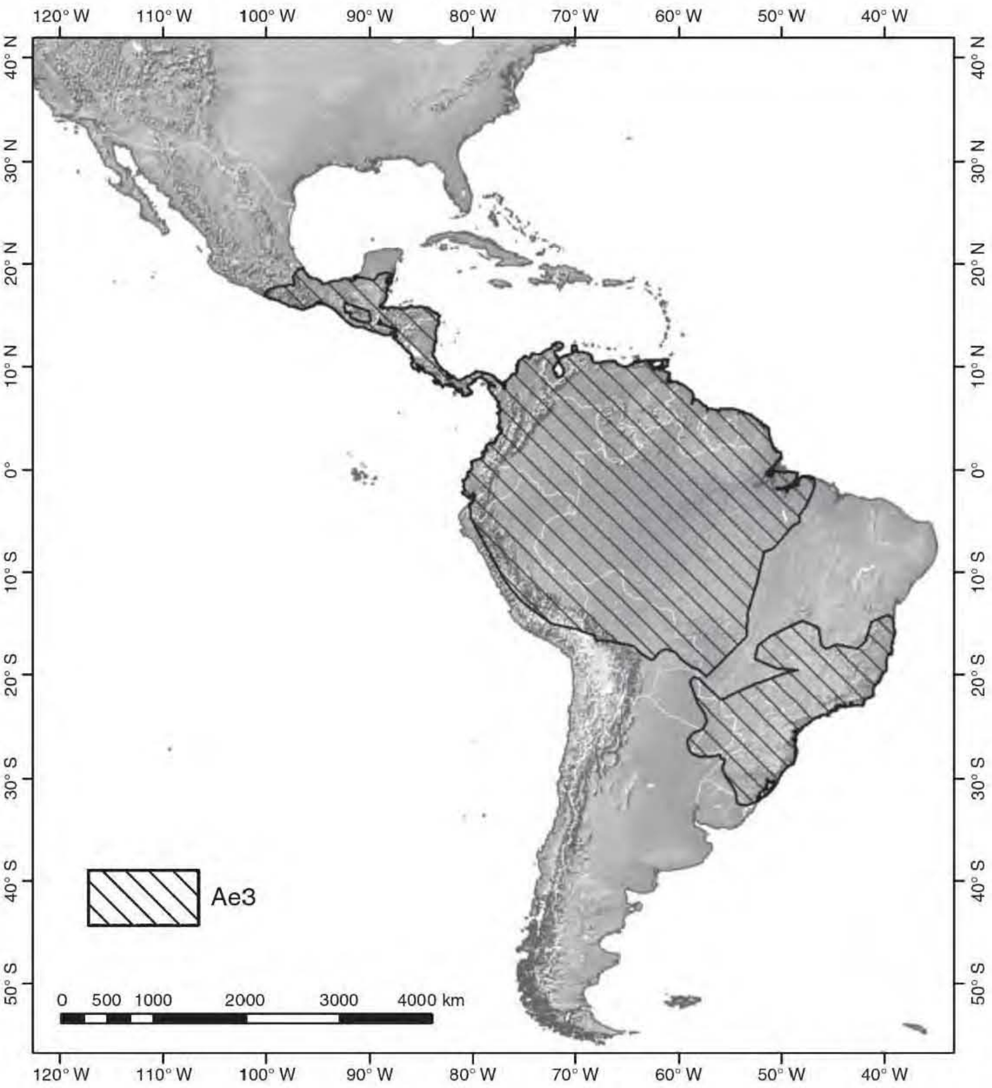

Fig. 4. Map of the Neotropical area of endemism Ae3.

(Argentina, Paraguay) and the Atlantic Coast and the Caatinga in Brazil were excluded from the area. It was supported by six taxa (Table 2).

Neotropical Ae6

This area extends from the Sierra Madre del Sur and coast of Veracruz (excluding the Trans-Mexican Volcanic Belt) to Bolivia, northern Peru and southern Brazil. The coast and desert of Peru, and the Puna in Bolivia were excluded from the pattern (Fig. 7). It was supported by eight taxa (Table 2).

Neotropical Ae7

This area ranged from the southern coast of Texas, over the Mexican Mountain Component and the Sierra Madre Occidental, to central Argentina. This Ae excludes Puna in Bolivia and Argentina (Fig. 8). It is supported by 10 taxa (Table 2).

Neotropical Ae8

This area extended from the Pacific Lowlands, Sierra Madre Occidental and Oriental, and the coast of Veracruz in Mexico to northern Argentina and southern Uruguay. It excluded southern Peru, western Bolivia and Uruguay (Fig. 9). The northern zone of the pattern included Jamaica. It was supported by 10 taxa (Table 2).

Neotropical Ae9

It ranged from the Mexican Mountain Component (excluding the Sierra Madre Occidental) and Veracruz coast in Mexico, to northern Argentina and southern Uruguay. This Ae excluded

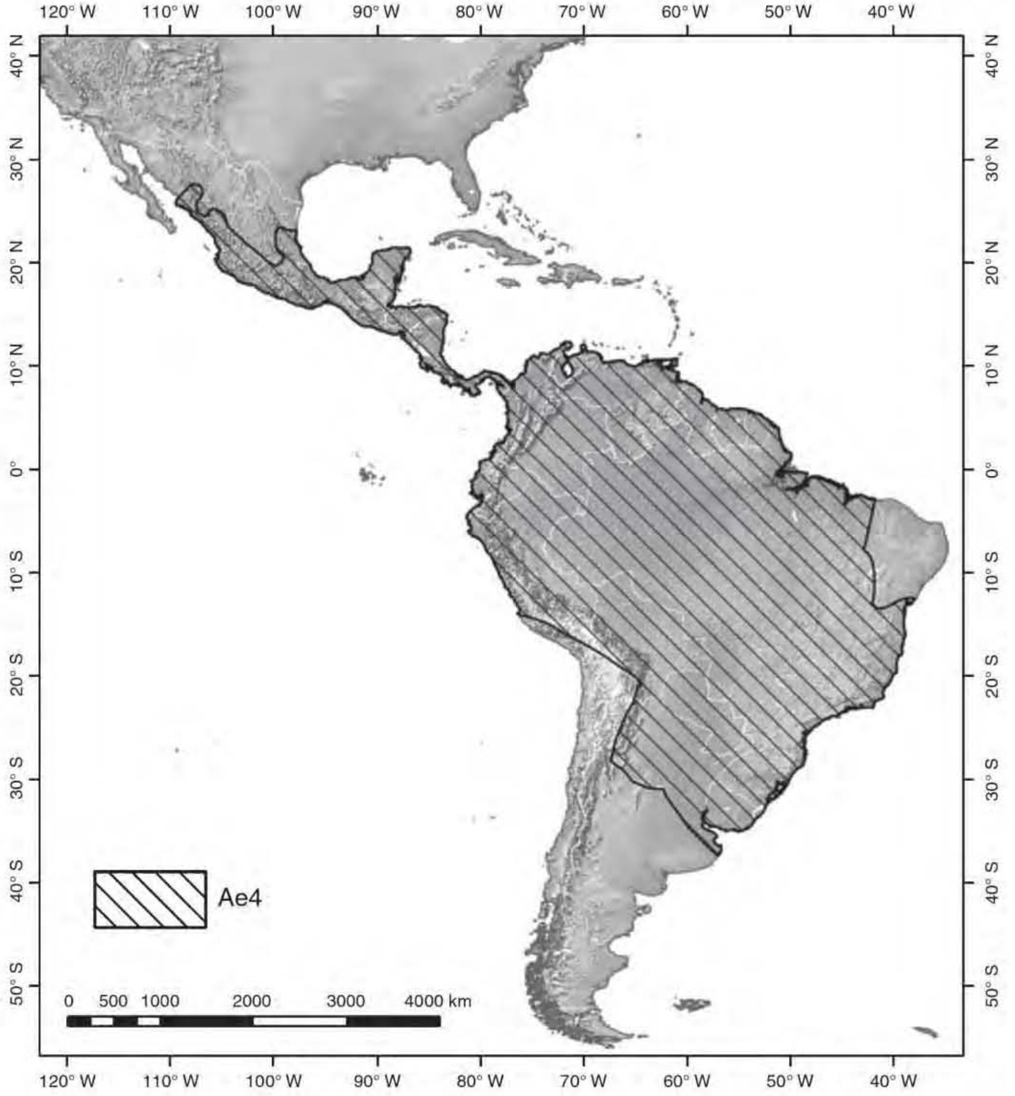

Fig. 5. Map of the Neotropical area of endemism Ae4.

the coast of Peru, Puna in Bolivia and Argentina (Fig. 10). This area had the highest number of endemic taxa (36 taxa; Table 2).

Overlap of the OAE in the NR

The OAE map resulted in a NR with multiple boundaries and geographical configurations (Fig. 11), because there are areas include regions that other areas do not include. There was an observed decrease in the OAE from the Equatorial parallel to northern and southern America (Fig. 11). The highest OAE extended from the Veracruz and Pacific coasts of Mexico to Amazonia in Brazil. We obtained two correlations between latitude and the OAE (Fig. 11), namely, a negative correlation from Equatorial parallel (0°) to Southern USA (38°; $\rho = -0.91$, $P < 2.2e{-}16$) and a positive correlation from the Equatorial parallel (0°) to Argentina (–38°; $\rho = 0.7$, $P < 2.2e{-}16$).

Discussion

Areas of endemism and endemic taxa

Wallace (1876) and Sclater (1895) proposed that the biogeographical divisions of the Earth surface are characterised by different taxonomic levels. Our results corroborated this idea, in showing that the delimitation of the Neotropical region is supported by three levels of endemic taxa, namely, families, genera and species. Noguera-Urbano and Escalante (2015) proposed that the Neotropical region is supported by only two endemic families (Cebidae, Echimyidae); our results added five endemic families to this number (Atelidae, Dasyproctidae, Erethizontidae, Mormoopidae and Tayassuidae). Other studies suggested that the Neotropical region was characterised by the presence of 10 families (Bradypodidae, Caviidea, Cebidae, Dasyproctidae, Dinomyidae, Echimyidae, Hapalidae,

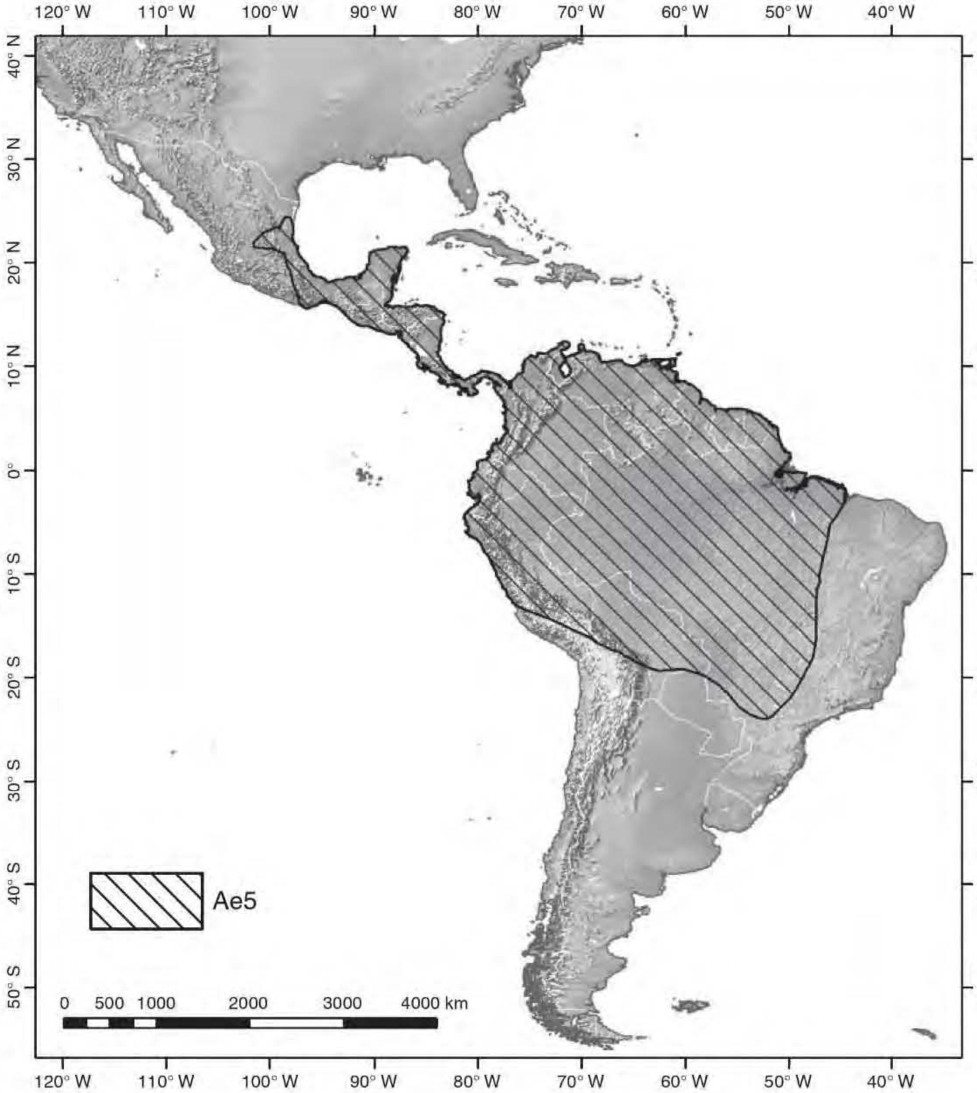

Fig. 6. Map of the Neotropical area of endemism Ae5.

Myrmecophagidae, Phyllostomidae and Thyropteridae; Wallace 1876; Sclater 1895; Hershkovitz 1969). Some of the disagreement between our results and previous characterisations of the NR are due to taxonomic changes. In the case of Atelidae and Cebidae, for example, Wallace (1876) and other authors considered Cebidae as endemics, following the traditional primate taxonomic arrangement that comprised only two families (the Callitrichidae (before: Hapalidae, marmosets and tamarins), and Cebidae (all others)). However, since then, Cebidae has been redefined and other families such as Atelidae have been split from that taxonomic group (Rylands and Mittermeier 2009). Other inconsistencies are caused by taxa that define only a patch of the NR, not the broad distribution pattern that defines the NR as a unit. This is the case of Bradypodidae, which includes species that inhabit tropical forests that exclude the Rio Orinoco Basin and the llanos of Colombia and Venezuela (Gardner 2007), or Myrmecophagidae, which is restricted to South America. In contrast, Erethizontidae includes genera widespread in America (e.g. *Erethizon*: Mexico, United States and Canada; *Coendou*: South America); Thyropteridae comprises five species, of which only one (*Thyroptera tricolor*) is found from Brazil to Mexico (Neotropics). Caviidea inhabits ecosystems from Argentina to southern Panama, and Dinomyidae is restricted to the Andean forests (Patton *et al.* 2015). Our results do not support Phyllostomidae as an endemic family of the NR, because some of its species occur in the United States (Neartic region), such as *Choeronycteris mexicana*, *Leptonycteris nivalis* or *Macrotus californicus* (Simmons 2005).

At the genus level, Noguera-Urbano and Escalante (2015) reported 15 endemic genera of the NR, a number that is here increased to 20 Neotropical endemic genera. In contrast,

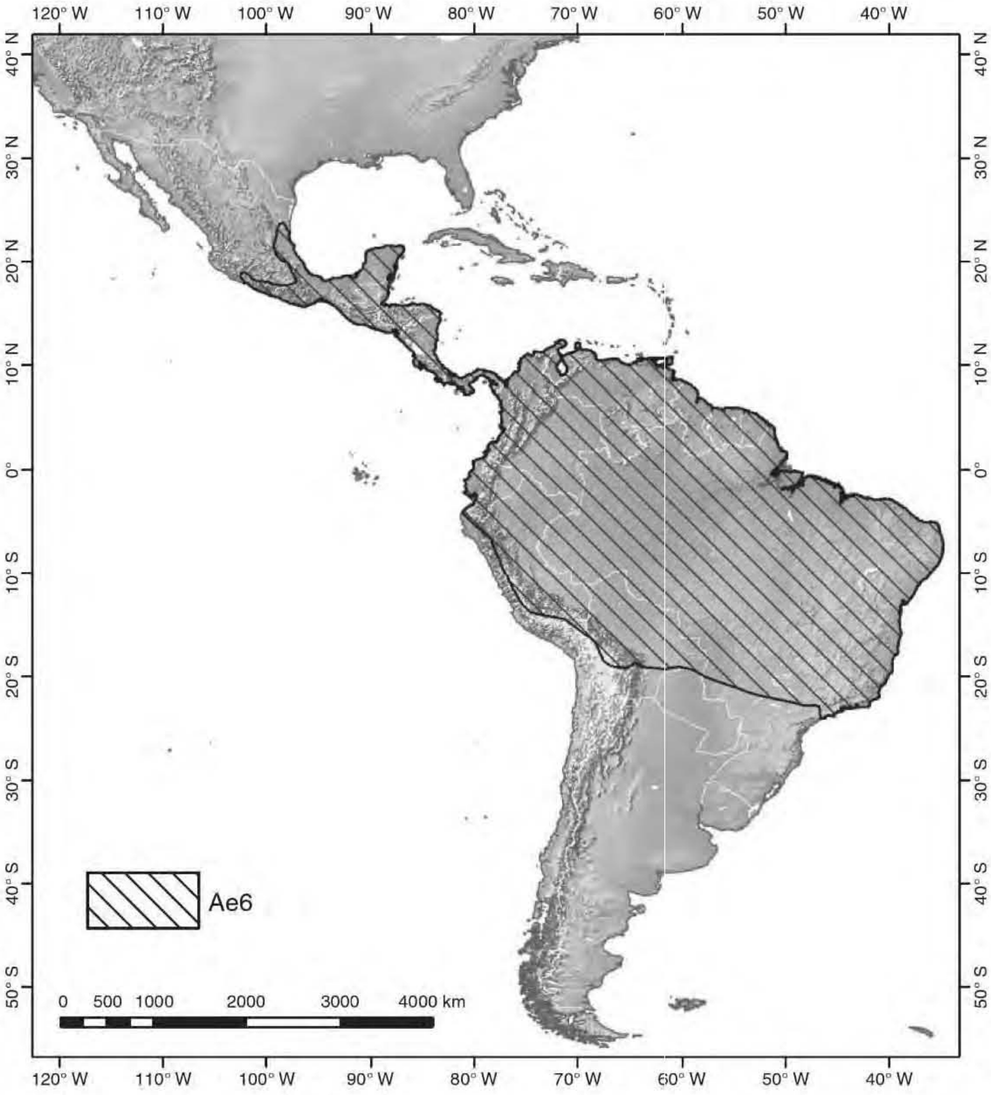

Fig. 7. Map of the Neotropical area of endemism Ae6.

Procheş and Ramdhani (2012) reported 89 mammal genera characteristic of the NR, of which 29 are also recognised in our analyses. We believe the incongruence between our results and those of Procheş and Ramdhani (2012) is due to the use of different criteria to define the NR. For example, Procheş and Ramdhani (2012) used the degree of match between the taxa and zoogeographical regions to select characteristic taxa; the degree selected was 'Match $\geq$0.5'. Thus, they defined as characteristic taxa those genera that occupy at least 50% of the ecoregions in a given zoogeographical region. Instead, the software NDM/VNDM secures the selection of Ae with as much consistency as possible among the sets (areas of endemism) and the distributional areas of the species ($E > 2.0$). In this regard, the software NDM/VNDM retains Ae with a high E and endemic species with a high 'e'; consequently, small and medium-sized distributional areas are excluded.

In addition to these characteristic genera, Procheş and Ramdhani (2012) mentioned four genera restricted to the NR (*Didelphis*, *Procyon*, *Puma*, and *Speothos*) that were not detected by our analysis. Currently, the distribution of the genera *Didelphis*, *Procyon* and *Puma* extends from Canada to Argentina. This means that they are endemic to America. However, *Didelphis* includes the species *Didelphis marsupialis*, which is endemic to the Ae5. The genus *Speothos* includes an extant species, *Speothos venaticus*, which extends from Panama to Brazil, northern Argentina, central Bolivia and Paraguay (South America). It was not detected in our analysis because its distributional area was incongruent with the distributional areas of other species of mammals.

Each of the Neotropical Ae identified in our analysis partially agrees with earlier biogeographic schemes of the NR (Sclater 1858, 1895; Wallace 1876; Cabrera and Willink 1973;

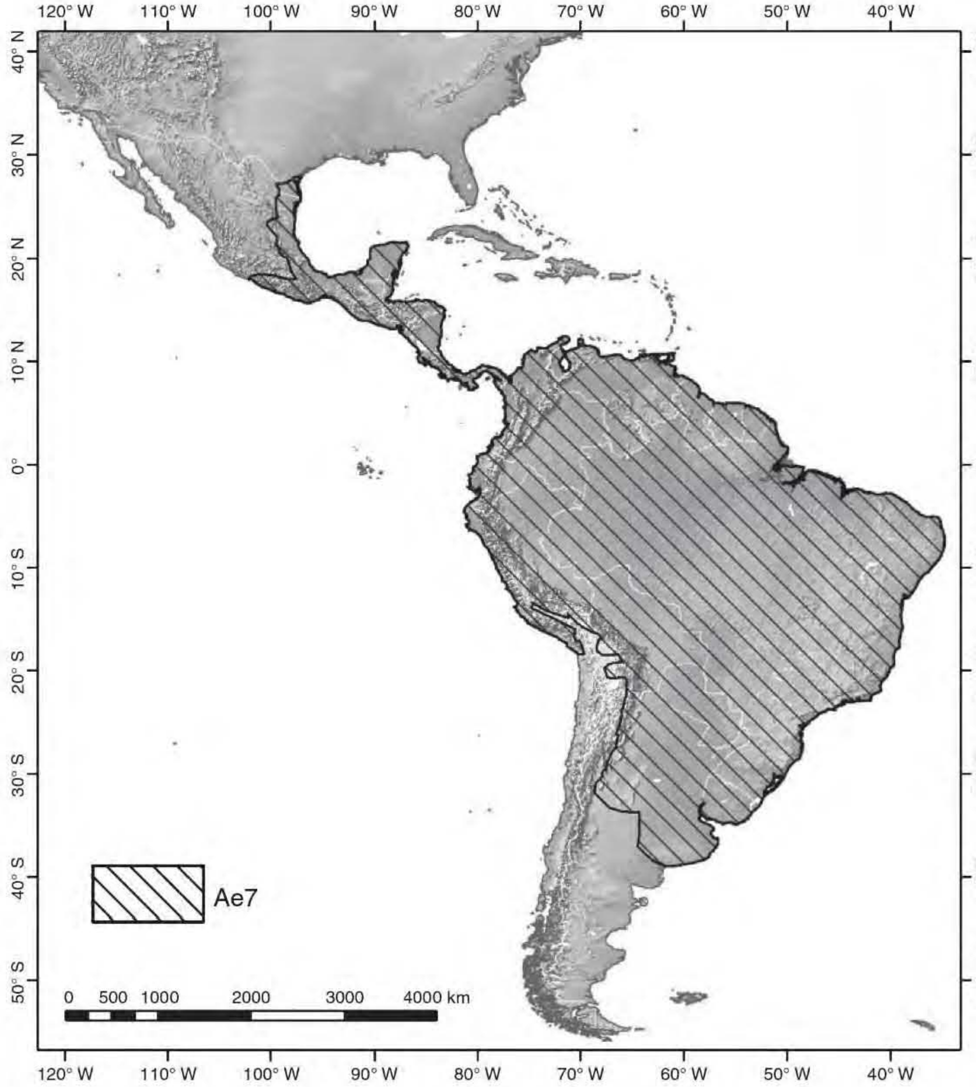

Fig. 8. Map of the Neotropical area of endemism Ae7.

Udvardy 1975; Smith 1983; Morrone 2001*b*, 2014*a*, 2015; Kreft and Jetz, 2010; Holt *et al*. 2013). The Neotropical Ae1 and the Neotropical Ae2 match at 38°N (Figs 2, 3), extending beyond the northern limit of the NR in Mexico (Sclater 1858, 1895; Wallace 1876; Cabrera and Willink 1973; Udvardy 1975; Morrone 2001*b*; Kreft and Jetz 2010; Holt *et al*. 2013; Rueda *et al*. 2013; Morrone 2004, 2014*a*). Escalante *et al*. (2014) mentioned that the southern Nearctic region (United States) has ecological similarities to the Neotropical ecosystems of Mexico, allowing some Neotropical species to extend their areas of distribution to the Nearctic region.

Seven Neotropical areas (Ae3–9, Figs 4–10) had a 'Y' shaped northern border formed by the Sierra Madre Oriental and Sierra Madre Occidental in Mexico. Those borders have been described by other authors (Wallace 1876; Sclater 1895; Hershkovitz 1958; Cox 2001; Morrone 2004, 2014*a*, 2015) to identify the Mexican transition zone. The Mexican transition zone is a topographically, climatically and biogeographically complex zone, with a high number of subareas of endemism (Noguera-Urbano and Escalante 2015) and species richness (Escalante *et al*. 2014), turnover of species assemblages (Kreft and Jetz, 2010), and phylogenetic turnover (Holt *et al*. 2013), possibly owing to the contact between the Nearctic region and the NR.

In South America, the Neotropical Ae1 area (Fig. 2) partially agrees with the biogeographic schemes of the NR proposed by Morrone (2004, 2014*a*, 2015). The difference resides in the fact that the Ae1 is limited by the cis-Andean lands and the northern Patagonia (Argentina), whereas NR by Morrone (2004, 2014*a*, 2015) includes the Andean mountains (South American transition zone) and the central Patagonia (Monte province, Argentina). However, the Neotropical Ae2 (Fig. 3)

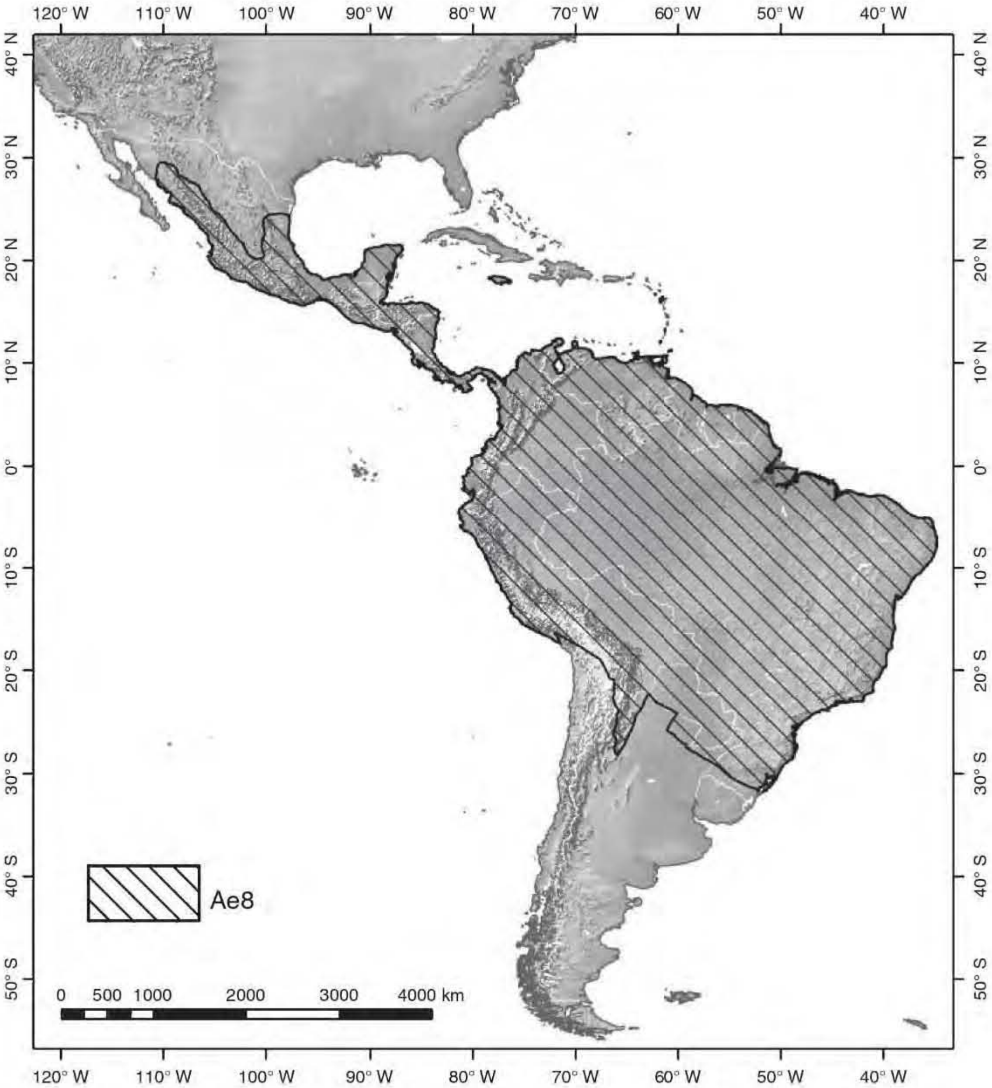

Fig. 9. Map of the Neotropical area of endemism Ae8.

partially agrees with the southern NR of Holt *et al.* (2013), in that its southern boundary is the centre of Bolivia and it excludes the Atlantic rainforest. The southern boundary of the Neotropical Ae4 (Fig. 5) agrees with the NR proposed by Kreft and Jetz (2010), the Neotropical Ae5 (Fig. 6) agrees with Holt *et al.* (2013), and the Neotropical Ae7, Ae8 and Ae9 (Figs 8–10) partially agree with Morrone (2004, 2014*a*, 2015) in that they partially exclude the central Andes mountains as well as the southern Andes and Patagonia. Morrone (2014*a*, 2015) proposed that the NR excludes the Andean highlands from western Venezuela to central western Argentina (South American transition zone) and southern South America (Andean region). The southern Andes and Patagonia have been problematic in their biogeographical definition because of their transitional nature, and, therefore, different names have been adopted for this area, including Chilean subregion (Wallace 1876), Patagonian subregion (Sclater 1895; Hershkovitz 1958), Argentine (Smith 1983), South American transition zone and Andean region (Morrone 2004, 2014*a*), temperate South America (Kreft and Jetz 2010) and the Andean region (Procheş and Ramdhani 2012).

With respect to the south-eastern limit of the NR, it is interesting that four Neotropical areas (Ae2, Ae3, Ae4, Ae5) did not include some zones in the south-eastern or eastern Brazil (e.g. Caatinga in Ae3 and Ae4, Figs 4, 5). This is important because those zones have generally been considered as part of the NR (Sclater 1858, 1895; Wallace 1876; Cabrera and Willink 1973; Udvardy 1975; Smith 1983; Morrone 2001*b*, 2014*a*; Kreft and Jetz 2010; Holt et *al.* 2013). Costa *et al.* (2000) and Morrone (2014*a*) mentioned that south-eastern Brazil, including the entire Atlantic rainforest and the Caatinga regions, comprises a distinct biogeographic area from the Amazonian

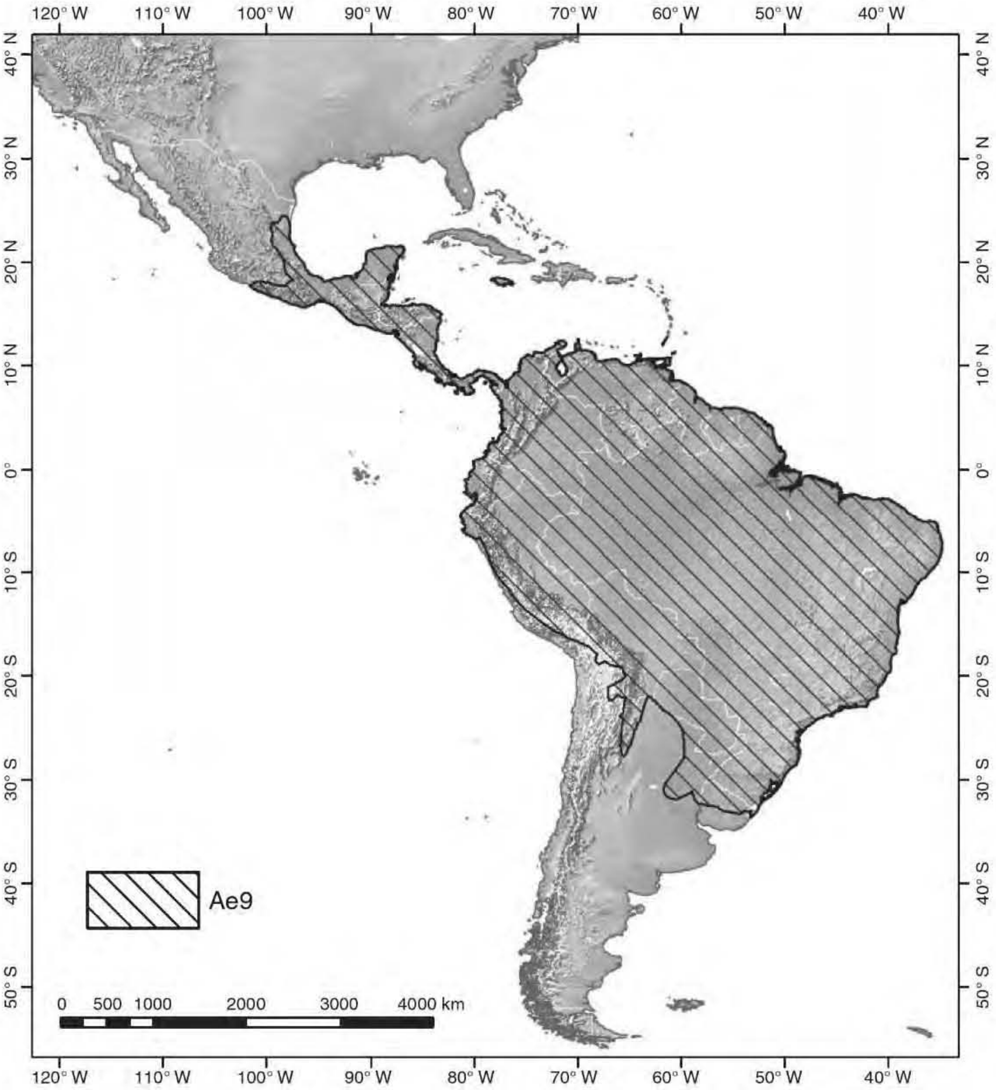

Fig. 10. Map of the Neotropical area of endemism Ae9.

rainforest and the Cerrado. For example, the Caatinga is considered a dry savanna, which acts as an environmental barrier for some mammals (rodents and opossums) because of its hot and dry climate, and a marked seasonal rainfall regime (Carmignotto *et al.* 2012). The Atlantic rainforest is separated from the Cerrado by extensive mountain ranges, which act also as a barrier restricting the distributional range of some mammals (Carmignotto *et al.* 2012).

Overlap of the OAE in the NR

It has been proposed that the boundaries of the NR are delimited by transition zones that represent areas of biotic overlap between the NR and the neighbouring regions (Hershkovitz 1958; Morrone 2004, 2014*a*). The Mexican transition zone is located between the Nearctic and Neotropical regions, whereas the South American transition zone is located between the Neotropical and Andean regions (Hershkovitz 1958; Morrone 2004, 2014*a*). Low Neotropical endemism values and high values of OAE are characteristic of the complex zones (transitional zones). It is possible that the transitional zones act as dispersal barriers or biotic barriers, constraining the distributional ranges of Neotropical endemic mammals and affecting the number of endemic taxa around the boundaries of the NR. In North America, Escalante *et al.* (2010) showed changes in species richness at the Mexican transitional zone (north of Mexico), with the number of species increasing to the tropics. Therefore, it is possible that the temperate climates of North America prevent the dispersal of Neotropical endemic species. In South America, Ruggiero *et al.* (1998) suggested that the land shape and likely differences in the history of the fauna affect the size and shape of the geographical distributions. Moreover, the Andean mountains and environmental resistance

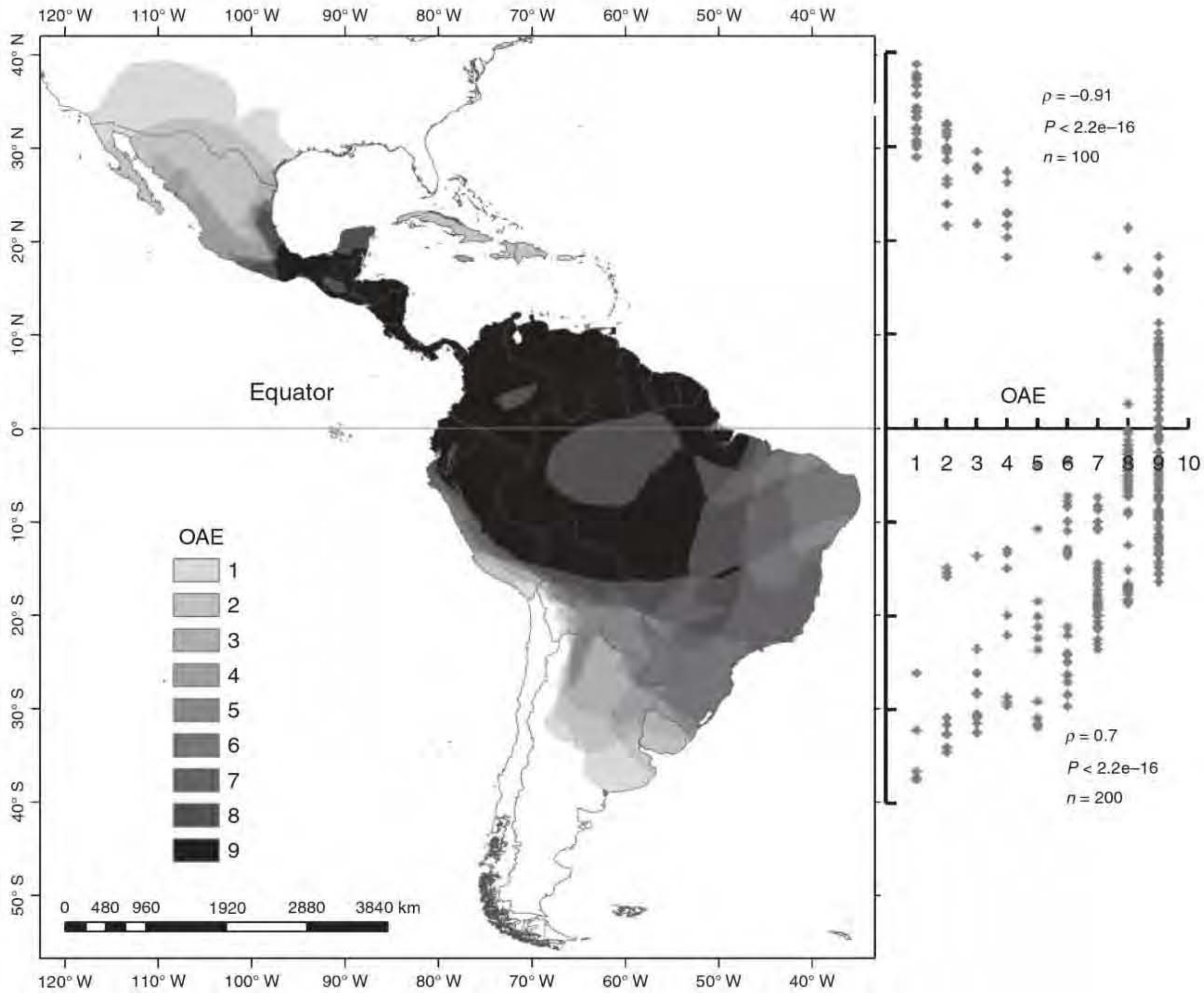

Fig. 11. Map of the variation of the endemism of the Neotropical region and the tendency of the overlap of the areas of endemism (OAE) values (*x*-axis) considering latitude variations (*y*-axis). In the map, the numbers and colour variations indicate the OAE with higher (dark) and lower (light) overlapping of areas of endemism.

act as barriers against the expansion of distributional areas of mammals in the southern half of South America. Thus, the OAE is likely to be influenced by ecological, geographical or historical processes, which, therefore, modulate shape and size of the area of the NR.

The results obtained here for extant mammal species suggest that the boundaries of the NR based on Ae vary strikingly with latitude, resulting in significant differences in the OAE between the temperate and tropical biomes. The OAE decreases from the Equatorial parallel towards the transitional zones (above 39°N and above 39°S; Fig. 11). The core zone of the OAE and the latitudinal gradient observed here agrees well with the hypothesis of an evolutionary uniqueness zone (Holt *et al.* 2013), with higher mammal species richness, and phylogenetic diversity around the Equatorial parallel (Davies and Buckley 2011). Possibly, the same hypotheses proposed to explain the latitudinal diversity gradient of mammals in the tropics can be used to explain the OAE in the NR. Thus, the gradient observed in the OAE (from the Equator decreasing towards the transition zones to the south and north) may be explained by processes such as the time-to-speciation effect (the longer time since the Neotropical species colonised the region, higher speciation rates, lower extinction rates, multiple dispersal events, higher climatic stability, lower competition, higher productivity and spatial heterogeneity; Pianka 1966; Antonelli and Sanmartín 2011; Rolland *et al.* 2014). However, disentangling these competing explanations would require phylogenetic and biogeographic studies, as well as those addressing the ecology of the species implied. Only considering these historical and ecological aspects, an integrative regionalisation of the NR region might be achieved. Other studies taking into account the endemic Neotropical mammals are necessary to go beyond to spatial congruence (Noguera-Urbano 2016), and propose biological and ecological explanations for the biotic integration of endemic mammals in the NR.

Conclusions

For many years, different authors (Sclater 1858, 1895; Wallace 1876; Hershkovitz 1958; Smith 1983; Cabrera and Willink 1973; Udvardy 1975; Cox 2001; Morrone 2001*b*, 2014*a*, 2015; Kreft and Jetz 2010; Holt *et al.* 2013) have suggested schemes with specific boundaries for the NR. The boundaries of the nine Neotropical Ae found in the present study based on mammals agree with several schemes of the NR (Sclater 1858, 1895; Wallace 1876; Hershkovitz 1958; Udvardy 1975; Kreft and Jetz 2010; Holt *et al.* 2013; Rueda *et al.* 2013; Morrone 2014*a*, 2015), rather than with only one. Therefore, our analysis suggests that, in combination, these Ae are a good representation of the NR as a whole (e.g. overlap of the Ae map). Thus, if we consider that the distributional areas of mammals and other biological groups are not stable over time (Gaston 2003; Antonelli and Sanmartín 2011), but rather move in response to, for example, biological interactions or in concert with climatic change, fluctuations in sea level, the movement of the continents (Holt 2001), we may suppose that, given time, the Neotropical endemic species could extend or contract their areas of distribution towards the Equatorial parallel or over the transitional zones, modifying the current picture of the NR. Several authors have proposed changes in the current biogeographic patterns. For example, Morrone (2014*b*) proposed a biogeographical regionalisation of the NR, and tested the relationships between the biotic components (subregions and domains). The author described six major evolutionary events (the former connection between the North American and South American landmasses, the vicariance between the Antilles and the rest of the NR, the vicariance between the north-western and south-eastern continental components of the NR, the vicariance between northern Amazonia and the remaining areas of the north-eastern continental component, the vicariance between south-western Amazonia and north-western South America–Mesoamerica, and the vicariance between Chaco and Parana) related with the integration of subunits in the NR, which has led to a re-organisation of the structure of the NR. However, other factors have also played a role in the evolution of the Neotropical biodiversity and the origins of the present diversity, such as time evolution, rainfall changes, temperature variations, modifications of the geographic areas, mountain uplift, hydrological changes; Hoorn *et al.* 2010; Antonelli and Sanmartín 2011).

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgments

We are grateful to Irene Goyenechea for definitive comments to improve this manuscript. Thanks go to Hector Ramírez-Chaves, Laura Rengifo and Amparo Echeverry for crucial comments on a previous draft of this manuscript that greatly improved it. This paper constitutes a partial fulfillment of the requirements to obtain a doctoral degree from Posgrado en Ciencias Biológicas of the National Autonomous University of México (UNAM) of E. A. Noguera-Urbano. Funding was provided by the Consejo Nacional de Ciencia y Tecnología from Mexico (CONACyT, scholarship 262582) and the Posgrado en Ciencias Biológicas of the National Autonomous University of Mexico (UNAM). We are also grateful to the Associate Editor and anonymous reviewers for valuable comments on the manuscript. Special thanks go to Lynna Kiere for reviewing the English writing of this manuscript.

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Handling editor: Isabel Sanmartin

Australian Systematic Botany, 2017, **30**, 470–484
doi:10.1071/SB16053_AC

Supplementary material

The Neotropical region *sensu* the areas of endemism of terrestrial mammals

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Table S1. List of taxa processed

Number	Taxon
1	*Abrawayaomys ruschii*
2	*Abrocoma*
3	*Abrocoma bennettii*
4	*Abrocoma boliviensis*
5	*Abrocoma budini*
6	*Abrocoma cinerea*
7	*Abrocoma famatina*
8	*Abrocoma shistacea*
9	*Abrocoma uspallata*
10	*Abrocoma vaccarum*
11	*Abrocomidae*
12	*Abrothrix*
13	*Abrothrix andinus*
14	*Abrothrix hershkovitzi*
15	*Abrothrix illuteus*
16	*Abrothrix jelskii*
17	*Abrothrix lanosus*
18	*Abrothrix longipilis*
19	*Abrothrix markhami*
20	*Abrothrix olivaceus*
21	*Abrothrix sanborni*
22	*Aconaemys*
23	*Aconaemys fuscus*
24	*Aconaemys porteri*
25	*Aconaemys sagei*
26	*Aegialomys*
27	*Aegialomys galapagoensis*
28	*Aegialomys xanthaeolus*
29	*Aepeomys*
30	*Aepeomys lugens*
31	*Aepeomys reigi*
32	*Akodon*
33	*Akodon aerosus*
34	*Akodon affinis*
35	*Akodon albiventer*
36	*Akodon aliquantulus*
37	*Akodon azarae*
38	*Akodon bogotensis*
39	*Akodon boliviensis*
40	*Akodon budini*
41	*Akodon cursor*
42	*Akodon dayi*
43	*Akodon dolores*
44	*Akodon fumeus*
45	*Akodon iniscatus*
46	*Akodon juninensis*
47	*Akodon kofordi*
48	*Akodon latebricola*
49	*Akodon leucolimnaeus*
50	*Akodon lindberghi*
51	*Akodon lutescens*
52	*Akodon mimus*
53	*Akodon molinae*
54	*Akodon mollis*
55	*Akodon montensis*
56	*Akodon mystax*
57	*Akodon neocenus*
58	*Akodon oenos*
59	*Akodon orophilus*
60	*Akodon paranaensis*
61	*Akodon pervalens*
62	*Akodon philipmyersi*
63	*Akodon reigi*
64	*Akodon sanctipaulensis*
65	*Akodon serrensis*
66	*Akodon siberiae*
67	*Akodon simulator*
68	*Akodon spegazzinii*
69	*Akodon subfuscus*
70	*Akodon surdus*
71	*Akodon sylvanus*
72	*Akodon toba*
73	*Akodon torques*
74	*Akodon varius*
75	*Alouatta*
76	*Alouatta arctoidea*
77	*Alouatta belzebul*
78	*Alouatta caraya*
79	*Alouatta discolor*
80	*Alouatta guariba*
81	*Alouatta juara*
82	*Alouatta macconnelli*
83	*Alouatta nigerrima*
84	*Alouatta palliata*
85	*Alouatta pigra*
86	*Alouatta puruensis*
87	*Alouatta sara*
88	*Alouatta seniculus*
89	*Alouatta ululata*
90	*Ametrida centurio*
91	*Ammospermophilus harrisii*
92	*Ammospermophilus interpres*
93	*Ammospermophilus nelsoni*
94	*Amorphochilus schnablii*
95	*Amphinectomys savamis*
96	*Andalgalomys*
97	*Andalgalomys olrogi*
98	*Andalgalomys pearsoni*
99	*Andinomys edax*
100	*Anotomys leander*
101	*Anoura*
102	*Anoura caudifer*
103	*Anoura cultrata*
104	*Anoura fistulata*
105	*Anoura geoffroyi*
106	*Anoura latidens*
107	*Anoura luismanueli*
108	*Aotus*

Number	Taxon
109	*Aotus azarae*
110	*Aotus brumbacki*
111	*Aotus griseimembra*
112	*Aotus jorgehernandezi*
113	*Aotus lemurinus*
114	*Aotus miconax*
115	*Aotus nancymaae*
116	*Aotus nigriceps*
117	*Aotus trivirgatus*
118	*Aotus vociferans*
119	*Aotus zonalis*
120	*Ardops nichollsi*
121	*Ariteus flavescens*
122	*Artibeus*
123	*Artibeus amplus*
124	*Artibeus anderseni*
125	*Artibeus aztecus*
126	*Artibeus cinereus*
127	*Artibeus concolor*
128	*Artibeus fimbriatus*
129	*Artibeus fraterculus*
130	*Artibeus glaucus*
131	*Artibeus gnomus*
132	*Artibeus hirsutus*
133	*Artibeus inopinatus*
134	*Artibeus jamaicensis*
135	*Artibeus lituratus*
136	*Artibeus obscurus*
137	*Artibeus phaeotis*
138	*Artibeus planirostris*
139	*Artibeus rosenbergii*
140	*Artibeus toltecus*
141	*Artibeus watsoni*
142	*Ateles*
143	*Ateles belzebuth*
144	*Ateles chamek*
145	*Ateles fusciceps*
146	*Ateles geoffroyi*
147	*Ateles hybridus*
148	*Ateles marginatus*
149	*Ateles paniscus*
150	*Atelidae*
151	*Atelocynus microtis*
152	*Auliscomys*
153	*Auliscomys boliviensis*
154	*Auliscomys pictus*
155	*Auliscomys sublimis*
156	*Baiomys*
157	*Baiomys musculus*
158	*Baiomys taylori*
159	*Balantiopteryx*
160	*Balantiopteryx infusca*
161	*Balantiopteryx io*
162	*Balantiopteryx plicata*
163	*Bassaricyon*

Number	Taxon
164	*Bassaricyon alleni*
165	*Bassaricyon beddardi*
166	*Bassaricyon gabbii*
167	*Bassaricyon lasius*
168	*Bassaricyon pauli*
169	*Bassariscus sumichrasti*
170	*Bauerus dubiaquercus*
171	*Bibimys*
172	*Bibimys chacoensis*
173	*Bibimys labiosus*
174	*Bibimys torresi*
175	*Blarina carolinensis*
176	*Blarina hylophaga*
177	*Blarinomys breviceps*
178	*Blastocerus dichotomus*
179	*Brachyphylla*
180	*Brachyphylla cavernarum*
181	*Brachyphylla nana*
182	*Brachyteles*
183	*Brachyteles arachnoides*
184	*Brachyteles hypoxanthus*
185	*Bradypus*
186	*Bradypus torquatus*
187	*Bradypus tridactylus*
188	*Bradypus variegatus*
189	*Brucepattersonius*
190	*Brucepattersonius albinasus*
191	*Brucepattersonius griserufescens*
192	*Brucepattersonius guarani*
193	*Brucepattersonius igniventris*
194	*Brucepattersonius iheringi*
195	*Brucepattersonius misionensis*
196	*Brucepattersonius paradisus*
197	*Brucepattersonius soricinus*
198	*Cabassous*
199	*Cabassous centralis*
200	*Cabassous chacoensis*
201	*Cabassous tatouay*
202	*Cabassous unicinctus*
203	*Cacajao*
204	*Cacajao ayresi*
205	*Cacajao calvus*
206	*Cacajao hosomi*
207	*Cacajao melanocephalus*
208	*Caenolestes*
209	*Caenolestes caniventer*
210	*Caenolestes condorensis*
211	*Caenolestes convelatus*
212	*Caenolestes fuliginosus*
213	*Caenolestidae*
214	*Callibella humilis*
215	*Callicebus*
216	*Callicebus aureipalatii*
217	*Callicebus baptista*
218	*Callicebus barbarabrownae*

Number	Taxon
219	*Callicebus bernhardi*
220	*Callicebus brunneus*
221	*Callicebus caligatus*
222	*Callicebus caquetensis*
223	*Callicebus cinerascens*
224	*Callicebus coimbrai*
225	*Callicebus cupreus*
226	*Callicebus discolor*
227	*Callicebus donacophilus*
228	*Callicebus dubius*
229	*Callicebus hoffmannsi*
230	*Callicebus lucifer*
231	*Callicebus lugens*
232	*Callicebus medemi*
233	*Callicebus melanochir*
234	*Callicebus modestus*
235	*Callicebus moloch*
236	*Callicebus nigrifrons*
237	*Callicebus oenanthe*
238	*Callicebus olallae*
239	*Callicebus ornatus*
240	*Callicebus pallescens*
241	*Callicebus personatus*
242	*Callicebus purinus*
243	*Callicebus regulus*
244	*Callicebus stephennashi*
245	*Callicebus torquatus*
246	*Callimico goeldii*
247	*Callistomys pictus*
248	*Callithrix*
249	*Callithrix aurita*
250	*Callithrix flaviceps*
251	*Callithrix geoffroyi*
252	*Callithrix jacchus*
253	*Callithrix kuhlii*
254	*Callithrix penicillata*
255	*Callitrichidae*
256	*Calomys*
257	*Calomys boliviae*
258	*Calomys callidus*
259	*Calomys callosus*
260	*Calomys expulsus*
261	*Calomys fecundus*
262	*Calomys hummelincki*
263	*Calomys laucha*
264	*Calomys lepidus*
265	*Calomys musculinus*
266	*Calomys sorellus*
267	*Calomys tener*
268	*Calomys tocantinsi*
269	*Calomys venustus*
270	*Caluromys*
271	*Caluromys derbianus*
272	*Caluromys lanatus*
273	*Caluromys philander*
274	*Caluromysiops irrupta*
275	*Calyptophractus retusus*
276	*Capromyidae*
277	*Capromys pilorides*
278	*Carollia*
279	*Carollia brevicauda*
280	*Carollia castanea*
281	*Carollia manu*
282	*Carollia perspicillata*
283	*Carollia sowelli*
284	*Carollia subrufa*
285	*Carterodon sulcidens*
286	*Catagonus wagneri*
287	*Cavia*
288	*Cavia aperea*
289	*Cavia fulgida*
290	*Cavia magna*
291	*Cavia tschudii*
292	*Caviidae*
293	*Cebidae*
294	*Cebuella pygmaea*
295	*Cebus*
296	*Cebus albifrons*
297	*Cebus apella*
298	*Cebus capucinus*
299	*Cebus cay*
300	*Cebus flavius*
301	*Cebus kaapori*
302	*Cebus libidinosus*
303	*Cebus macrocephalus*
304	*Cebus nigritus*
305	*Cebus olivaceus*
306	*Cebus robustus*
307	*Cebus xanthosternos*
308	*Centronycteris*
309	*Centronycteris centralis*
310	*Centronycteris maximiliani*
311	*Centurio senex*
312	*Cerdocyon thous*
313	*Cerradomys*
314	*Cerradomys andersoni*
315	*Cerradomys maracajuensis*
316	*Cerradomys marinhus*
317	*Cerradomys scotti*
318	*Cerradomys subflavus*
319	*Chacodelphys formosa*
320	*Chaetodipus arenarius*
321	*Chaetodipus artus*
322	*Chaetodipus baileyi*
323	*Chaetodipus californicus*
324	*Chaetodipus dalquesti*
325	*Chaetodipus eremicus*
326	*Chaetodipus fallax*
327	*Chaetodipus goldmani*
328	*Chaetodipus intermedius*

Number	Taxon
329	*Chaetodipus lineatus*
330	*Chaetodipus nelsoni*
331	*Chaetodipus penicillatus*
332	*Chaetodipus pernix*
333	*Chaetodipus rudinoris*
334	*Chaetodipus spinatus*
335	*Chaetomys subspinosus*
336	*Chaetophractus*
337	*Chaetophractus nationi*
338	*Chaetophractus vellerosus*
339	*Chaetophractus villosus*
340	*Chelemys*
341	*Chelemys delfini*
342	*Chelemys macronyx*
343	*Chelemys megalonyx*
344	*Chibchanomys*
345	*Chibchanomys orcesi*
346	*Chibchanomys trichotis*
347	*Chilomys instans*
348	*Chilonatalus*
349	*Chilonatalus micropus*
350	*Chilonatalus tumidifrons*
351	*Chinchilla*
352	*Chinchilla chinchilla*
353	*Chinchilla lanigera*
354	*Chinchillidae*
355	*Chinchillula sahamae*
356	*Chiroderma*
357	*Chiroderma doriae*
358	*Chiroderma improvisum*
359	*Chiroderma salvini*
360	*Chiroderma trinitatum*
361	*Chiroderma villosum*
362	*Chironectes minimus*
363	*Chiropotes*
364	*Chiropotes albinasus*
365	*Chiropotes chiropotes*
366	*Chiropotes satanas*
367	*Chiropotes utahickae*
368	*Chlamyphorus truncatus*
369	*Choeroniscus*
370	*Choeroniscus godmani*
371	*Choeroniscus minor*
372	*Choeroniscus periosus*
373	*Choeronycteris mexicana*
374	*Choloepus*
375	*Choloepus didactylus*
376	*Choloepus hoffmanni*
377	*Chrotopterus auritus*
378	*Chrysocyon brachyurus*
379	*Clyomys*
380	*Clyomys bishopi*
381	*Clyomys laticeps*
382	*Coendou*
383	*Coendou bicolor*
384	*Coendou nycthemera*
385	*Coendou prehensilis*
386	*Coendou quichua*
387	*Coendou rothschildi*
388	*Coendou sanctamartae*
389	*Conepatus*
390	*Conepatus chinga*
391	*Conepatus humboldtii*
392	*Conepatus leuconotus*
393	*Conepatus semistriatus*
394	*Cormura brevirostris*
395	*Corynorhinus mexicanus*
396	*Corynorhinus rafinesquii*
397	*Cratogeomys*
398	*Cratogeomys castanops*
399	*Cratogeomys fulvescens*
400	*Cratogeomys fumosus*
401	*Cratogeomys goldmani*
402	*Cratogeomys merriami*
403	*Cratogeomys perotensis*
404	*Cratogeomys planiceps*
405	*Cricetidae*
406	*Cryptonanus*
407	*Cryptonanus agricolai*
408	*Cryptonanus chacoensis*
409	*Cryptonanus guahybae*
410	*Cryptonanus unduaviensis*
411	*Cryptotis alticola*
412	*Cryptotis brachyonyx*
413	*Cryptotis colombiana*
414	*Cryptotis endersi*
415	*Cryptotis equatoris*
416	*Cryptotis goldmani*
417	*Cryptotis goodwini*
418	*Cryptotis gracilis*
419	*Cryptotis griseoventris*
420	*Cryptotis hondurensis*
421	*Cryptotis magna*
422	*Cryptotis mayensis*
423	*Cryptotis medellinia*
424	*Cryptotis mera*
425	*Cryptotis meridensis*
426	*Cryptotis merriami*
427	*Cryptotis mexicana*
428	*Cryptotis montivaga*
429	*Cryptotis nelsoni*
430	*Cryptotis nigrescens*
431	*Cryptotis obscura*
432	*Cryptotis orophila*
433	*Cryptotis peregrina*
434	*Cryptotis peruviensis*
435	*Cryptotis phillipsii*
436	*Cryptotis squamipes*
437	*Cryptotis tamensis*
438	*Cryptotis thomasi*

Number	Taxon
439	*Cryptotis tropicalis*
440	*Ctenomys*
441	*Ctenomys argentinus*
442	*Ctenomys australis*
443	*Ctenomys azarae*
444	*Ctenomys bergi*
445	*Ctenomys boliviensis*
446	*Ctenomys bonettoi*
447	*Ctenomys brasiliensis*
448	*Ctenomys budini*
449	*Ctenomys colburni*
450	*Ctenomys coludo*
451	*Ctenomys conoveri*
452	*Ctenomys coyhaiquensis*
453	*Ctenomys dorbignyi*
454	*Ctenomys dorsalis*
455	*Ctenomys emilianus*
456	*Ctenomys famosus*
457	*Ctenomys flamarioni*
458	*Ctenomys fochi*
459	*Ctenomys fodax*
460	*Ctenomys frater*
461	*Ctenomys fulvus*
462	*Ctenomys goodfellowi*
463	*Ctenomys haigi*
464	*Ctenomys johannis*
465	*Ctenomys juris*
466	*Ctenomys knighti*
467	*Ctenomys lami*
468	*Ctenomys latro*
469	*Ctenomys leucodon*
470	*Ctenomys lewisi*
471	*Ctenomys magellanicus*
472	*Ctenomys maulinus*
473	*Ctenomys mendocinus*
474	*Ctenomys minutus*
475	*Ctenomys occultus*
476	*Ctenomys opimus*
477	*Ctenomys osvaldoreigi*
478	*Ctenomys pearsoni*
479	*Ctenomys perrensi*
480	*Ctenomys peruanus*
481	*Ctenomys pilarensis*
482	*Ctenomys pontifex*
483	*Ctenomys porteousi*
484	*Ctenomys pundti*
485	*Ctenomys rionegrensis*
486	*Ctenomys roigi*
487	*Ctenomys saltarius*
488	*Ctenomys scagliai*
489	*Ctenomys sericeus*
490	*Ctenomys sociabilis*
491	*Ctenomys steinbachi*
492	*Ctenomys sylvanus*
493	*Ctenomys talarum*

Number	Taxon
494	*Ctenomys torquatus*
495	*Ctenomys tuconax*
496	*Ctenomys tucumanus*
497	*Ctenomys tulduco*
498	*Ctenomys validus*
499	*Ctenomys viperinus*
500	*Ctenomys yolandae*
501	*Cuniculus paca*
502	*Cuniculus taczanowskii*
503	*Cuscomys ashaninka*
504	*Cyclopes didactylus*
505	*Cynomops*
506	*Cynomops abrasus*
507	*Cynomops greenhalli*
508	*Cynomops mexicanus*
509	*Cynomops paranus*
510	*Cynomops planirostris*
511	*Cynomys gunnisoni*
512	*Cynomys mexicanus*
513	*Cynomys parvidens*
514	*Cyttarops alecto*
515	*Dactylomys*
516	*Dactylomys boliviensis*
517	*Dactylomys dactylinus*
518	*Dactylomys peruanus*
519	*Dasypodidae*
520	*Dasyprocta*
521	*Dasyprocta azarae*
522	*Dasyprocta coibae*
523	*Dasyprocta cristata*
524	*Dasyprocta fuliginosa*
525	*Dasyprocta guamara*
526	*Dasyprocta kalinowskii*
527	*Dasyprocta leporina*
528	*Dasyprocta mexicana*
529	*Dasyprocta prymnolopha*
530	*Dasyprocta punctata*
531	*Dasyprocta ruatanica*
532	*Dasyproctidae*
533	*Dasypus hybridus*
534	*Dasypus kappleri*
535	*Dasypus novemcinctus*
536	*Dasypus pilosus*
537	*Dasypus sabanicola*
538	*Dasypus septemcinctus*
539	*Dasypus yepesi*
540	*Delomys*
541	*Delomys collinus*
542	*Delomys dorsalis*
543	*Delomys sublineatus*
544	*Deltamys kempi*
545	*Desmodus rotundus*
546	*Diaemus youngi*
547	*Diclidurus*
548	*Diclidurus albus*

Number	Taxon	Number	Taxon
549	*Diclidurus ingens*	604	*Eptesicus innoxius*
550	*Diclidurus isabellus*	605	*Eremoryzomys polius*
551	*Diclidurus scutatus*	606	*Erethizontidae*
552	*Didelphis albiventris*	607	*Erophylla*
553	*Didelphis aurita*	608	*Erophylla bombifrons*
554	*Didelphis imperfecta*	609	*Erophylla sezekorni*
555	*Didelphis marsupialis*	610	*Eumops*
556	*Didelphis pernigra*	611	*Eumops auripendulus*
557	*Dinomys branickii*	612	*Eumops bonariensis*
558	*Diphylla ecaudata*	613	*Eumops dabbenei*
559	*Diplomys*	614	*Eumops floridanus*
560	*Diplomys caniceps*	615	*Eumops glaucinus*
561	*Diplomys labilis*	616	*Eumops hansae*
562	*Dipodomys agilis*	617	*Eumops maurus*
563	*Dipodomys compactus*	618	*Eumops patagonicus*
564	*Dipodomys deserti*	619	*Eumops perotis*
565	*Dipodomys elator*	620	*Eumops trumbulli*
566	*Dipodomys gravipes*	621	*Eumops underwoodi*
567	*Dipodomys heermanni*	622	*Euneomys*
568	*Dipodomys ingens*	623	*Euneomys chinchilloides*
569	*Dipodomys insularis*	624	*Euneomys fossor*
570	*Dipodomys margaritae*	625	*Euneomys mordax*
571	*Dipodomys merriami*	626	*Euneomys petersoni*
572	*Dipodomys nelsoni*	627	*Euphractus sexcinctus*
573	*Dipodomys nitratoides*	628	*Euryoryzomys*
574	*Dipodomys panamintinus*	629	*Euryoryzomys emmonsae*
575	*Dipodomys phillipsii*	630	*Euryoryzomys lamia*
576	*Dipodomys simulans*	631	*Euryoryzomys legatus*
577	*Dipodomys spectabilis*	632	*Euryoryzomys macconnelli*
578	*Dipodomys stephensi*	633	*Euryoryzomys nitidus*
579	*Dipodomys venustus*	634	*Euryoryzomys russatus*
580	*Dolichotis*	635	*Euryzygomatomys spinosus*
581	*Dolichotis patagonum*	636	*Furipteridae*
582	*Dolichotis salinicola*	637	*Furipterus horrens*
583	*Dromiciops gliroides*	638	*Galea*
584	*Echimyidae*	639	*Galea flavidens*
585	*Echimys*	640	*Galea monasteriensis*
586	*Echimys chrysurus*	641	*Galea musteloides*
587	*Echimys saturnus*	642	*Galea spixii*
588	*Echimys vieirai*	643	*Galenomys garleppi*
589	*Echinoprocta rufescens*	644	*Galictis*
590	*Ectophylla alba*	645	*Galictis cuja*
591	*Eira barbara*	646	*Galictis vittata*
592	*Eligmodontia*	647	*Geocapromys*
593	*Eligmodontia moreni*	648	*Geocapromys brownii*
594	*Eligmodontia morgani*	649	*Geomys arenarius*
595	*Eligmodontia puerulus*	650	*Geomys attwateri*
596	*Eligmodontia typus*	651	*Geomys breviceps*
597	*Enchisthenes hartii*	652	*Geomys knoxjonesi*
598	*Eptesicus andinus*	653	*Geomys personatus*
599	*Eptesicus brasiliensis*	654	*Geomys pinetis*
600	*Eptesicus chiriquinus*	655	*Geomys texensis*
601	*Eptesicus diminutus*	656	*Geomys tropicalis*
602	*Eptesicus furinalis*	657	*Geoxus valdivianus*
603	*Eptesicus guadeloupensis*	658	*Glironia venusta*

Number	Taxon
659	*Glossophaga*
660	*Glossophaga commissarisi*
661	*Glossophaga leachii*
662	*Glossophaga longirostris*
663	*Glossophaga morenoi*
664	*Glossophaga soricina*
665	*Glyphonycteris*
666	*Glyphonycteris behnii*
667	*Glyphonycteris daviesi*
668	*Glyphonycteris sylvestris*
669	*Gracilinanus*
670	*Gracilinanus aceramarcae*
671	*Gracilinanus agilis*
672	*Gracilinanus dryas*
673	*Gracilinanus emiliae*
674	*Gracilinanus marica*
675	*Gracilinanus microtarsus*
676	*Graomys*
677	*Graomys centralis*
678	*Graomys domorum*
679	*Graomys edithae*
680	*Graomys griseoflavus*
681	*Habromys*
682	*Habromys chinanteco*
683	*Habromys delicatulus*
684	*Habromys ixtlani*
685	*Habromys lepturus*
686	*Habromys lophurus*
687	*Habromys schmidlyi*
688	*Habromys simulatus*
689	*Handleyomys*
690	*Handleyomys alfaroi*
691	*Handleyomys chapmani*
692	*Handleyomys fuscatus*
693	*Handleyomys intectus*
694	*Handleyomys melanotis*
695	*Handleyomys rhabdops*
696	*Handleyomys rostratus*
697	*Handleyomys saturatior*
698	*Herpailurus yagouaroundi*
699	*Heteromys*
700	*Heteromys anomalus*
701	*Heteromys australis*
702	*Heteromys desmarestianus*
703	*Heteromys gaumeri*
704	*Heteromys nelsoni*
705	*Heteromys oasicus*
706	*Heteromys oresterus*
707	*Heteromys teleus*
708	*Hippocamelus*
709	*Hippocamelus antisensis*
710	*Hippocamelus bisulcus*
711	*Histiotus*
712	*Histiotus alienus*
713	*Histiotus humboldti*
714	*Histiotus laephotis*
715	*Histiotus macrotus*
716	*Histiotus magellanicus*
717	*Histiotus montanus*
718	*Histiotus velatus*
719	*Hodomys alleni*
720	*Holochilus*
721	*Holochilus brasiliensis*
722	*Holochilus chacarius*
723	*Holochilus sciureus*
724	*Hoplomys gymnurus*
725	*Hydrochoerus*
726	*Hydrochoerus hydrochaeris*
727	*Hydrochoerus isthmius*
728	*Hyladelphys kalinowskii*
729	*Hylaeamys*
730	*Hylaeamys acritus*
731	*Hylaeamys laticeps*
732	*Hylaeamys megacephalus*
733	*Hylaeamys oniscus*
734	*Hylaeamys perenensis*
735	*Hylaeamys tatei*
736	*Hylaeamys yunganus*
737	*Hylonycteris underwoodi*
738	*Ichthyomys*
739	*Ichthyomys hydrobates*
740	*Ichthyomys pittieri*
741	*Ichthyomys stolzmanni*
742	*Ichthyomys tweedii*
743	*Idionycteris phyllotis*
744	*Irenomys tarsalis*
745	*Isothrix*
746	*Isothrix barbarabrownae*
747	*Isothrix bistriata*
748	*Isothrix negrensis*
749	*Isothrix pagurus*
750	*Isothrix sinnamariensis*
751	*Isthmomys*
752	*Isthmomys flavidus*
753	*Isthmomys pirrensis*
754	*Juliomys*
755	*Juliomys pictipes*
756	*Juliomys rimofrons*
757	*Juscelinomys*
758	*Juscelinomys guaporensis*
759	*Juscelinomys huanchacae*
760	*Kannabateomys amblyonyx*
761	*Kerodon*
762	*Kerodon acrobata*
763	*Kerodon rupestris*
764	*Kunsia*
765	*Kunsia fronto*
766	*Kunsia tomentosus*
767	*Lagidium*
768	*Lagidium peruanum*

Number	Taxon
769	*Lagidium viscacia*
770	*Lagidium wolffsohni*
771	*Lagostomus maximus*
772	*Lagothrix*
773	*Lagothrix cana*
774	*Lagothrix lagotricha*
775	*Lagothrix lugens*
776	*Lagothrix poeppigii*
777	*Lama guanicoe*
778	*Lampronycteris brachyotis*
779	*Lasiurus atratus*
780	*Lasiurus castaneus*
781	*Lasiurus degelidus*
782	*Lasiurus ebenus*
783	*Lasiurus ega*
784	*Lasiurus egregius*
785	*Lasiurus insularis*
786	*Lasiurus intermedius*
787	*Lasiurus minor*
788	*Lasiurus pfeifferi*
789	*Lasiurus varius*
790	*Lasiurus xanthinus*
791	*Lenoxus apicalis*
792	*Leontopithecus*
793	*Leontopithecus caissara*
794	*Leontopithecus chrysomelas*
795	*Leontopithecus chrysopygus*
796	*Leontopithecus rosalia*
797	*Leopardus*
798	*Leopardus colocolo*
799	*Leopardus geoffroyi*
800	*Leopardus guigna*
801	*Leopardus jacobita*
802	*Leopardus pardalis*
803	*Leopardus tigrinus*
804	*Leopardus wiedii*
805	*Leptonycteris*
806	*Leptonycteris curasoae*
807	*Leptonycteris nivalis*
808	*Leptonycteris yerbabuenae*
809	*Lepus alleni*
810	*Lepus callotis*
811	*Lepus flavigularis*
812	*Lepus insularis*
813	*Lestodelphys halli*
814	*Lestoros inca*
815	*Lichonycteris obscura*
816	*Liomys*
817	*Liomys adspersus*
818	*Liomys irroratus*
819	*Liomys pictus*
820	*Liomys salvini*
821	*Liomys spectabilis*
822	*Lionycteris spurrelli*
823	*Lonchophylla*

Number	Taxon
824	*Lonchophylla bokermanni*
825	*Lonchophylla chocoana*
826	*Lonchophylla concava*
827	*Lonchophylla dekeyseri*
828	*Lonchophylla handleyi*
829	*Lonchophylla hesperia*
830	*Lonchophylla mordax*
831	*Lonchophylla orcesi*
832	*Lonchophylla robusta*
833	*Lonchophylla thomasi*
834	*Lonchorhina*
835	*Lonchorhina aurita*
836	*Lonchorhina fernandezi*
837	*Lonchorhina inusitata*
838	*Lonchorhina marinkellei*
839	*Lonchorhina orinocensis*
840	*Lonchothrix emiliae*
841	*Lontra longicaudis*
842	*Lontra provocax*
843	*Lophostoma*
844	*Lophostoma aequatorialis*
845	*Lophostoma brasiliense*
846	*Lophostoma carrikeri*
847	*Lophostoma evotis*
848	*Lophostoma schulzi*
849	*Lophostoma silvicolum*
850	*Lophostoma yasuni*
851	*Loxodontomys*
852	*Loxodontomys micropus*
853	*Loxodontomys pikumche*
854	*Lundomys molitor*
855	*Lutreolina crassicaudata*
856	*Lyncodon patagonicus*
857	*Macrophyllum macrophyllum*
858	*Macrotus*
859	*Macrotus californicus*
860	*Macrotus waterhousii*
861	*Makalata*
862	*Makalata didelphoides*
863	*Makalata macrura*
864	*Makalata rhipidura*
865	*Marmosa*
866	*Marmosa alstoni*
867	*Marmosa andersoni*
868	*Marmosa constantiae*
869	*Marmosa demerarae*
870	*Marmosa lepida*
871	*Marmosa mexicana*
872	*Marmosa murina*
873	*Marmosa paraguayanus*
874	*Marmosa phaea*
875	*Marmosa quichua*
876	*Marmosa regina*
877	*Marmosa robinsoni*
878	*Marmosa rubra*

Number	Taxon
879	*Marmosa tyleriana*
880	*Marmosa xerophila*
881	*Marmosops*
882	*Marmosops bishopi*
883	*Marmosops cracens*
884	*Marmosops creightoni*
885	*Marmosops fuscatus*
886	*Marmosops handleyi*
887	*Marmosops impavidus*
888	*Marmosops incanus*
889	*Marmosops invictus*
890	*Marmosops juninensis*
891	*Marmosops neblina*
892	*Marmosops noctivagus*
893	*Marmosops ocellatus*
894	*Marmosops parvidens*
895	*Marmosops paulensis*
896	*Marmosops pinheiroi*
897	*Mazama*
898	*Mazama americana*
899	*Mazama bororo*
900	*Mazama bricenii*
901	*Mazama chunyi*
902	*Mazama gouazoubira*
903	*Mazama nana*
904	*Mazama nemorivaga*
905	*Mazama pandora*
906	*Mazama rufina*
907	*Mazama temama*
908	*Megadontomys*
909	*Megadontomys cryophilus*
910	*Megadontomys nelsoni*
911	*Megadontomys thomasi*
912	*Megasorex gigas*
913	*Melanomys*
914	*Melanomys caliginosus*
915	*Melanomys robustulus*
916	*Melanomys zunigae*
917	*Mephitis macroura*
918	*Mesocapromys*
919	*Mesocapromys angelcabrerai*
920	*Mesocapromys auritus*
921	*Mesocapromys nanus*
922	*Mesomys*
923	*Mesomys hispidus*
924	*Mesomys leniceps*
925	*Mesomys occultus*
926	*Mesomys stimulax*
927	*Mesophylla macconnelli*
928	*Metachirus nudicaudatus*
929	*Mico*
930	*Mico acariensis*
931	*Mico argentatus*
932	*Mico chrysoleucus*
933	*Mico emiliae*

Number	Taxon
934	*Mico humeralifer*
935	*Mico intermedius*
936	*Mico leucippe*
937	*Mico manicorensis*
938	*Mico marcai*
939	*Mico mauesi*
940	*Mico melanurus*
941	*Mico nigriceps*
942	*Mico rondoni*
943	*Mico saterei*
944	*Microakodontomys transitorius*
945	*Microcavia*
946	*Microcavia australis*
947	*Microcavia niata*
948	*Microcavia shiptoni*
949	*Microdipodops pallidus*
950	*Micronycteris*
951	*Micronycteris brosseti*
952	*Micronycteris hirsuta*
953	*Micronycteris matses*
954	*Micronycteris megalotis*
955	*Micronycteris microtis*
956	*Micronycteris minuta*
957	*Micronycteris sanborni*
958	*Micronycteris schmidtorum*
959	*Microryzomys*
960	*Microryzomys altissimus*
961	*Microryzomys minutus*
962	*Microsciurus*
963	*Microsciurus alfari*
964	*Microsciurus flaviventer*
965	*Microsciurus mimulus*
966	*Microsciurus santanderensis*
967	*Microtus guatemalensis*
968	*Microtus mexicanus*
969	*Microtus oaxacensis*
970	*Microtus quasiater*
971	*Microtus umbrosus*
972	*Mimon*
973	*Mimon bennettii*
974	*Mimon cozumelae*
975	*Mimon crenulatum*
976	*Mimon koepckeae*
977	*Mindomys hammondi*
978	*Molossops*
979	*Molossops aequatorianus*
980	*Molossops mattogrossensis*
981	*Molossops neglectus*
982	*Molossops temminckii*
983	*Molossus*
984	*Molossus aztecus*
985	*Molossus barnesi*
986	*Molossus coibensis*
987	*Molossus currentium*
988	*Molossus molossus*

Number	Taxon
989	*Molossus pretiosus*
990	*Molossus rufus*
991	*Molossus sinaloae*
992	*Monodelphis*
993	*Monodelphis adusta*
994	*Monodelphis americana*
995	*Monodelphis brevicaudata*
996	*Monodelphis dimidiata*
997	*Monodelphis domestica*
998	*Monodelphis emiliae*
999	*Monodelphis glirina*
1000	*Monodelphis handleyi*
1001	*Monodelphis iheringi*
1002	*Monodelphis kunsi*
1003	*Monodelphis maraxina*
1004	*Monodelphis osgoodi*
1005	*Monodelphis palliolata*
1006	*Monodelphis reigi*
1007	*Monodelphis ronaldi*
1008	*Monodelphis rubida*
1009	*Monodelphis scalops*
1010	*Monodelphis theresa*
1011	*Monodelphis umbristriatus*
1012	*Monodelphis unistriatus*
1013	*Monophyllus*
1014	*Monophyllus plethodon*
1015	*Monophyllus redmani*
1016	*Mormoopidae*
1017	*Mormoops*
1018	*Mormoops blainvillei*
1019	*Mormoops megalophylla*
1020	*Mormopterus kalinowskii*
1021	*Mormopterus minutus*
1022	*Mormopterus phrudus*
1023	*Musonycteris harrisoni*
1024	*Mustela africana*
1025	*Mustela felipei*
1026	*Myocastor coypus*
1027	*Myoprocta*
1028	*Myoprocta acouchy*
1029	*Myoprocta pratti*
1030	*Myotis aelleni*
1031	*Myotis albescens*
1032	*Myotis atacamensis*
1033	*Myotis auriculus*
1034	*Myotis austroriparius*
1035	*Myotis chiloensis*
1036	*Myotis cobanensis*
1037	*Myotis dinellii*
1038	*Myotis dominicensis*
1039	*Myotis elegans*
1040	*Myotis findleyi*
1041	*Myotis fortidens*
1042	*Myotis grisescens*
1043	*Myotis keaysi*
1044	*Myotis levis*
1045	*Myotis martiniquensis*
1046	*Myotis nesopolus*
1047	*Myotis nigricans*
1048	*Myotis occultus*
1049	*Myotis oxyotus*
1050	*Myotis peninsularis*
1051	*Myotis planiceps*
1052	*Myotis riparius*
1053	*Myotis ruber*
1054	*Myotis simus*
1055	*Myotis velifer*
1056	*Myotis vivesi*
1057	*Myrmecophaga tridactyla*
1058	*Myrmecophagidae*
1059	*Mysateles gundlachi*
1060	*Mysateles melanurus*
1061	*Mysateles meridionalis*
1062	*Mysateles prehensilis*
1063	*Nasua*
1064	*Nasua narica*
1065	*Nasua nasua*
1066	*Nasuella olivacea*
1067	*Natalus*
1068	*Natalus espiritosantensis*
1069	*Natalus jamaicensis*
1070	*Natalus lanatus*
1071	*Natalus major*
1072	*Natalus mexicanus*
1073	*Natalus primus*
1074	*Natalus stramineus*
1075	*Natalus tumidirostris*
1076	*Neacomys*
1077	*Neacomys dubosti*
1078	*Neacomys guianae*
1079	*Neacomys minutus*
1080	*Neacomys musseri*
1081	*Neacomys paracou*
1082	*Neacomys pictus*
1083	*Neacomys spinosus*
1084	*Neacomys tenuipes*
1085	*Necromys*
1086	*Necromys amoenus*
1087	*Necromys benefactus*
1088	*Necromys lactens*
1089	*Necromys lasiurus*
1090	*Necromys lenguarum*
1091	*Necromys obscurus*
1092	*Necromys punctulatus*
1093	*Necromys temchuki*
1094	*Necromys urichi*
1095	*Nectomys*
1096	*Nectomys apicalis*
1097	*Nectomys magdalenae*
1098	*Nectomys palmipes*

Number	Taxon
1099	*Nectomys rattus*
1100	*Nectomys squamipes*
1101	*Nelsonia*
1102	*Nelsonia goldmani*
1103	*Nelsonia neotomodon*
1104	*Neofiber alleni*
1105	*Neonycteris pusilla*
1106	*Neotoma albigula*
1107	*Neotoma angustapalata*
1108	*Neotoma bryanti*
1109	*Neotoma chrysomelas*
1110	*Neotoma devia*
1111	*Neotoma goldmani*
1112	*Neotoma leucodon*
1113	*Neotoma macrotis*
1114	*Neotoma mexicana*
1115	*Neotoma micropus*
1116	*Neotoma nelsoni*
1117	*Neotoma palatina*
1118	*Neotoma phenax*
1119	*Neotoma stephensi*
1120	*Neotomodon alstoni*
1121	*Neotomys ebriosus*
1122	*Nephelomys*
1123	*Nephelomys albigularis*
1124	*Nephelomys auriventer*
1125	*Nephelomys caracolus*
1126	*Nephelomys devius*
1127	*Nephelomys keaysi*
1128	*Nephelomys levipes*
1129	*Nephelomys meridensis*
1130	*Nesoryzomys*
1131	*Nesoryzomys fernandinae*
1132	*Nesoryzomys narboroughi*
1133	*Nesoryzomys swarthi*
1134	*Neusticomys*
1135	*Neusticomys ferreirai*
1136	*Neusticomys monticolus*
1137	*Neusticomys mussoi*
1138	*Neusticomys oyapocki*
1139	*Neusticomys peruviensis*
1140	*Neusticomys venezuelae*
1141	*Noctilio*
1142	*Noctilio albiventris*
1143	*Noctilio leporinus*
1144	*Notiomys edwardsii*
1145	*Notiosorex*
1146	*Notiosorex cockrumi*
1147	*Notiosorex crawfordi*
1148	*Notiosorex evotis*
1149	*Notiosorex villai*
1150	*Nycticeius cubanus*
1151	*Nyctiellus lepidus*
1152	*Nyctinomops*
1153	*Nyctinomops aurispinosus*
1154	*Nyctinomops femorosaccus*
1155	*Nyctinomops laticaudatus*
1156	*Nyctinomops macrotis*
1157	*Nyctomys sumichrasti*
1158	*Ochrotomys nuttalli*
1159	*Octodon*
1160	*Octodon bridgesi*
1161	*Octodon degus*
1162	*Octodon lunatus*
1163	*Octodon pacificus*
1164	*Octodontidae*
1165	*Octodontomys gliroides*
1166	*Octomys mimax*
1167	*Oecomys*
1168	*Oecomys auyantepui*
1169	*Oecomys bicolor*
1170	*Oecomys catherinae*
1171	*Oecomys cleberi*
1172	*Oecomys concolor*
1173	*Oecomys flavicans*
1174	*Oecomys mamorae*
1175	*Oecomys paricola*
1176	*Oecomys phaeotis*
1177	*Oecomys rex*
1178	*Oecomys roberti*
1179	*Oecomys rutilus*
1180	*Oecomys speciosus*
1181	*Oecomys superans*
1182	*Oecomys trinitatis*
1183	*Olallamys*
1184	*Olallamys albicauda*
1185	*Olallamys edax*
1186	*Oligoryzomys*
1187	*Oligoryzomys andinus*
1188	*Oligoryzomys arenalis*
1189	*Oligoryzomys brendae*
1190	*Oligoryzomys chacoensis*
1191	*Oligoryzomys delticola*
1192	*Oligoryzomys destructor*
1193	*Oligoryzomys eliurus*
1194	*Oligoryzomys flavescens*
1195	*Oligoryzomys fornesi*
1196	*Oligoryzomys fulvescens*
1197	*Oligoryzomys griseolus*
1198	*Oligoryzomys longicaudatus*
1199	*Oligoryzomys magellanicus*
1200	*Oligoryzomys microtis*
1201	*Oligoryzomys moojeni*
1202	*Oligoryzomys nigripes*
1203	*Oligoryzomys rupestris*
1204	*Oligoryzomys stramineus*
1205	*Oligoryzomys vegetus*
1206	*Onychomys arenicola*
1207	*Oreonax flavicauda*
1208	*Oreoryzomys balneator*

Number	Taxon
1209	*Orthogeomys*
1210	*Orthogeomys cavator*
1211	*Orthogeomys cherriei*
1212	*Orthogeomys cuniculus*
1213	*Orthogeomys dariensis*
1214	*Orthogeomys grandis*
1215	*Orthogeomys heterodus*
1216	*Orthogeomys hispidus*
1217	*Orthogeomys lanius*
1218	*Orthogeomys matagalpae*
1219	*Orthogeomys thaeleri*
1220	*Orthogeomys underwoodi*
1221	*Oryzomys couesi*
1222	*Oryzomys dimidiatus*
1223	*Oryzomys gorgasi*
1224	*Osgoodomys banderanus*
1225	*Otonyctomys hatti*
1226	*Ototylomys phyllotis*
1227	*Oxymycterus*
1228	*Oxymycterus akodontius*
1229	*Oxymycterus amazonicus*
1230	*Oxymycterus angularis*
1231	*Oxymycterus caparoae*
1232	*Oxymycterus dasytrichus*
1233	*Oxymycterus delator*
1234	*Oxymycterus hiska*
1235	*Oxymycterus hispidus*
1236	*Oxymycterus hucucha*
1237	*Oxymycterus inca*
1238	*Oxymycterus josei*
1239	*Oxymycterus nasutus*
1240	*Oxymycterus paramensis*
1241	*Oxymycterus quaestor*
1242	*Oxymycterus roberti*
1243	*Oxymycterus rufus*
1244	*Ozotoceros bezoarticus*
1245	*Panthera onca*
1246	*Pappogeomys*
1247	*Pappogeomys alcorni*
1248	*Pappogeomys bulleri*
1249	*Paralomys gerbillus*
1250	*Pattonomys*
1251	*Pattonomys occasius*
1252	*Pattonomys semivillosus*
1253	*Pearsonomys annectens*
1254	*Pecari tajacu*
1255	*Pennatomys nivalis*
1256	*Perognathus alticolus*
1257	*Perognathus amplus*
1258	*Perognathus inornatus*
1259	*Perognathus merriami*
1260	*Peromyscus attwateri*
1261	*Peromyscus aztecus*
1262	*Peromyscus beatae*
1263	*Peromyscus bullatus*
1264	*Peromyscus californicus*
1265	*Peromyscus difficilis*
1266	*Peromyscus eremicus*
1267	*Peromyscus eva*
1268	*Peromyscus fraterculus*
1269	*Peromyscus furvus*
1270	*Peromyscus gossypinus*
1271	*Peromyscus grandis*
1272	*Peromyscus gratus*
1273	*Peromyscus guardia*
1274	*Peromyscus guatemalensis*
1275	*Peromyscus gymnotis*
1276	*Peromyscus hooperi*
1277	*Peromyscus hylocetes*
1278	*Peromyscus levipes*
1279	*Peromyscus madrensis*
1280	*Peromyscus mayensis*
1281	*Peromyscus megalops*
1282	*Peromyscus mekisturus*
1283	*Peromyscus melanocarpus*
1284	*Peromyscus melanophrys*
1285	*Peromyscus melanotis*
1286	*Peromyscus melanurus*
1287	*Peromyscus merriami*
1288	*Peromyscus mexicanus*
1289	*Peromyscus nasutus*
1290	*Peromyscus ochraventer*
1291	*Peromyscus pectoralis*
1292	*Peromyscus perfulvus*
1293	*Peromyscus polionotus*
1294	*Peromyscus polius*
1295	*Peromyscus sagax*
1296	*Peromyscus schmidlyi*
1297	*Peromyscus simulus*
1298	*Peromyscus spicilegus*
1299	*Peromyscus stirtoni*
1300	*Peromyscus winkelmanni*
1301	*Peromyscus yucatanicus*
1302	*Peromyscus zarhynchus*
1303	*Peropteryx*
1304	*Peropteryx kappleri*
1305	*Peropteryx leucoptera*
1306	*Peropteryx macrotis*
1307	*Peropteryx trinitatis*
1308	*Phaenomys ferrugineus*
1309	*Philander*
1310	*Philander andersoni*
1311	*Philander deltae*
1312	*Philander frenatus*
1313	*Philander mcilhennyi*
1314	*Philander mondolfii*
1315	*Philander olrogi*
1316	*Philander opossum*
1317	*Phylloderma stenops*
1318	*Phyllomys*

Number	Taxon
1319	*Phyllomys blainvillii*
1320	*Phyllomys brasiliensis*
1321	*Phyllomys dasythrix*
1322	*Phyllomys kerri*
1323	*Phyllomys lamarum*
1324	*Phyllomys lundi*
1325	*Phyllomys mantiqueirensis*
1326	*Phyllomys medius*
1327	*Phyllomys nigrispinus*
1328	*Phyllomys pattoni*
1329	*Phyllomys thomasi*
1330	*Phyllomys unicolor*
1331	*Phyllonycteris*
1332	*Phyllonycteris aphylla*
1333	*Phyllonycteris poeyi*
1334	*Phyllops falcatus*
1335	*Phyllostomidae*
1336	*Phyllostomus*
1337	*Phyllostomus discolor*
1338	*Phyllostomus elongatus*
1339	*Phyllostomus hastatus*
1340	*Phyllostomus latifolius*
1341	*Phyllotis*
1342	*Phyllotis amicus*
1343	*Phyllotis andium*
1344	*Phyllotis anitae*
1345	*Phyllotis bonariensis*
1346	*Phyllotis caprinus*
1347	*Phyllotis darwini*
1348	*Phyllotis definitus*
1349	*Phyllotis haggardi*
1350	*Phyllotis limatus*
1351	*Phyllotis magister*
1352	*Phyllotis osgoodi*
1353	*Phyllotis osilae*
1354	*Phyllotis wolffsohni*
1355	*Phyllotis xanthopygus*
1356	*Pipanacoctomys aureus*
1357	*Pithecia*
1358	*Pithecia aequatorialis*
1359	*Pithecia irrorata*
1360	*Pithecia monachus*
1361	*Pithecia pithecia*
1362	*Pitheciidae*
1363	*Plagiodontia aedium*
1364	*Platalina genovensium*
1365	*Platyrrhinus*
1366	*Platyrrhinus albericoi*
1367	*Platyrrhinus aurarius*
1368	*Platyrrhinus brachycephalus*
1369	*Platyrrhinus chocoensis*
1370	*Platyrrhinus dorsalis*
1371	*Platyrrhinus infuscus*
1372	*Platyrrhinus ismaeli*
1373	*Platyrrhinus lineatus*
1374	*Platyrrhinus masu*
1375	*Platyrrhinus matapalensis*
1376	*Platyrrhinus nigellus*
1377	*Platyrrhinus recifinus*
1378	*Platyrrhinus umbratus*
1379	*Platyrrhinus vittatus*
1380	*Podomys floridanus*
1381	*Podoxymys roraimae*
1382	*Potos flavus*
1383	*Priodontes maximus*
1384	*Procyon cancrivorus*
1385	*Procyon pygmaeus*
1386	*Proechimys*
1387	*Proechimys brevicauda*
1388	*Proechimys canicollis*
1389	*Proechimys chrysaeolus*
1390	*Proechimys cuvieri*
1391	*Proechimys decumanus*
1392	*Proechimys echinothrix*
1393	*Proechimys gardneri*
1394	*Proechimys goeldii*
1395	*Proechimys guairae*
1396	*Proechimys guyannensis*
1397	*Proechimys hoplomyoides*
1398	*Proechimys kulinae*
1399	*Proechimys longicaudatus*
1400	*Proechimys magdalenae*
1401	*Proechimys mincae*
1402	*Proechimys oconnelli*
1403	*Proechimys pattoni*
1404	*Proechimys poliopus*
1405	*Proechimys quadruplicatus*
1406	*Proechimys roberti*
1407	*Proechimys semispinosus*
1408	*Proechimys simonsi*
1409	*Proechimys steerei*
1410	*Proechimys trinitatus*
1411	*Proechimys urichi*
1412	*Promops*
1413	*Promops centralis*
1414	*Promops nasutus*
1415	*Pseudalopex*
1416	*Pseudalopex culpaeus*
1417	*Pseudalopex fulvipes*
1418	*Pseudalopex griseus*
1419	*Pseudalopex gymnocercus*
1420	*Pseudalopex sechurae*
1421	*Pseudalopex vetulus*
1422	*Pseudoryzomys simplex*
1423	*Pteronotus*
1424	*Pteronotus davyi*
1425	*Pteronotus gymnonotus*
1426	*Pteronotus macleayii*
1427	*Pteronotus paraguanensis*
1428	*Pteronotus parnellii*

Number	Taxon
1429	*Pteronotus personatus*
1430	*Pteronotus quadridens*
1431	*Pteronura brasiliensis*
1432	*Pudu*
1433	*Pudu mephistophiles*
1434	*Pudu puda*
1435	*Punomys*
1436	*Punomys kofordi*
1437	*Punomys lemminus*
1438	*Pygoderma bilabiatum*
1439	*Reithrodon*
1440	*Reithrodon auritus*
1441	*Reithrodon typicus*
1442	*Reithrodontomys bakeri*
1443	*Reithrodontomys brevirostris*
1444	*Reithrodontomys burti*
1445	*Reithrodontomys chrysopsis*
1446	*Reithrodontomys creper*
1447	*Reithrodontomys darienensis*
1448	*Reithrodontomys fulvescens*
1449	*Reithrodontomys gracilis*
1450	*Reithrodontomys hirsutus*
1451	*Reithrodontomys humulis*
1452	*Reithrodontomys mexicanus*
1453	*Reithrodontomys microdon*
1454	*Reithrodontomys paradoxus*
1455	*Reithrodontomys raviventris*
1456	*Reithrodontomys rodriguezi*
1457	*Reithrodontomys spectabilis*
1458	*Reithrodontomys sumichrasti*
1459	*Reithrodontomys tenuirostris*
1460	*Reithrodontomys zacatecae*
1461	*Rhagomys*
1462	*Rhagomys longilingua*
1463	*Rhagomys rufescens*
1464	*Rheomys*
1465	*Rheomys mexicanus*
1466	*Rheomys raptor*
1467	*Rheomys thomasi*
1468	*Rheomys underwoodi*
1469	*Rhinophylla*
1470	*Rhinophylla alethina*
1471	*Rhinophylla fischerae*
1472	*Rhinophylla pumilio*
1473	*Rhipidomys*
1474	*Rhipidomys austrinus*
1475	*Rhipidomys cariri*
1476	*Rhipidomys caucensis*
1477	*Rhipidomys couesi*
1478	*Rhipidomys emiliae*
1479	*Rhipidomys fulviventer*
1480	*Rhipidomys gardneri*
1481	*Rhipidomys latimanus*
1482	*Rhipidomys leucodactylus*
1483	*Rhipidomys macconnelli*

Number	Taxon
1484	*Rhipidomys macrurus*
1485	*Rhipidomys mastacalis*
1486	*Rhipidomys modicus*
1487	*Rhipidomys nitela*
1488	*Rhipidomys ochrogaster*
1489	*Rhipidomys venezuelae*
1490	*Rhipidomys venustus*
1491	*Rhipidomys wetzeli*
1492	*Rhogeessa*
1493	*Rhogeessa aeneus*
1494	*Rhogeessa alleni*
1495	*Rhogeessa genowaysi*
1496	*Rhogeessa gracilis*
1497	*Rhogeessa hussoni*
1498	*Rhogeessa io*
1499	*Rhogeessa minutilla*
1500	*Rhogeessa mira*
1501	*Rhogeessa parvula*
1502	*Rhogeessa tumida*
1503	*Rhyncholestes raphanurus*
1504	*Rhynchonycteris naso*
1505	*Romerolagus diazi*
1506	*Saccopteryx*
1507	*Saccopteryx antioquensis*
1508	*Saccopteryx bilineata*
1509	*Saccopteryx canescens*
1510	*Saccopteryx gymnura*
1511	*Saccopteryx leptura*
1512	*Saguinus*
1513	*Saguinus bicolor*
1514	*Saguinus fuscicollis*
1515	*Saguinus geoffroyi*
1516	*Saguinus imperator*
1517	*Saguinus inustus*
1518	*Saguinus labiatus*
1519	*Saguinus leucopus*
1520	*Saguinus martinsi*
1521	*Saguinus melanoleucus*
1522	*Saguinus midas*
1523	*Saguinus mystax*
1524	*Saguinus niger*
1525	*Saguinus nigricollis*
1526	*Saguinus oedipus*
1527	*Saguinus tripartitus*
1528	*Saimiri*
1529	*Saimiri boliviensis*
1530	*Saimiri oerstedii*
1531	*Saimiri sciureus*
1532	*Saimiri ustus*
1533	*Saimiri vanzolinii*
1534	*Salinoctomys loschalchalerosorum*
1535	*Salinomys delicatus*
1536	*Santamartamys rufodorsalis*
1537	*Scapteromys*
1538	*Scapteromys aquaticus*

Number	Taxon
1539	*Scapteromys tumidus*
1540	*Sciurillus pusillus*
1541	*Sciurus aestuans*
1542	*Sciurus alleni*
1543	*Sciurus arizonensis*
1544	*Sciurus aureogaster*
1545	*Sciurus colliaei*
1546	*Sciurus deppei*
1547	*Sciurus flammifer*
1548	*Sciurus gilvigularis*
1549	*Sciurus granatensis*
1550	*Sciurus ignitus*
1551	*Sciurus igniventris*
1552	*Sciurus nayaritensis*
1553	*Sciurus oculatus*
1554	*Sciurus pucheranii*
1555	*Sciurus pyrrhinus*
1556	*Sciurus richmondi*
1557	*Sciurus sanborni*
1558	*Sciurus spadiceus*
1559	*Sciurus stramineus*
1560	*Sciurus variegatoides*
1561	*Sciurus yucatanensis*
1562	*Scleronycteris ega*
1563	*Scolomys*
1564	*Scolomys melanops*
1565	*Scolomys ucayalensis*
1566	*Scotinomys*
1567	*Scotinomys teguina*
1568	*Scotinomys xerampelinus*
1569	*Sigmodon alleni*
1570	*Sigmodon alstoni*
1571	*Sigmodon arizonae*
1572	*Sigmodon fulviventer*
1573	*Sigmodon hirsutus*
1574	*Sigmodon hispidus*
1575	*Sigmodon inopinatus*
1576	*Sigmodon leucotis*
1577	*Sigmodon mascotensis*
1578	*Sigmodon ochrognathus*
1579	*Sigmodon peruanus*
1580	*Sigmodon planifrons*
1581	*Sigmodon toltecus*
1582	*Sigmodontomys*
1583	*Sigmodontomys alfari*
1584	*Sigmodontomys aphrastus*
1585	*Solenodon*
1586	*Solenodon cubanus*
1587	*Solenodon paradoxus*
1588	*Sooretamys angouya*
1589	*Sorex arizonae*
1590	*Sorex emarginatus*
1591	*Sorex ixtlanensis*
1592	*Sorex lyelli*
1593	*Sorex macrodon*

Number	Taxon
1594	*Sorex mediopua*
1595	*Sorex milleri*
1596	*Sorex neomexicanus*
1597	*Sorex oreopolus*
1598	*Sorex orizabae*
1599	*Sorex ornatus*
1600	*Sorex saussurei*
1601	*Sorex sclateri*
1602	*Sorex stizodon*
1603	*Sorex tenellus*
1604	*Sorex ventralis*
1605	*Sorex veraecrucis*
1606	*Sorex veraepacis*
1607	*Spalacopus cyanus*
1608	*Speothos venaticus*
1609	*Spermophilus adocetus*
1610	*Spermophilus annulatus*
1611	*Spermophilus atricapillus*
1612	*Spermophilus madrensis*
1613	*Spermophilus mexicanus*
1614	*Spermophilus mohavensis*
1615	*Spermophilus perotensis*
1616	*Spermophilus tereticaudus*
1617	*Sphaeronycteris toxophyllum*
1618	*Sphiggurus*
1619	*Sphiggurus ichillus*
1620	*Sphiggurus insidiosus*
1621	*Sphiggurus melanurus*
1622	*Sphiggurus mexicanus*
1623	*Sphiggurus pruinosus*
1624	*Sphiggurus roosmalenorum*
1625	*Sphiggurus spinosus*
1626	*Sphiggurus vestitus*
1627	*Sphiggurus villosus*
1628	*Spilogale angustifrons*
1629	*Spilogale pygmaea*
1630	*Stenoderma rufum*
1631	*Sturnira*
1632	*Sturnira aratathomasi*
1633	*Sturnira bidens*
1634	*Sturnira bogotensis*
1635	*Sturnira erythromos*
1636	*Sturnira ludovici*
1637	*Sturnira luisi*
1638	*Sturnira magna*
1639	*Sturnira mistratensis*
1640	*Sturnira mordax*
1641	*Sturnira nana*
1642	*Sturnira oporaphilum*
1643	*Sturnira sorianoi*
1644	*Sturnira thomasi*
1645	*Sturnira tildae*
1646	*Sylvilagus aquaticus*
1647	*Sylvilagus brasiliensis*
1648	*Sylvilagus cognatus*

Number	Taxon	Number	Taxon
1649	*Sylvilagus cunicularius*	1704	*Thomasomys macrotis*
1650	*Sylvilagus dicei*	1705	*Thomasomys monochromos*
1651	*Sylvilagus graysoni*	1706	*Thomasomys niveipes*
1652	*Sylvilagus insonus*	1707	*Thomasomys notatus*
1653	*Sylvilagus mansuetus*	1708	*Thomasomys onkiro*
1654	*Sylvilagus palustris*	1709	*Thomasomys oreas*
1655	*Sylvilagus robustus*	1710	*Thomasomys paramorum*
1656	*Sylvilagus varynaensis*	1711	*Thomasomys popayanus*
1657	*Syntheosciurus brochus*	1712	*Thomasomys praetor*
1658	*Tamandua*	1713	*Thomasomys pyrrhonotus*
1659	*Tamandua mexicana*	1714	*Thomasomys rhoadsi*
1660	*Tamandua tetradactyla*	1715	*Thomasomys rosalinda*
1661	*Tamias alpinus*	1716	*Thomasomys silvestris*
1662	*Tamias bulleri*	1717	*Thomasomys taczanowskii*
1663	*Tamias canipes*	1718	*Thomasomys ucucha*
1664	*Tamias cinereicollis*	1719	*Thomasomys vestitus*
1665	*Tamias durangae*	1720	*Thomasomys vulcani*
1666	*Tamias merriami*	1721	*Thomomys umbrinus*
1667	*Tamias obscurus*	1722	*Thrichomys*
1668	*Tamias palmeri*	1723	*Thrichomys apereoides*
1669	*Tamias panamintinus*	1724	*Thrichomys inermis*
1670	*Tamias quadrimaculatus*	1725	*Thrichomys pachyurus*
1671	*Tamias quadrivittatus*	1726	*Thylamys*
1672	*Tamias rufus*	1727	*Thylamys cinderella*
1673	*Tamias speciosus*	1728	*Thylamys citellus*
1674	*Tamiasciurus mearnsi*	1729	*Thylamys elegans*
1675	*Tapecomys primus*	1730	*Thylamys fenestrae*
1676	*Tapirus bairdii*	1731	*Thylamys karimii*
1677	*Tapirus pinchaque*	1732	*Thylamys macrurus*
1678	*Tapirus terrestris*	1733	*Thylamys pallidior*
1679	*Tayassu pecari*	1734	*Thylamys pulchellus*
1680	*Tayassuidae*	1735	*Thylamys pusillus*
1681	*Thalpomys*	1736	*Thylamys sponsorius*
1682	*Thalpomys cerradensis*	1737	*Thylamys tatei*
1683	*Thalpomys lasiotis*	1738	*Thylamys velutinus*
1684	*Thaptomys nigrita*	1739	*Thylamys venustus*
1685	*Thomasomys*	1740	*Thyroptera*
1686	*Thomasomys apeco*	1741	*Thyroptera devivoi*
1687	*Thomasomys aureus*	1742	*Thyroptera discifera*
1688	*Thomasomys baeops*	1743	*Thyroptera lavali*
1689	*Thomasomys bombycinus*	1744	*Thyroptera tricolor*
1690	*Thomasomys caudivarius*	1745	*Tlacuatzin canescens*
1691	*Thomasomys cinereiventer*	1746	*Tolypeutes*
1692	*Thomasomys cinereus*	1747	*Tolypeutes matacus*
1693	*Thomasomys cinnameus*	1748	*Tolypeutes tricinctus*
1694	*Thomasomys daphne*	1749	*Tomopeas ravus*
1695	*Thomasomys eleusis*	1750	*Tonatia*
1696	*Thomasomys erro*	1751	*Tonatia bidens*
1697	*Thomasomys gracilis*	1752	*Tonatia saurophila*
1698	*Thomasomys hudsoni*	1753	*Toromys grandis*
1699	*Thomasomys hylophilus*	1754	*Trachops cirrhosus*
1700	*Thomasomys incanus*	1755	*Transandinomys*
1701	*Thomasomys ischyrus*	1756	*Transandinomys bolivaris*
1702	*Thomasomys kalinowskii*	1757	*Transandinomys talamancae*
1703	*Thomasomys ladewi*	1758	*Tremarctos ornatus*

Number	Taxon
1759	*Trinomys*
1760	*Trinomys albispinus*
1761	*Trinomys dimidiatus*
1762	*Trinomys eliasi*
1763	*Trinomys gratiosus*
1764	*Trinomys iheringi*
1765	*Trinomys mirapitanga*
1766	*Trinomys moojeni*
1767	*Trinomys myosuros*
1768	*Trinomys paratus*
1769	*Trinomys setosus*
1770	*Trinomys yonenagae*
1771	*Trinycteris nicefori*
1772	*Tylomys*
1773	*Tylomys bullaris*
1774	*Tylomys fulviventer*
1775	*Tylomys mirae*
1776	*Tylomys nudicaudus*
1777	*Tylomys panamensis*
1778	*Tylomys tumbalensis*
1779	*Tylomys watsoni*
1780	*Tympanoctomys barrerae*
1781	*Urocyon littoralis*
1782	*Uroderma*
1783	*Uroderma bilobatum*
1784	*Uroderma magnirostrum*
1785	*Vampyressa*
1786	*Vampyressa bidens*
1787	*Vampyressa brocki*
1788	*Vampyressa melissa*
1789	*Vampyressa nymphaea*
1790	*Vampyressa pusilla*
1791	*Vampyressa thyone*
1792	*Vampyrum spectrum*
1793	*Vicugna vicugna*
1794	*Wiedomys*
1795	*Wiedomys cerradensis*
1796	*Wiedomys pyrrhorhinos*
1797	*Wilfredomys oenax*
1798	*Xenomys nelsoni*
1799	*Xeronycteris vieirai*
1800	*Zaedyus pichiy*
1801	*Zygodontomys*
1802	*Zygodontomys brevicauda*
1803	*Zygodontomys brunneus*
1804	*Zygogeomys trichopus*

Evolutionary biogeography of mammals (Mammalia): phylogenetic and ecological relationships in the Neotropical region

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Word count: 6492
Running head: **Evolutionary biogeography of Neotropical mammals** (Enviado *Journal of Natural History*)

ABSTRACT

Evolutionary biogeography combines different biological data to describe biogeographic patterns and propose the historical changes that have shaped them. Areas of endemism (Ae) of Neotropical mammals are biogeographic patterns promoted by historical and ecological processes that assume a correspondence between the phylogenetic relationship of mammals and their geographic distributions. Herein, we examine the phylogenetic structure of Ae of mammals at the scale of the Neotropical region. We identified Ae and endemic mammals at regional scale applying the Analysis of Endemicity method (NDM/VNDM). Then we assessed the phylogenetic structure applying Faith's index as phylogenetic diversity metric (PD), the net relatedness index and the nearest taxon index at the Ae of mammals and the Neotropical region as whole pattern. We examined if there is a matching between Ae and the geographic ancestral distributions of the endemic mammals to propose a biotic scenario composed by cenocrons and to explain their integration in the Neotropical region. Six Ae and 51 endemic mammal species were identified, a single area (Ae0) was significantly phylogenetically overdispersed while the Neotropical region was clustered. The clustering pattern of the Neotropical region could be showing the phylogenetic signal due to the phylogenetic relatedness of the endemic mammals that evolved in South America. A core of endemism is located in the tropics around of the equator. A hypothetical scenario to explain the integration of endemic mammals into South America is as follows: endemic Neotropical mammals expanded from tropics in South America to north and south of the Neotropical region, while others mammals expanded into Neotropical zone. The Neotropical endemic mammals have several ages and geographic ancestral distributions integrated in five cenocrons, suggesting that a set of barriers and corridors shaped by geological evolve, together with climatic complexity, affected the Neotropical mammals' diversification and dispersion at different time and spatial scales.

KEYWORDS

Biotic scenario; cenocron; dispersal; Neotropics; phylogenetic diversity.

Introduction

Evolutionary biogeography combines distributional, phylogenetical and molecular data to describe biogeographic patterns and propose the historical and changes that have shaped them (Morrone 2007; Morrone 2009). Accordingly, areas of endemism are evolutionary and ecological patterns that assume a correspondence between the phylogenetic relationships among taxa and their geographic distributions (Müller 1973; Cracraft 1985; Szumik et al. 2002; Morrone 2009; Murray and Crother 2016; Noguera-Urbano 2016). Hence, some species have evolved together with the earth itself, generating areas of endemism. In a practical sense, areas of endemism are identified by comparing the areas of distribution of species. Therefore, a species can be considered endemic if it shares its area of distribution with at least one other species, and they are both restricted to that area (Cracraft 1985; Platnick 1991; Morrone 1994; Espinosa et al. 2001; Szumik et al. 2002; Noguera-Urbano 2016). Thus, a high spatial congruence among species supports areas of endemism (Cracraft 1985; Morrone 2001; Morrone 2009; Noguera-Urbano 2016). Congruence among areas of distribution is promoted by species' parallel and simultaneous responses to historical and macroecological processes such as speciation, extinction, migration, niche evolution, evolutionary convergence and colonization (Müller 1973; Cracraft 1985; Anderson 1994;

Szumik et al. 2002; Villalobos et al. 2013; Murray and Crother 2016; Noguera-Urbano 2016). In addition, the congruence is related with a physiographic or climatic barrier (Cracraft 1985; Noguera-Urbano and Escalante 2015).

Areas of endemism evolve when endemic species confront similar ecological or geographical changes (Cracraft 1985; Anderson 1994; Murray and Crother 2016; Noguera-Urbano 2016). For example, the structure and shape of the areas of endemism change according to the responses of their endemic species to processes driven by climate change (Gámez et al. 2014; Aguado-Bautista and Escalante 2015). In some cases, areas of endemism disappear altogether due to the divergence, migration or extinction of the endemic species (Anderson 1994; Murray and Crother 2016). However, little is known about the ecological processes and phylogenetic relationships of the endemic species within areas of endemism (Noguera-Urbano 2016).

Phylogenetic information using phylogenetic community methods can be directly integrated to analyze the ecological and phylogenetic process within areas of endemism. Phylogenetic community addresses the relationship between the phylogenetic structure of an assemblage (nonrandom subsets of the regional pool of species) and their distribution (Webb 2000; Webb et al. 2002), and the nature of the non-randomness may provide clues to the historical and ecological processes promoting assemblage formation at large geographical scales (Cardillo et al. 2008; Cardillo 2011; Villalobos et al. 2013; Swenson 2014). Phylogenetic structure refers to the degree of phylogenetic relatedness of two or more spatially congruent species (Haydon et al. 1993). Currently there are specific indices that use phylogenetic diversity (PD) as an indicator of the phylogenetic structure of assemblages (Webb 2000; Webb et al. 2002; Cardillo 2011; Swenson 2014), which include Faith's index (Faith 1992) that represents the phylogenetic diversity, the net relatedness index (NRI) measures the degree of phylogenetic clustering (species more closely related than expected) or overdispersion (species less closely related than expected) throughout the phylogeny and the nearest taxon index (NTI) reflects clustering or overdispersion at the tips of the phylogeny. Two basic hypotheses are proposed to explain the phylogenetic structure of spatially congruent species. On one hand, niche evolution, evolutionary convergence and colonization could lead to "phylogenetic overdispersion" (Cardillo et al. 2008; Cardillo 2011; Villalobos et al. 2013), in which differences in size and diet promote the coexistence of distantly related species. On the other hand, "phylogenetic clustering" occurs when spatially congruent species are also phylogenetically grouped, and can be caused by processes such as high *in situ* speciation and niche conservatism (Cardillo et al. 2008; Cardillo 2011; Villalobos et al. 2013). On the other hand, the species–area relationship has been crucial to the development of ecological theory, and it is considered one of the few general laws in ecology (Preston 1962, Morlon et al. 2011). Although, empirical observations show that PD increases with area at a slower pace than species richness (Rodrigues and Gaston 2002, Morlon et al. 2011), spatial scaling of PD remains vaguely known (Morlon et al. 2011). Therefore, we believe that using areas of endemism at regional scale could reveal how is the ecological relationship and tendency between PD and area.

Mammals are found on all continents, and they live in all biomes and types of habitats. They have been used to define biogeographic units (regions, subregions, provinces) at different scales (Wallace 1876; Smith 1983; Holt et al. 2013; Noguera-Urbano and Escalante 2015). A formal biogeographic scheme of the world was proposed based on the mammals patterns of distribution (Wallace 1876), and currently, the biogeographic patterns of mammals have been used in multiple studies to explain ecological and evolutionary processes (e.g. dispersion, vicariance, extension) (Hershkovitz 1958, 1969, Cox 2001, Escalante et al. 2010, Kreft and Jetz 2010, Holt et al. 2013, Rueda et al. 2013, Morrone 2014, Noguera-Urbano and Escalante 2015). In addition, some analyses of phylogenetic structure have focused on 'regional-scale' communities (e.g. Cardillo & Meijaard, 2010; Cardillo, 2011; Villalobos *et al.*, 2013; Cantalapiedra, Fernández, & Morales, 2014; Fergnani & Ruggiero, 2015), and the biogeographic processes that have promoted the distribution of mammals have been widely described (e.g. Cardillo 2011, 2015; Carrillo et al. 2015; Juñent 1994; Rojas, Warsi, and Dávalos 2016; Schenk, Rowe, and Steppan 2013; Webb 2011).

The Neotropical region has been described as a pattern of multiple boundaries on the basis of the identification of areas of endemism (Noguera-Urbano 2013; Noguera-Urbano and Escalante 2015). Initially, it was proposed that the Neotropical boundaries were composed of seven areas of endemism (Noguera-Urbano 2013), but recently two additional patterns were identified (Noguera-Urbano and Escalante 2015) supported mainly by the differing taxonomic composition of primarily bats (Chiroptera) and rodents (Rodentia). Although it is proposed that the endemic species in areas of endemism could be phylogenetically related when the variance is the promoter of their evolve (Nelson and Platnick 1981; Rosen and Smith 1988; Anderson 1994; Harold and Mooi 1994), currently it is unknown which hypotheses explains the phylogenetic structure of the endemic species in the Neotropical areas of endemism. Therefore, it is necessity to integrate the biogeographic and phylogenetical approaches in order to disentangle the influences of evolutionary history and ecological processes on patterns of distribution (Weeks et al. 2016; Noguera-Urbano 2016). We consider that areas of endemism represent subsets of the regional pool of species, and that they are equivalent to an assemblage of species in a geographical space, since both terms refer to a group of species with spatial congruence.

Here, we examine the phylogenetic structure of areas of endemism of mammals at the scale of the Neotropical region. We identify the areas of endemism equivalents to Neotropical region *sensu lato* (Smith 1983; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt et al. 2013; Rueda et al. 2013; Morrone 2014a) and analyze their phylogenetic structure. Thus, we make tree specific predictions about the phylogenetic structure of Neotropical endemic mammals: (i) It is suggested that "if assemblages within a biogeographic region are mainly made up of species of a certain subclade, due to within-region radiation these assemblages will tend to exhibit phylogenetic clustering" (Catalapieda et al. 2014). Therefore, if the Neotropical region is defined by endemic species that exhibit phylogenetic clustering, the areas of endemism could represent systems of species integrated in space and time, this means similar evolutionary history. To test such a prediction, we first assessed whether phylogenetic structure varies among areas of endemism or if a regional or world species pool makes a difference for detecting significant structure. (ii) We predicted that PD would increase with the number of endemic species and size of the geographical area following some macroecological tendencies (Morlon et al. 2011; Helmus and Ives 2012), such that a larger Neotropical region with higher richness of endemics would have a higher PD. Thus, we evaluate whether PD is related to the number of endemic species or geographic descriptors such as size, shape longitude, and latitude centroids of the areas of endemism. Cenocron refers specifically to assemblages that disperse into a biota and have different ages (Morrone 2014b), consequently the cenocrons that characterize the areas of endemism of Neotropical mammals can be resumed according to the geographic ancestral distributions. (iii) So we suppose that there is a close relationship between the grouping of the species in a geographic area and the geographic ancestral distribution or cenocrons, due to the endemic species are space-temporally integrated (Anderson 1994; Morrone 2009; Murray and Crother 2016; Noguera-Urbano 2016); therefore, we test the match between areas of endemism and geographic ancestral distributions of the endemic mammals to propose a biotic scenario to explain the integration of the endemic mammals and the cenocrons in the current Neotropical region.

Material and methods

Areas of endemism and endemic species

The Neotropical areas of endemism based on mammals were described by (Noguera-Urbano 2013) and Noguera-Urbano and Escalante (2015) by analyzing the endemism at three taxonomic levels (families, genera and species). Because we were interested in the phylogenetic structure of species-level areas of endemism, we excluded families and genera taxonomic levels and re-analyzed a species matrix using the maps of distribution of 1,605 species of neotropical mammals proposed by the International Union for Conservation of Nature (IUCN 2014). IUCN´s maps of distribution follows the nomenclature proposed by Wilson and Reeder (2005). The maps of distribution were cut with a rectangular mask that extends from the United States of America (USA) to Patagonia (38°N- 56°S and 122°W-34°W) to avoid that the analysis is biased toward some biogeographic scheme. The species distribution maps were overlapped in a 4° × 4° latitude-longitude grid to produce a presence/absence matrix (1605 species as columns and 210 rows). This grid-size was chosen because it allows the identification of regional areas of endemism (Escalante et al. 2010; Escalante et al. 2013; Noguera-Urbano 2013).

To identify areas of endemism, we processed the presence/absence matrix using the Analysis of Endemicity method (Szumik et al. 2002; Szumik and Goloboff 2004), which is implemented in NDM/VNDM software, version 3.0 (Goloboff 2014). A heuristic search was applied, keeping areas with at least two endemic species and an area endemicity score (E) greater than 2.0. The option of proportion of grid-cells was not used because it limited the searching of sets (Noguera-Urbano and Escalante 2015). Areas of endemism identified by NDM/VNMD can share a percentage of endemic taxa (Szumik et al. 2002; Szumik and Goloboff 2004), thus “keep overlapping subsets > 98%” was applied (Noguera-Urbano and

Escalante 2015). We performed 100 NDM/VNDM analysis, changing the randomization parameter (Noguera-Urbano and Escalante 2015) to retain the results from the random seed number (r.s.n. =341) with the highest number of areas of endemism (104). We disable four widely distributed species (*Platyrrhinus helleri*, *Sturnira lilium*, *Uroderma bilobatum* and *Vampyrodes caraccioli*) in the NDM/VNDM software, which were recently split into several species and restricted to specific zones along Central or South America (Velazco et al. 2010, Mantilla-Meluk 2014, Velazco and Patterson 2014, Lopes et al. 2016). We excluded this new species arrangement, due to their maps of distribution are unavailable.

Several boundaries have been proposed for the Neotropical region (Wallace 1876; Udvardy 1975; Smith 1983; Procheş and Ramdhani 2012; Holt et al. 2013; Rueda et al. 2013; Morrone 2014a). We therefore selected the regional scale areas of endemism considering current schemes of the Neotropical region (Central America zones plus South America zones) (Smith 1983; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt et al. 2013; Rueda et al. 2013; Morrone 2014a). A 'loose' consensus analysis (50% against any of the other areas in the consensus) was applied to the regional areas of endemism; this consensus is agglomerative and combines areas when overlapping patterns of distribution exist (Aagesen et al. 2013). The endemicity score of the area (*E*), the number of endemic taxa, and the endemic taxa with their endemicity score (*e*) are reported for each consensus area of endemism (Ae). The areas of endemism were mapped by merging the maps of distribution of their endemic species.

Phylogenetic structure of each area of endemism

Each Ae was considered an assemblage to analyze phylogenetic structure. In a practical sense, this analysis allows the comparison among several Neotropical patterns (areas of endemism at the regional scale), which were identified with the same methodology and biological group. This facilitates comparisons and generalizations at the level of the Neotropical region. To calculate the phylogenetic structure of areas of endemism, we made a binary matrix (endemic species vs area of endemism) to represent the community data. The presence of each endemic species in an Ae was encoded with a "1", and absence with a "0".

The phylogenetic information was obtained from the ultrametric supertree of mammals proposed by Fritz et al. (2009). The original phylogeny was pruned to obtain a subtree composed by the endemic species previously identified, this allowed to simplify the analysis. Polytomies were resolved with random order (Swenson 2014). Three metrics of phylogenetic structure were applied to the community data: (1) Faith's Index of phylogenetic diversity (PD), (2) the net relatedness index (NRI), and (3) the nearest taxon index (NTI). PD was calculated as the total length of the branches in the tree (Faith 1992). Communities with a higher number of ancient linages show high PD (more disrupted), while phylogenetically related communities have low PD. NRI is a standardized measure of the average pairwise phylogenetic distance of the sample. NTI considers the branch length separating each species from its nearest relative (Webb et al. 2002; Swenson 2014). Positive values of NRI and NTI ($p<0.05$) indicate increase of clustering and become negative ($p>0.95$) with overdispersion (Webb 2000; Webb et al. 2002; Cardillo 2011; Swenson 2014). Both NTI and NRI suggesting overdispersion or clustering; however, NTI reflects structure at the tips of the phylogeny while NRI is sensitive to structure throughout the phylogeny (Webb et al. 2002; Cardillo 2011). NTI and NRI describe the difference between average phylogenetic distances in the observed assemblages and random simulations, standardized by the standard deviation of phylogenetic distances in the random simulations (Webb 2000; Webb et al. 2002; Cardillo 2011). PD, NRI and NTI were calculated using the functions "ses.pd", 'ses.mpd' and 'ses.mntd' (null model: taxa labels; runs: 999), respectively, in the Picante library (Kembel et al. 2010) for R (R Core Team 2015). This null model randomizes the tip labels across the tips of the phylogeny while fixing the observed community data matrix since we are asking about whether my community has a higher phylogenetic diversity than expected. Thus, phylogenetic structure can be calculated for NRI and NTI by compared observed phylogenetic relatedness to the pattern expected under the null model of phylogeny randomization (Webb et al. 2002). Together these three metrics give a good synthesis of the phylogenetic structure of species groups (Webb 2000; Webb et al. 2002; Cardillo 2011; Mazel et al. 2015).

In addition, NRI and NTI were calculated to describe the phylogenetic structure of the Neotropical region as a single pattern that includes all endemic species. For this, two levels of source pool were considered: "World", the entire phylogeny of Fritz et al. (2009) which represents a world super-community of mammals, and "Regional", the pruned phylogeny containing the 1605 species of mammals used to identify the areas of endemism, which represents a regional super-community of mammals.

Macroecological trends in phylogenetic structure

We calculated five metrics to describe each area of endemism using QGIS software (QGIS Development Team 2015): the size, perimeter, perimeter-√size ratio (RPS; shape: high values indicated maps with irregular shape) (Rapoport 1975), the latitude centroid and the longitude centroid. It is suggested that those metrics are good geographical descriptors of the distribution areas and their patterns (Rapoport 1975; Brown et al. 1996; Sexton et al. 2009; Cardillo 2015), therefore we predicted that PD would increase with the number of endemic species and size of the geographical area (Morlon et al. 2011; Helmus and Ives 2012), such that a larger Neotropical region with higher richness of endemics would have a higher PD. Because the form and extend among areas of endemism at Region scale can be different, we suppose that there is a relationship among PD and the other geographic descriptors. The relationship between the phylogenetic diversity of the areas of endemism and their number of endemic species, the size of area of endemism, the RPS (Rapoport 1975), and the absolute values of the latitude centroid and the longitude centroid were evaluated using Pearson´s tests (Ho: correlation is equal to 0; reject Ho if $p \leq 0.05$). All variables were log10 transformed.

Phylogenetic diversity of the Neotropical region and its temporal strata

The IUCN's maps of maps of distribution of the endemic species were overlapped with a grid of 5 km latitude-longitude cells to produce a presence/absence matrix (grid cell x species). For each grid cell the PDs were calculated and represented in a map. We selected this new grid size to obtain PD maps close to the scale of the maps of distribution, thereby improving the representation of the boundaries of the Neotropical region in the PD maps. This analysis included all endemic species as elements of a single biogeographic pattern. The PD in the Neotropical region was then mapped. Areas of endemism are composed of temporal strata (Noguera-Urbano 2016); therefore the temporal strata that compose the Neotropical region were described by classifying each Neotropical endemic mammal according to its geographic ancestral reconstruction and cenocrons.

Geographic ancestral reconstructions are hypothesis about the geographical distribution at the time of speciation of sister species, and it is assumed that distributions are so static that ancestral geographical distributions can be inferred from the ranges of their descendants (Losos and Glor 2003). The geographic ancestral distribution for each endemic species was extracted from several references, due to the absence of a proposal that included all endemic species and their ancestral geographical distributions (Appendix 1). Additionally, cenocron term is as follow “It can deal with the process of geodispersal and refer specifically to assemblages that disperse into a biota and have different ages. Dating cenocrons depends largely on dating the clades that are assigned to them, which in turn depends on the fossil record, geological information and molecular-based age estimates” (Morrone 2014b). From this standpoint, the cenocrons that characterize the areas of endemism of Neotropical mammals can be resumed according to the geographic ancestral distributions. Therefore, a frequency diagram was made with the divergence times of the endemic species, which were organized by geographic ancestral distribution to define the cenocrons.

Finally, because current groupings of species in areas of endemism could be derived from groupings in geographic ancestral distributions due to the temporal and spatial integration of endemic mammals, a Mantel test using the Spearman method was applied to test for correlation between the binary matrices (areas of endemism and geographic ancestral distributions). The binary matrices were made by coding as “1” the presence of the endemic species in both the areas of endemism and geographic ancestral distributions. The Jaccard distances were obtained from both binary matrices to run the Mantel test.

Results

Areas of endemism and endemic species

The NDM/VNDM analyses resulted in 104 systems, of which eight matched with the Neotropical region *sensu lato* (Id NDM: 3, 18, 28, 47, 52, 63, 85, 86). The consensus analysis resulted in six areas supported by 51 endemic mammal species (Table 1) and the areas showed several boundaries (Table 1; Appendix 2 Figures). Ae0 had the highest number of endemic species (22) and Ae2 and Ae3 the lowest (4) (Table 1).

Table 1. Neotropical areas of endemism obtained using the Analysis of endemicity (NDM/VNDM). Area of endemism consensus (Ae); endemicity score of the areas (E: minimum to maximum); number of endemic species (ES); species with its interval of endemicity score taxa (e: minimum to maximum); phylogenetical diversity (PD); perimeter (P), perimeter-√size ratio (RPA).; the centroids of the latitude (CLa) and longitude (CLo) in degrees.

Ae	E	# ES	Species (e)	PD	Size (km^2)	P (km)	RPA (km^{-1})	CLa	CLo
Ae0	13.8-15.5	22	*Carollia perspicillata (0.878-0.977), Chrotopterus auritus (0.850-0.946), Cuniculus paca (0.000-0.911), Diaemus youngi (0.000-0.929), Eptesicus brasiliensis (0.908-0.945), Eumops auripendulus (0.845-0.939), Leopardus pardalis (0.000-0.845), Lonchorhina aurita (0.000-0.919), Macrophyllum macrophyllum (0.950-0.976), Metachirus nudicaudatus (0.912-0.941), Micronycteris minuta (0.000-0.946), Myotis nigricans (0.000-0.873), Myrmecophaga tridactyla (0.000-0.847), Noctilio albiventris (0.914-0.932), Peropteryx macrotis (0.894-0.936), Phylloderma stenops (0.000-0.955), Phyllostomus discolor (0.000-0.947), Phyllostomus hastatus (0.000-0.960), Saccopteryx leptura (0.931-0.960), Sylvilagus brasiliensis (0.000-0.871), Tayassu pecari (0.000-0.867), Trachops cirrhosus (0.938-0.958)*	1.261	13,140,000	4,573,000	0.348021	-7.845	-61.16

Ae1	6.2-6.4	7	*Galictis vittata (-0.891), Lichonycteris obscura (-0.856), Mimon crenulatum (-0.898), Peropteryx kappleri (-0.905), Potos flavus (-0.847), Rhynchonycteris naso (-0.947), Uroderma magnirostrum (-0.903)*	425	10,850,000	3,777,000	0.348111	-4.538	-61.37
Ae2	3.6-3.8	4	*Chiroderma trinitatum (-0.9), Cormura brevirostris (-0.928), Mesophylla macconnelli (-0.971), Oecomys bicolor (-0.847)*	324	8,179,000	2,537,000	0.310185	-4.526	-62.87
Ae3	3.2-3.4	4	*Lophostoma brasiliense (-1), Micronycteris hirsuta (-0.755), Micronycteris schmidtorum (-0.75), Thyroptera tricolor (-0.715)*	248	9,374,000	3,631,000	0.387348	-3.796	-61.14
Ae4	8-8.3	9	*Artibeus lituratus (-0.931), Eira barbara (-0.93), Eptesicus furinalis (-0.852), Glossophaga soricina (-0.898), Leopardus wiedii (-0.919), Molossus molossus (-0.885), Molossus rufus (-0.907), Noctilio leporinus (-0.896), Nyctinomops laticaudatus (-0.876)*	534	14,790,000	5,861,000	0.396281	-7.608	-63.24
Ae5	4-4.3	5	*Carollia castanea (-0.881), Eumops hansae (-0.812), Philander opossum (-0.747), Vampyressa thyone (-0.843), Vampyrum spectrum (-0.81)*	406	7,753,000	2,817,000	0.363343	-2.54	-66.73

Phylogenetic structure of each area of endemism

PD differed among areas of endemism (Figure1); Ae0 had the highest PD, while the Ae2 and Ae3 had the lowest PD (Table 1), despite all three areas having similar species richness (4 species). NRI showed no consistent pattern of phylogenetic under- or overdispersion (Table 2). NTI showed overdispersion at the tips of the phylogeny in Ae0, but no structure in the other areas of endemism (Table 2). NRI values showed that the 51 endemic mammal species were clustered at the base of the phylogenies using both the World and Regional species pools (Table 2). NTI values indicated clustering at the tips of the phylogenies when using the World species pool, but not the Regional pool (Table 2). Using nested Neotropical areas of endemism showed unclear phylogenetic patterns, while considering the areas of endemism as a single Neotropical region showed a clustered phylogenetic pattern (Table 2).

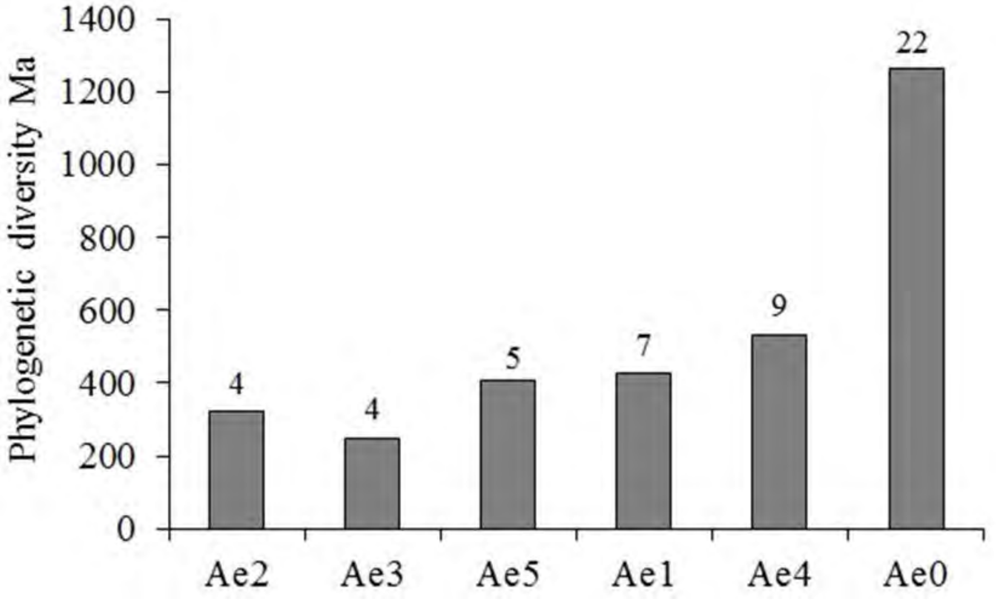

Figure 1. Phylogenetic diversity of the Neotropical areas of endemism. The number above each bar is the number of endemic species.

Table 2. The net relatedness index (NRI) and nearest taxon index (NTI) values of the Neotropical areas of endemism. Phylogenetic clustering is indicated with an asterisk (*), and phylogenetic overdispersion is indicated with a cross (+).

Area	NRI			NTI		
	Observed	Calculated	*p-value*	Observed	Calculated	*p-value*
Ae0	149.60	0.65	0.714	95.06	2.46	**0.995**$^{+}$
Ae1	135.62	-0.21	0.432	62.29	-1.31	0.089
Ae2	146.17	0.15	0.595	94.05	-0.39	0.4
Ae3	83.37	-1.39	0.057	56.50	-1.41	0.0765
Ae4	130.28	-0.37	0.385	78.78	-0.60	0.297
Ae5	170.00	0.75	0.786	112.76	0.37	0.6685
World pool	140.73	-5.59	**0.001***	49.89	-3.29	**0.001***
Regional pool	140.73	-4.15	**0.001***	49.89	-0.24	0.414

Notes: p<0.05 indicates phylogenetic clustering, while p>0.95 indicates phylogenetic overdispersion.

Macroecological trends of phylogenetic structure

The geographic variables varied among areas of endemism (Table 3). The mean size and perimeter of the areas of endemism were 10,681,000 km2 and 3,866,000 km, respectively. The perimeter-√size ratio showed that the Neotropical areas of endemism are irregularly shaped and differ from each other in shape (Table3; Appendix 2 Figures). Four areas of endemism (Ae0, Ae1, Ae3 and Ae5) had a similar shape, while Ae2 had a less irregular shape and Ae4 had the most irregular shape (Table 3). All areas of endemism had their centroids in South America, around of the equator. Ae5 was shifted more to the north and east than the other areas, while Ae0 had the southernmost centroid. We found a strong relationship between the number of endemic species and the PD (r=0.97, p< 0.01; Figure 2). On another hand, the relationship between PD and each of the five geographic descriptors of the Neotropical areas of endemism was non-significant (Table 3).

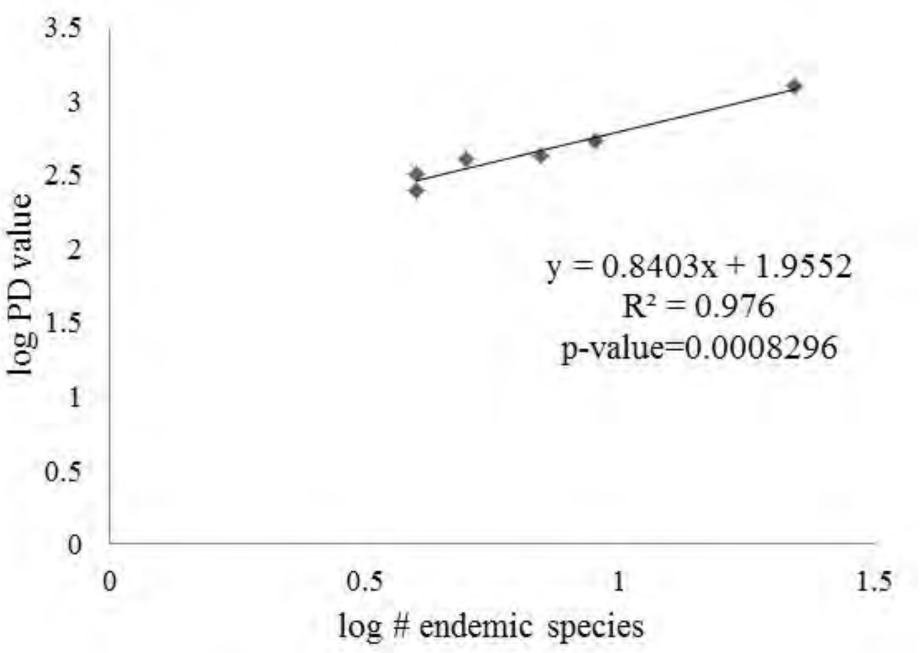

Figure 2. Correlation between the number of endemic species and the phylogenetic diversity of the Neotropical areas of endemism.

Table 3. Results of the Pearson´s correlation analysis among the phylogenetic diversity (PD) and the five geographic descriptors of the Neotropical areas of endemism. RPS = perimeter-√size ratio.

Correlation	Pearson's product	*p-value*	Conclusion
PD-# Endemic species	0.976	0	Positive correlation
PD-Size	0.65	0.16	No correlation
PD-Perimeter	0.53	0.28	No correlation
PD-RPS	-0.05	0.93	No correlation
PD-Centroid latitude	0.68	0.14	No correlation
PD-Centroid longitude	-0.16	0.76	No correlation

Phylogenetic diversity of the Neotropical region and its temporal strata

The PD of the Neotropical region decreases in the Andean mountains, Mexico and central Argentina, and reaches its maximum value (1,9 million years; Ma) around of the equator representing a core zone of PD (Figure 3). We found that the Neotropical endemic mammals belong to six hypothetical geographic ancestral distributions or cenocrons (America; North America; North America and Central America; Central America; Antilles and South America), with South America being the geographic ancestral distribution of the most species (39 species; Appendix 1 Table). The divergence times of the Neotropical endemic mammals showed that the Neotropical region is a biogeographic pattern with multitemporal strata (Figure 4). However, no Ae agreed completely with the geographic ancestral distribution groupings (Figure 5), and the Mantel test showed no correlation (r= -0.01328, *p*= 0.579) between the current and ancestral groupings of Neotropical endemic mammal species.

Discussion

The Neotropical region contains multiple areas of endemism of mammals (Noguera-Urbano and Escalante; Noguera-Urbano and Escalante 2015) composed of several taxonomic orders. We found that the majority of the endemic mammals are bats, and that the number of endemic species varied among the areas of endemism. Ae0 and Ae4 were the main consensus areas due to the higher number of endemic species and PD. They were the largest areas, and matched with a wide Neotropical region (excluding Patagonia) (Smith 1983; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Rueda et al. 2013; Morrone 2014a). The remaining areas of endemism are consistent with a narrow Neotropical region for mammals, which excludes some zones of the Caatinga and Patagonia (Holt et al. 2013). Ae1, Ae2, Ae3 and Ae5 share geographical similarities, such as the presence of a Neotropical core around the equator.

The PD showed that the Neotropical region is a pattern structured by areas of endemism with different evolutionary histories and taxonomic lineages (e.g. taxonomic orders). The differences in PD values, number of endemic species and list of endemic species among the areas of endemism indicate the varied position of the endemic mammals in the phylogeny, and suggest that each area of endemism is phylogenetically distinct (Morlon et al. 2011), and that represents long, complex and distinct histories in South America.

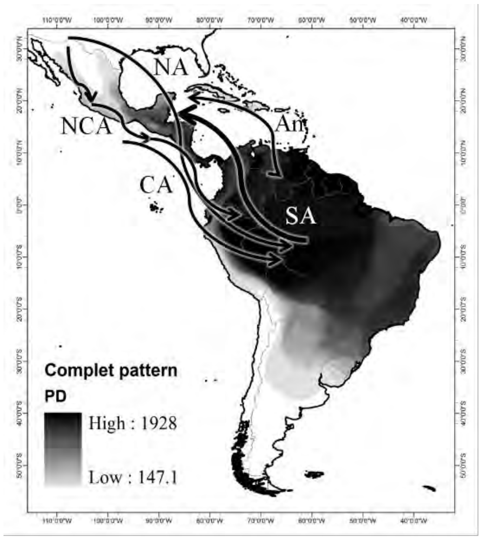

Figure 3. Map of the phylogenetical diversity (PD) of endemic mammals in the Neotropical region. Arrows indicate the hypothetical dispersal direction of endemic mammals. North America (NA), North America and Central America (NCA), Central America (CA), Antilles (An) and South America (SA).

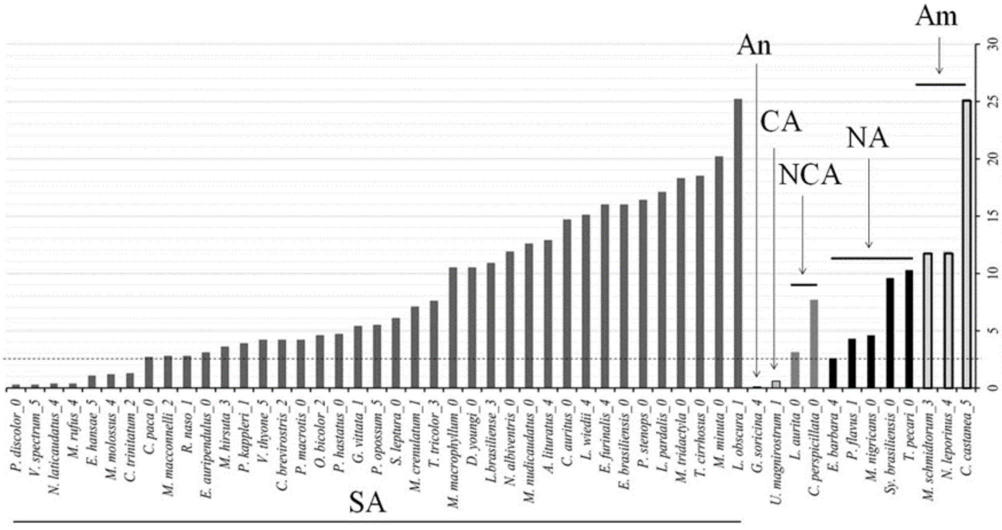

Figure 4. Bar plot with the time of lineage divergence (Ma: millions of years) of the endemic mammals. Six geographic ancestral distributions are indicated as follow: America (Am), North America (NA), North America and Central America (NCA), Central America (CA), Antilles (An) and South America (SA). The dotted line indicates the boundary between the Quaternary and Tertiary ~2.6 Ma.

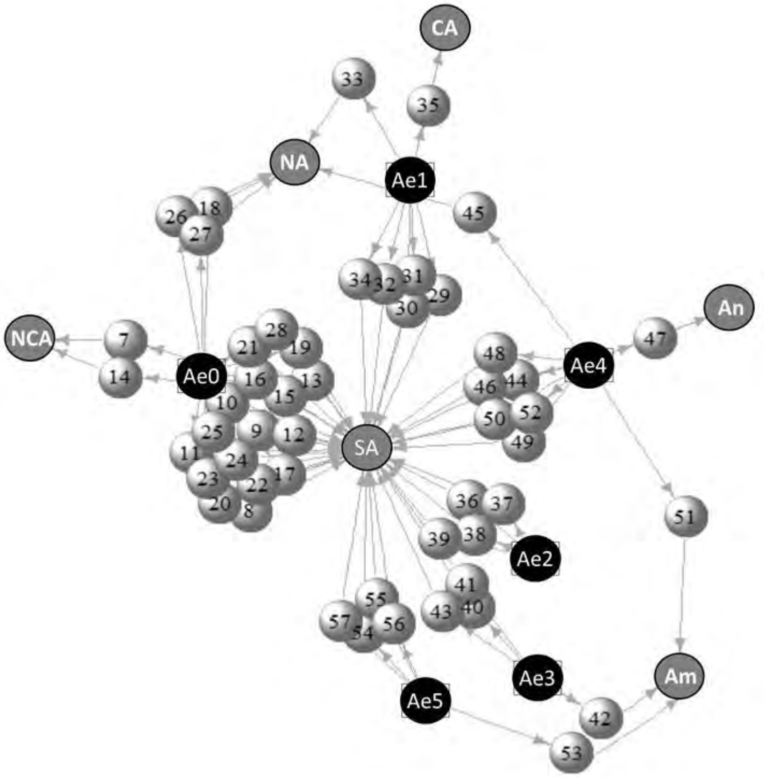

Figure 5. Network of the areas of endemism (Ae) and the geographic ancestral distributions of the Neotropical endemic mammals. The numbers indicate the species: (7). *C. perspicillata*, (8). *C. auritus*, (9). *C. paca*, (10). *D. youngi*, (11). *E. brasiliensis*, (12). *E. auripendulus*, (13). *L. pardalis*, (14). *L. aurita*, (15). *M. macrophyllum*, (16). *M. nudicaudatus*, (17). *M. minuta*, (18). *M. nigricans*, (19). *M. tridactyla*, (20). *N. albiventris*, (21). *P. macrotis*, (22). *P. stenops*, (23). *P. discolor*, (24). *P. hastatus*, (25). *S. leptura*, (26). *S. brasiliensis*, (27). *T. pecari*, (28). *T. cirrhosus*, (29). *G. vittata*, (30). *L. obscura*, (31). *M. crenulatum*, (32). *P. kappleri*, (33). *P. flavus*, (34). *R. naso*, (35). *U. magnirostrum*, (36). *C. trinitatum*, (37). *C. brevirostris*, (38). *M. macconnelli*, (39). *O. bicolor*, (40). *L. brasiliense*, (41). *M. hirsuta*, (42). *M. schmidtorum*, (43). *T. tricolor*, (44). *A. lituratus*, (45). *E. barbara*, (46). *E. furinalis*, (47). *G. soricina*, (48). *L. wiedii*, (49). *M. molossus*, (50). *M. rufus*, (51). *N. leporinus*, (52). *N. laticaudatus*, (53). *C. castanea*, (54). *E. hansae*, (55). *P. opossum*, (56). *V. thyone*, (57). *V. spectrum*.

The NRI showed no clear pattern of phylogenetic clustering or overdispersion in the overall phylogeny in any Ae, but the NTI showed phylogenetic overdispersion in Ae0, probably related to biological differences among distantly related species due to niche evolution, evolutionary convergence and colonization (Cardillo and Meijaard 2010; Cardillo 2011; Villalobos et al. 2013). This overdispersion could be explained by the effect of similar abiotic factors that determined the boundaries of the areas of distribution of mammals in the Ae0, or may be the endemic Neotropical mammals have long-distant immigration rates, rapid speciation and lower extinction rates. Bats accounted for the majority of the endemic mammals in Ae0 (15 species), and due to their phenotypic similarities related to flight, it is possible that they tolerate similar abiotic environments without exclusion (Webb et al. 2002).

Bats are more vagile than rats and opossums (Ditchfield 2000), this could explain why there is more sympatry among bat species than rat and opossum species. On another hand, the endemic bats exhibited quite different cranial, dentary and wing morphologies. These traits allow them to occupy distinct habitats and dietary guilds in the same area (Weinbeer and Kalko 2004), promoting the high number of coexistent Neotropical bats.

It is possible that low number of endemic species in Ae1-5 masks a phylogenetic pattern compared to Ae0, consequently the phylogenetic structure of each Neotropical area of endemism separately may obscure the overall phylogenetic structure of the Neotropical region. This is consistent with assemblages that show phylogenetic structure only at a given biogeographical level (Realms, region or landscape) (Cantalapiedra et al. 2014). When NRI and NTI are analyzed in each area separately, patterns could be hidden by the spatial scaling of species diversity (Morlon et al. 2011). In addition, it is suggested that assembly processes on the macroecological scale have shaped the phylogenetic structure of the regions, which in turn affect phylogenetic relationships within the biogeographic units that make up each region (Cantalapiedra et al. 2014).

The NRI and NTI values calculated using both world and regional phylogenies suggested that the Neotropical region as a single pattern is primarily explained by phylogenetic clustering (Table 2), which indicates that endemic mammals are space-temporally integrated, due to the phylogenetic clustering be caused by processes such as high in situ speciation and niche conservatism (Cardillo et al. 2008; Cardillo 2011; Villalobos et al. 2013). This integration is likely due to the specialization of lineages to their habitats, which allows them to adapt and radiate within that habitat (Cantalapiedra et al. 2014). The clustering of the endemic mammals could also indicate phylogenetic signal, since crown age and species richness are positively associated with phylogenetic signal (Cardillo 2015). For example, Chiroptera (bats) are split into Megachiroptera (Pteropodidae) and Microchiroptera. The Microchiroptera are further divided into two major clades: the Yangochiroptera, and a modified version of the "Rhinolophoidea" Yinpterochiroptera (remaining microbat families: Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae, and Rhinopomatidae) (Agnarsson et al. 2011). Yangochiroptera have had a panglobal distribution, however within this suborder, the emballonurids have an exclusively tropical distribution, and some living noctilionoids (phyllostomids, mormoopids, noctilionids, furipterids, and thyropterids) are mainly confined to the Neotropic (Teeling et al. 2005). Ancestral reconstructions suggest that noctilionoids originated in Gondwana, perhaps in South Americ (Teeling et al. 2005). Therefore, phylogenetic signal of the Chiroptera New world suborders and families would probably contribute substantially to the clustering pattern in the Neotropical areas of endemism, since most endemic species identified are bats (39 species).

The diversification of the Neotropical endemic species was likely ecologically driven, and could represent mixed histories, suggesting radiation at the base or toward the tips of the phylogeny. This pattern is consistent with the scenario of radiating clades spreading out rapidly to the boundaries of the biogeographic patterns or explosive radiation, rather than a gradual diffusion from areas of evolution to current areas of distributions (Cardillo 2011; Cantalapiedra et al. 2014). It is suggest that many dispersals events of mammals have occurred along the Andes cordilleras and South America (Clare 2011; Parada et al. 2015; Rojas et al. 2016).

The Neotropical areas of endemism are all irregularly shaped and their centroids are all around the equator, but none of the geographical descriptors we examined predicted the PD. It is possible that the Neotropical areas of endemism are so similar that the values of the geographical descriptors have low variation. On the other hand, the endemism of the Neotropical region decreases along its borders with the Nearctic and Andean regions (Noguera-Urbano and Escalante 2015); this is supported by the strong relationship between the number of endemic mammals and the PD. Thus, the highest values of PD are in the zones around of the equator where endemic mammal and birds diversity is highest (Cracraft 1985, Prado et al. 2014, Noguera-Urbano and Escalante 2015). As is generally observed (Swenson 2014), we found a positive correlation between PD and number of endemic species, thus the addition of species to the analysis could increase the PD.

Attributes such as the age of the clades and the diversification rate of some taxonomic groups determine the structure of the geographical and ecological patterns (Procheş et al. 2006; Rabosky 2009; Cardillo 2011; Villalobos et al. 2013; Cardillo 2015). For that reason, the Neotropical phylogenetic pattern (clustering) and the higher PD around the equator are strong evidence that the endemic mammals in that zone are spatially and phylogenetical structured into an evolutionary and ecological unit. Cracraft (1985) proposed that the main ecological factors that delimit areas of endemism are climatic and geographic barriers. This explanation partially applies to the Neotropical region because the evidence supports an overdispersed pattern for the Ae0 and clustered pattern for the Neotropical region as a whole.

The endemic Neotropical mammals have a shared ancestry, which suggest that areas of endemism did not predict the geographic ancestral distributions of the endemic mammals. Therefore, some Neotropical endemic mammals extended from and forward the Neotropical core without confining to their geographic ancestral distribution. This is consistent with the evolve that each region has had since South America reached its equatorial position and connected with North America (Solari et al. 2012). Although no Ae agreed completely with the geographic ancestral distribution groupings, South America was the geographic ancestral distribution of 39 species of Neotropical endemic mammals. Those mammals, such as bats and rodents, mostly form integrated monophyletic groups and evolved in neotropical ecosystems (Müller 1973; Fritz et al. 2009; Lim 2009; Gutiérrez-García and Vázquez-Domínguez 2012; Schenk et al. 2013; Rojas et al. 2016).

A spatial and phylogenetic integration of the endemic mammals of the Neotropical region

The cenocrons that characterize the areas of endemism of Neotropical mammals can be resumed according to the geographic ancestral distributions (Appendix 1 Table) and the divergence times of the endemic mammals (Figure 3). Considering that the Neotropical endemic mammals have their hypothetical region of evolution in America, we propose that the Neotropical region is a complex scenario composed of five cenocrons (An, Ca, NA, NCA, SA) in which the role of dispersal has been important (Figure 3).

Five endemic mammals evolved in North America (NA), two in North and Central America (NCA), one in Central America (CA) and one in the Antilles (An). The remaining mammals compose the Neotropical cenocron (SA). Although the temporal integration of endemic Neotropical mammals is difficult to propose, we supposed that the northern cenocrons (CA, NA, NCA and An) moved toward the south of the Neotropical Region (Figure 3). This result is consistent with one proposed biogeographic scenario, in which the isolation of South America's mammal fauna ended by ~10–7 Ma, and then permanent connection was established with Central America approximately ~3 Ma (Carrillo et al. 2015), around that time the isthmian land bridge promoted the Great American Biotic Interchange (GABI) (Simpson 1980; Webb 2011). It is possible that the Great American Biotic Interchange was a phase of movement of the CA, NA, NCA and An cenocrons into South America between the Quaternary and the Tertiary at approximately 2.6 Ma, when a large majority of land mammal families were crossing reciprocally between North and South America (i e.g. Late Pliocene; Webb, 2011). For example, in Neotropical bats it is suggested that dispersal was more frequent than vicariance at cladogenesis (Rojas et al. 2016), and that some rodents dispersed and expanded during the Miocene–Pliocene from the north to South America (Gutiérrez-García and Vázquez-Domínguez 2012).

The South America cenocron is composed of mammals of a wide range of ages; for example, the oldest species is *Lichonycteris obscura* (25.2 Ma; Ae1), while *Phyllostomus discolor* (0.3 Ma; Ae0) is the youngest (Figure 3). In this cenocron seven species (*P. discolor*, *Chiroderma trinitatum*, *Eumops hansae*, *Molossus molossus*, *Molossus rufus*, *Nyctinomops laticaudatus* and *Vampyrum spectrum*) are older than the Quaternary/Tertiary boundary. These endemic mammals may have evolved during the Quaternary then expanded their area of distribution towards the northern Neotropical Region more recently due the development of tropical forest, savanna and open habitats in America. The remaining species evolved earlier than the permanent connection between Central and South America, suggesting that they used the Isthmian land bridge to extend their areas of distribution toward Central America between ~7 Ma or 10 Ma and 2 Ma, when the savannas, grasslands and rainforests expanded in the Neotropics and the Panama Isthmus was completely formed (Hoorn et al. 2010; Webb 2011; Carrillo et al. 2015).

The integration of the SA and NAC cenocrons in South America occurred during the middle and late Miocene (Webb 2011; Carrillo et al. 2015). For example, the Great American Biotic Interchange offered the opportunity for older species (*Tayassu pecari*) (Webb 2011) to move into South American forests, and the Andes Mountains could have served as route of migration of northern taxa toward temperate environments in South America (Webb, 1991). A hypothetical order of the integration of migrant cenocrons into South America based on the ages of the mammals is: NA, NCA, CA and An. This result is also supported by analyses of geographic distributions pointing to South America and Central and North America as two important centers of diversification of Neotropical mammals, as suggested by the bats (Lim 2009; Gutiérrez-García and Vázquez-Domínguez 2012; Arita et al. 2014; Rojas et al. 2016) and other mammal groups (Müller 1973; Simpson 1980; Juñent 1994; Webb 2011; Carrillo et al. 2015). A set of barriers and corridors shaped by geological evolve, together with climatic complexity, affected the Neotropical mammals' diversification and dispersion at different time and spatial scales. We consider that these hypotheses must be tested carefully given the absence of a geographic ancestral distributions scheme that include all endemic species of mammals.

Conclusions

The NRI and NTI values calculated using both world and regional phylogenies suggested that the Neotropical region is a clear pattern explained by phylogenetic clustering of endemic mammals mainly bats. Accordingly, the several biogeographical schemes proposed to define at the Neotropical region (Hershkovitz 1958, Kreft and Jetz 2010, Holt et al. 2013, Rueda et al. 2013; Morrone 2014b, Noguera-Urbano and Escalante 2015) could have similar structures and processes as wide areas of endemism, since the biological groups used have been affected by the same historical and ecological process. But, it is also possible that some of those biogeographical schemes do not have a specific phylogenetic pattern as occurs with single areas of endemism due to the lower richness of endemic species and the analysis scale. It is necessary to include several biological groups in biogeographic analysis to propose a single scheme. Areas of endemism are an alternative for proposing the boundaries of biogeographic units and describing their biogeographic patterns and process. The core of endemism located in the tropics around the equator had the highest PD values and number of endemic species, and a pattern of phylogenetic clustering was evident there. The Neotropical endemic mammals have several geographic ancestral distributions and a range of ages, suggesting that they had an asynchronous integration as proposed by Prado et al. (2014) and Noguera-Urbano (2016). They evolved and compose the current snapshot of the Neotropical region, which has geographic and phylogenetic structure.

On the other hand, the size, perimeter, perimeter-√size ratio, and centroids of the geographical area of endemism are poor descriptors of PD. However, there was a stronger correlation between the richness of endemic species and the PD. Consequently, it is necessary to explore this correlation in small-scale areas of endemism to describe their phylogenetical patterns and process. The integration of the Neotropical endemic species of mammals defined five cenocrons, which shows that the Neotropical region is composed of temporal strata of endemic mammals, and is evidence of the history of Neotropical species that are spatiotemporally integrated in an evolutionary unit (Neotropical region) as presented by Hershkovitz (1969), Simpson (1980), Webb (2011), and some other authorities. The integration of the SA cenocron and the other cenocrons in South America may have occurred after the middle and late Miocene. We suggest that while the hypothetical temporal strata and the history of integration proposed are a general scenario, this is an integrative explanation of the ecological, geographic, historical and phylogenetical patterns of the Neotropical region. This study shows evidence of an evolutionary trade-off between the historical and ecological tendencies in areas of endemism at the Neotropical region scale.

Acknowledgments

We are profoundly grateful to Fernando Cervantes and Octavio Rojas for insightful comments that greatly helped us to improve manuscript. This paper constitutes partial fulfillment of the requirements to obtain a Doctoral degree from Posgrado en Ciencias Biológicas of the National Autonomous University of México (UNAM). Special thanks to Lynna Kiere for reviewing the English writing of this manuscript. We are also grateful to the Associate Editor and anonymous reviewers for valuable comments on the manuscript.

Funding

EAN-U was supported by the Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM) and the Consejo Nacional de Ciencia y Tecnología of Mexico (CONACyT) (Doctoral scholarship 262582).

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Appendix 1. Table of Neotropical endemic species of mammals and their geographic ancestral distributions. Am: America; NA: North America; NCA: North America and Central America; CA: Central America; An: Antilles and SA: South America. Source refers to the bibliographic source of the geographic ancestral distribution, referenced in the list following the table.

Endemic specie	Ancestral area	Divergence age in Ma*	Source
Carollia castanea	Am	25.2	(Rojas et al. 2016)
Noctilio leporinus	Am	11.9	(Rojas et al. 2016)
Micronycteris schmidtorum	Am	11.6	(Rojas et al. 2016)
Tayassu pecari	NA	10.3	(Gasparini et al. 2013)
Sylvilagus brasiliensis	NA?	9.6	(Ge et al. 2013)
Myotis nigricans	NA	4.6	(Stadelmann et al. 2007)
Potos flavus	NA	4.3	(Rolland et al. 2015)
Eira barbara	NA	2.6	(Rolland et al. 2015)
Carollia perspicillata	NCA	7.7	(Rojas et al. 2016)
Lonchorhina aurita	NCA	3.1	(Rojas et al. 2016)
Uroderma magnirostrum	CA	0.6	(Holanda et al. 2012)
Glossophaga soricina	An	0.1	(Rojas et al. 2016)
Lichonycteris obscura	SA	25.2	(Rojas et al. 2016)
Micronycteris minuta	SA	20.2	(Rojas et al. 2016)
Trachops cirrhosus	SA	18.5	(Rojas et al. 2016)
Myrmecophaga tridactyla	SA	18.3	(McDonald et al. 2008)
Leopardus pardalis	SA	17.1	(de Oliveira 1998)
Phylloderma stenops	SA	16.4	(Rojas et al. 2016)
Eptesicus brasiliensis	SA	16	(Lim 2009)
Eptesicus furinalis	SA	16	(Lim 2009)
Leopardus wiedii	SA	15.1	(de Oliveira 1998)
Chrotopterus auritus	SA	14.7	(Rojas et al. 2016)
Artibeus lituratus	SA	12.9	(Larsen et al. 2013)
Metachirus nudicaudatus	SA	12.6	(Jansa et al. 2013)
Noctilio albiventris	SA	11.9	(Lim 2009)
Lophostoma brasiliense	SA	10.9	(Rojas et al. 2016)
Diaemus youngi	SA	10.5	(Rojas et al. 2016)
Macrophyllum macrophyllum	SA	10.5	(Rojas et al. 2016)

Thyroptera tricolor	SA	7.6	(Rojas et al. 2016)
Mimon crenulatum	SA	7.1	(Hurtado-Miranda and Pacheco-Torres 2014)
Saccopteryx leptura	SA	6.1	(Lim 2010)
Philander opossum	SA	5.5	(Jansa et al. 2013)
Galictis vittata	SA	5.4	(Koepfli et al. 2008)
Phyllostomus hastatus	SA	4.7	(Rojas et al. 2016)
Oecomys bicolor	SA	4.6	(Schenk et al. 2013)
Peropteryx macrotis	SA	4.2	(Lim et al. 2008)
Cormura brevirostris	SA	4.2	(Lim 2007)
Vampyressa thyone	SA	4.2	(Rojas et al. 2016)
Peropteryx kappleri	SA	3.9	(Lim 2010)
Micronycteris hirsuta	SA	3.6	(Rojas et al. 2016)
Eumops auripendulus	SA	3.1	(Ammerman 2012)
Rhynchonycteris naso	SA	2.8	(Lim 2010)
Mesophylla macconnelli	SA	2.8	(Rojas et al. 2016)
Cuniculus paca	SA	2.7	(Upham and Patterson 2012)
Chiroderma trinitatum	SA	1.3	(Rojas et al. 2016)
Molossus molossus	SA	1.2	(Lim 2009)
Eumops hansae	SA	1.1	(Ammerman 2012)
Molossus rufus	SA	0.4	(Lim 2009)
Nyctinomops laticaudatus	SA	0.4	(Lim 2009)
Vampyrum spectrum	SA	0.3	(Rojas et al. 2016)
Phyllostomus discolor	SA	0.3	(Rojas et al. 2016)

Notes: (?) Infered from the genus or its sister species; (*) Obtained from the "Optimal tree" by Fritz et al. (2009).

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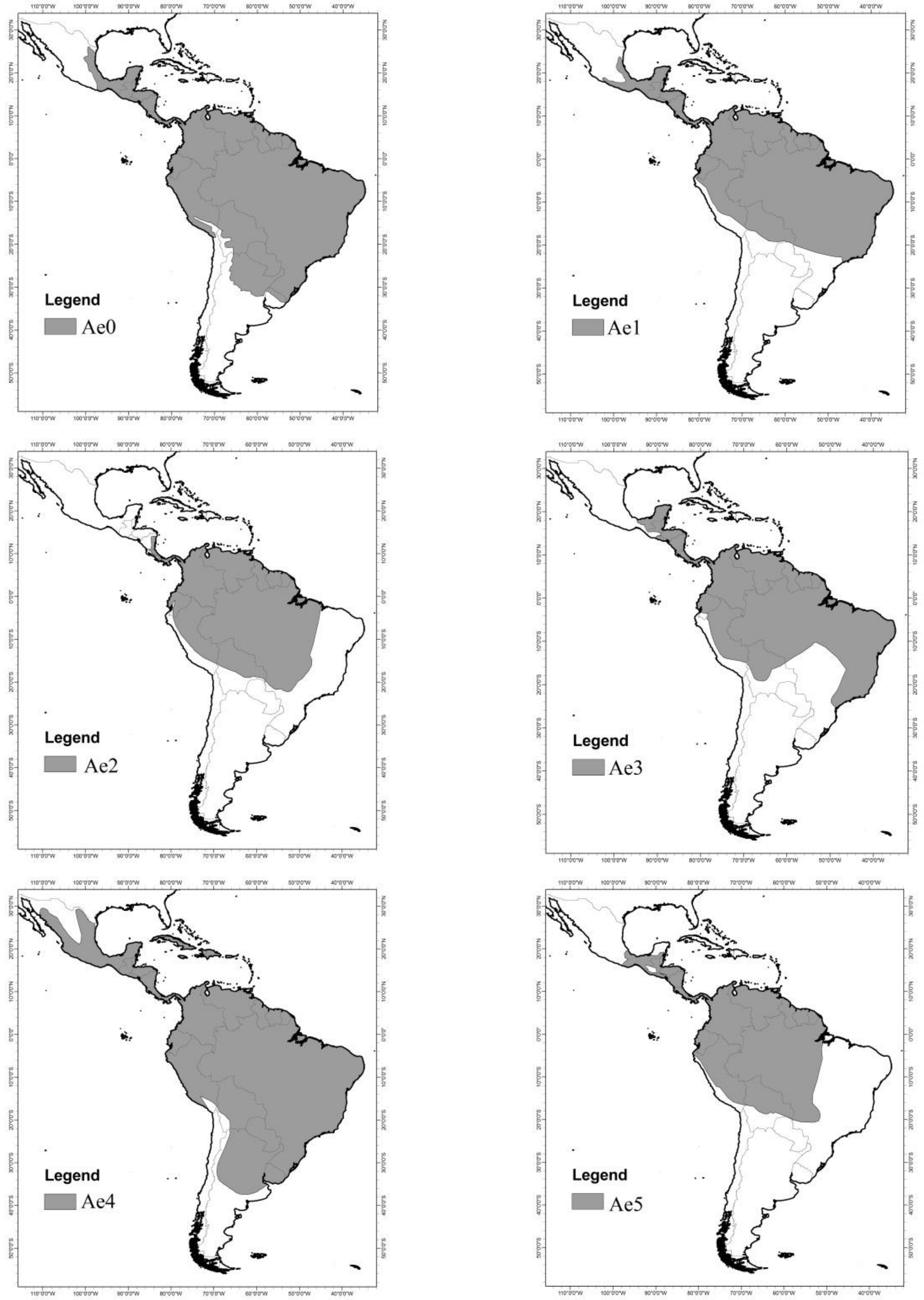
Appendix 2. Figs. Maps of the consensus areas of endemism (Ae), mapped by merging the maps of distribution of their endemic species.



CAPÍTULO III. SÍNTESIS DE LAS RELACIONES ECOLÓGICAS Y FILOGENÉTICAS EN LAS ÁREAS DE ENDEMISMO DE LOS MAMÍFEROS NEOTROPICALES

III.I Environmental factors related to biogeographical transition zones of Neotropical mammals' areas of endemism.

III.II Areas of endemism: travelling through space and the unexplored dimension.

CSIRO PUBLISHING
Australian Systematic Botany, 2017, **30**, 485–494
https://doi.org/10.1071/SB16055

Environmental factors related to biogeographical transition zones of areas of endemism of Neotropical mammals

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Abstract. Biogeographical transition zones are areas of a complex biotic mixture located at the borders between biogeographical units. Climatic, physical and ecological factors should play an important role in allowing coexistence of different biotic elements in the transition zone. Here, we explore the relationship between environmental factors and biogeographical transition zones, defined by Neotropical mammal distributions, by a model selection approach based on the Akaike information criterion and accounting for the spatial structure in the data. We detected three areas of high overlap between mammalian areas of endemism. Two of them corresponded to the well-established regional-level transition zones, namely Mexican (MTZ) and South American (SATZ) transition zones; the third was one located in south-eastern Brazil, approximately between the Paraná and Chacoan dominion that we call The Atlantic Forest integration zone (AF). Only one explicative variable was shared by the three transitions zones (precipitation of the warmest quarter). However, shared variables with great explanatory power indicated two environmental aspects as facilitators for the coexistence of different biotic components in a given geographical area. The first one was the heterogeneity component, either topographic for the SATZ and MTZ or climatic for the AF. The second one was related non-extreme thermal conditions: precipitation of the warmest quarter, interpreted as a thermal buffer, shared by AF and SATZ, and isothermality shared by MTZ and SATZ.

Received 30 November 2016, accepted 24 July 2017, published online 31 January 2018

Introduction

The biogeographical regions are defined by the occurrence of taxa in a particular geographical area, and nowhere else, namely endemic taxa. When several endemic taxa share similar geographical distribution ranges, this is frequently considered to be a consequence of barriers (physical or ecological) that have historically isolated biota, promoting speciation and shaping their distribution through evolutionary time (Nelson and Platnick 1981; Haffer 1982; Cracraft 1985). Such sets of co-distributed endemic taxa, or sets of spatiotemporally integrated taxa that coexist in given areas (biotic components *sensu* Morrone 2009), define areas of endemism. Areas of endemism are the basic units of evolutionary biogeography (Parenti and Ebach 2009, Noguera-Urbano 2016) used to propose biogeographical categories (region, domain, province; Escalante 2009). Biogeographical transition zones are areas of biotic mixture located at the borders of different biogeographical regions (Morrone 2006). Thus, the biogeographical transition zone occurs when two or more areas of endemism overlap each other (Naka 2011, Noguera-Urbano and Escalante 2015), leading to the blending of two distinct biotic components. The transition zone is a geographical area of overlap, replacement or partial segregation between these biotic components, either due to the attenuation of a pre-existing barrier or as an ongoing process of biotic limitation, such as progressive gradients of environmental conditions. Therefore, in a biographical transition zone, physical features, environmental conditions and ecological factors may all allow these biotas to mix but constrain their further diffusion into one another (Ferro and Morrone 2014).

Early zoogeographers recognised the Neotropical region on the basis of biotic singularity as a geographical area comprising South America, Central America, the southern half of Mexico and the Antilles, a scheme widely accepted by vertebrate zoogeographers (Cox 2001). Within South America, classical mammalian biogeographical regionalisation divides the continent into two subregions, namely, the north-eastern tropical lowlands (Guayano–Brazilian subregion) and the central Andean highlands and southern lowlands (Andean–Patagonian subregion; e.g. Wallace 1876; Sclater and Sclater 1899; Hershkovitz 1969). However, a more restrictive definition of the Neotropical region, proposed mainly by phytogeographers and invertebrate zoogeographers, considers the southern portion of South America as a different region, namely, The Andean region (see revision in Morrone 2014). This latter scheme defined the deepest transition of the biogeographical hierarchy in the American continent as follows: between the Holarctic kingdom and Holotropical kingdom in the Mexican transition zone (MTZ), and between Holotropical and Austral kingdom, in the South American transition zone (SATZ; Morrone 2015). Regardless of the hierarchical categorisation proposed by different authors (kingdom, region or subregion), this continental pattern of regionalisation has been repeatedly recovered by modern numerical techniques applied to vertebrate distributions (Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt *et al.* 2013; Noguera-Urbano and Escalante 2015; Escalante 2016).

Because transition zones occur between two or more biogeographical units, a desirable prerequisite for studying them is the definition of biogeographical units. In evolutionary biogeography, transition zones may be detected by conflicting results in cladistic biogeographical analyses (because a putative transition zone may be the sister area to different biogeographical areas) or by the presence of panbiogeographical nodes, namely areas where different generalised tracks converge (Morrone 2009). Although showing a mixture of biotic components, panbiogeographical nodes are unable to distinguish the geographical extent of transition zones. In contrast, hybridising areas of endemism on a general-area cladogram define transition zones with hard boundaries, thus neglecting the perception of spatial length and strength of transition zones (Ferro and Morrone 2014). Acknowledging that biotic component are spatio-temporal integrated sets of taxa and that may be either depicted as areas of endemism or as generalised tracks in panbiogeographical analysis (Morrone 2009), we used intersection of areas of endemism defined by mammal distributions to recognise transition zones in the present study. These areas of endemism were taken from a recently published analysis of Neotropical mammal endemism by Noguera-Urbano and Escalante (2015). On the basis of endemicity analysis, these authors identified areas of endemism that approximately coincided with classical biogeographical units. Also, they found two complex (transitional) areas and showed that these transitions matched with areas characterised by high topographic variability, namely, the Andes for SATZ and the Sierras Madres for MTZ. Nonetheless, the importance of environmental factors on the transitions zones remains unclear.

Here, we explored the relationship between biogeographical transition zones and environmental explanatory variables. Whereas the spatial pattern in species richness has been widely related to climatic and environmental factors, the relationships between such factors and biogeographical transition zones have been poorly explored and not quantified. Because a transition zone implies that several species from two or more areas of endemism have reached their distributional-range limits, physical and climatic factors should play an important role, and, at least, may partially explain the phenomenon. Therefore, we hypothesise that if there is a general process shaping the pattern of transition zones, then it acts in a similar manner in different transition zones and involves the same variables.

Materials and methods

Detection of biogeographical transition zones

To detect biogeographical transition zones, we used recently published analysis by Noguera-Urbano and Escalante (2015) that identified areas of endemism on the basis of mammal distributions taken from IUCN range maps (IUCN 2012). These authors analysed a matrix of 1782 mammal species in a grid of 2° latitude–longitude of the American continent by endemicity analysis. We defined our study area as the area between 32°N and 32°S latitude, encompassing the whole Neotropical region. Within this studied area, we transformed 84 areas of endemism found by Noguera-Urbano and Escalante (2015) from vector format to raster at 0.5° latitude–longitude resolution. Then, the areas of endemism in raster format were summed to obtain a resulting raster of the areas of endemism overlap (AEO) in the Neotropical region. Therefore, we obtained a map of biogeographical transition zones based on the intersection between two or more areas of endemism defined by mammal distributions. To reduce the number of pixels involved in the analysis of the relationship between AEO and environmental variables, we focused on those zones with high AEO. Thus, we identified regions where the highest AEO occur, and then use a buffer of 300 km around those areas. All spatial processes were executed in QGIS, ver. 2.18 (QGIS Development Team, Open Source Geospatial Foundation Project, see http://qgis.osgeo.org, accessed 12 May 2015).

Explanatory variable selections

Explanatory variables were taken from the 19 bioclimatic layers, ver. 1.4 (Hijmans *et al.* 2005, see http://biogeo.berkeley.edu/worldclim, accessed 24 February 2015), at the resolution of 2.5 min (~5 km^2) and a topographicvariable layer (altitude) was obtained from the digital elevation model (DEM) at the same resolution. All explanatory-variable layers were resampled using cubic technique to 0.5 degrees, which was the final spatial resolution of this analysis (~55 km^2). We evaluated multicollinearity among the 19 bioclimatic variables by the variance inflation factor (VIF; Zuur *et al.* 2010) and progressively eliminated variables until VIF was <2 for each variable (Pearson *r* of ~<0.5). Of the 19 bioclimatic variables, five (VIF of <2) were used for modelling biogeographical transition zones. The 14 variables removed after VIF analysis were used to build the climatic heterogeneity layer (see below). For the Mexican and the South American transition zones, the same five variables were retained for modelling (VIF of <2), and included isothermality (bio3), mean temperature of wettest quarter (bio8), precipitation seasonality (bio15), precipitation of the warmest quarter (bio18), precipitation of the coldest quarter (bio19). For the Atlantic Forest integration zone, mean diurnal range in temperature (bio2) and mean annual precipitation (bio12) were retained together with bio3, bio8 and bio18. This resulted in eight explanatory variables (including eigenvector filters, topographic and climatic heterogeneity) included in each transition zone for the model-selection analysis.

Environmental factors and topographical variation emerge as primary predictors of mammal biogeographic patterns (Kerr and Packer 1997). Therefore, we included as predictors two other variables, namely, climatic and topographic heterogeneities. The climatic heterogeneity was calculated for each transition zone using the 14 variables removed after VIF analysis. First, we reduced dimensionality of the bioclimatic variables by principal-component analysis (PCA). The PCA facilitates to consider multiple climatic variables at the same time and summarises them into synthetic variables. We then calculated the climatic heterogeneity, weighting the first three principal components by the amount of variation (percentage of eigenvalues; Table S1, available as Supplementary material for this paper) explained across the map layer, and summed them to produce the final heterogeneity layer (see Brown 2014 for procedure details). Topographic heterogeneity was quantified as the standard deviation of the elevation calculated from each raster pixel and the 24 cells neighbouring the focal cell (5 cells by 5 cells). Statistical analyses were performed using SDMtoolbox (Brown 2014) and R (R Foundation for Statistical Computing, see http://www.Rproject.org/, accessed 25 October 2013).

Statistical modelling of transition zones

All selected variables were standardised into units of variance for further analysis. For modelling the biogeographical transition zones, we used an Akaike information criterion (AIC) model-selection approach, accounting for the spatial structure (autocorrelation) in the data by a technique known as spatial eigenvector mapping (SEVM) or eigenvector-based spatial filters (Diniz-Filho and Bini 2005). The spatial filters (eigenvectors), representing the structure of the data at different spatial scales, were obtained from the principal coordinate analysis of neighbour matrices from a truncated pairwise-distance relationship among cells. We selected the combination of filters that minimised the spatial autocorrelation in the model residuals by keeping Moran's I below 0.05 in the first distance class. Spatial eigenvector filters were incorporated as explanatory variables for all models (Diniz-Filho *et al.* 2008). The model-selection routine was performed in Spatial Analysis in Macroecology (SAM) software, ver 3.1 (Rangel *et al.* 2006, 2010, see https://www.ecoevol.ufg.br/sam/, accessed 15 October 2014).

To evaluate the model that best explained each mammal biogeographical transition zone, we used the sample-corrected AIC (AICc) for each proposed model, selecting as the best models those with the minimum AICc. We evaluated models by calculating the difference between AICc of each model and the minimum AICc found for the set of models compared (ΔAICc). The relative contribution of each variable was estimated by the average of their coefficients across all models in which they were present, by the Akaike weight of each model w_i (Diniz-Filho *et al.* 2008).

Results

Detection of biogeographical transition zones

We detected three zones where areas of endemism were highly integrated (Fig. 1). One was located in Mesoamerica, approximately coinciding with the MTZ (Morrone 2014). Another one was located in the tropical Andes, coinciding with the Andean portion of the SATZ (*sensu* Morrone 2014). Finally, we detected a high mixture of areas of endemism located in south-eastern Brazil between the Paraná and the Chacoan dominion of the Neotropical region, that we call Atlantic Forest integration zone (Fig. 1).

Modelling biogeographical transition zone

Mexican transition zone

For the MTZ, of the 127 evaluated models, 6 were best models according to the AICc values, and can be considered equivalent according to their ΔAICc values of <2 (Burnham and Anderson 2002) (Table 1). All these models explained 94% of variation in this transition zone. Model length ranged from five to seven variables, but the best models were those with fewer variables. The two models with the lowest AICc were equal regarding the likelihood of being the best one (17%) according to w_i values, whereas the remaining models were below 8% according to w_i values. The following four variables were present in all selected models: precipitation of the warmest quarter (bio18); precipitation of the coldest quarter (bio19); isothermality (bio3); and topographic heterogeneity. The variable with the highest explanatory power, considering all models, was isothermality (bio 3) followed by topographic heterogeneity (see standardised coefficient in Table 2).

South American transition zone

Of the 127 possible models for the SATZ, four models with the lowest AICc were equivalent according to their ΔAICc (Table 1). Each model explained 89% of the variance in this biogeographical transition zone, including five to seven variables and different combinations across models. The model with the lowest AICc was the best one according to w_i values (21%). For the remaining three models, w_i values were below 12% (Table 1). Beyond eigenvector filters, which account for spatial structure in the data for every model (always present), of the seven alternative explanatory variables, the following four were present in all selected models: precipitation of warmest quarter (bio18); isothermality (bio3); topographic and climatic heterogeneity. The best model also included mean temperature of the wettest quarter (bio 8), which was present in three of the four best-ranked models. When considering the explanatory power of each variable across every model in which it was present, topographic heterogeneity was the variable with the largest standardised coefficient, followed by precipitation of the warmest quarter (bio18) and isothermality (bio3; Table 2).

Atlantic Forest integration zone

For this area, 14 models with ΔAICc < 2 were selected, each one explaining 96% of the variance (Table 1). The number of variables included in the selected models ranged from three to six, but best models included few variables. Only one variable

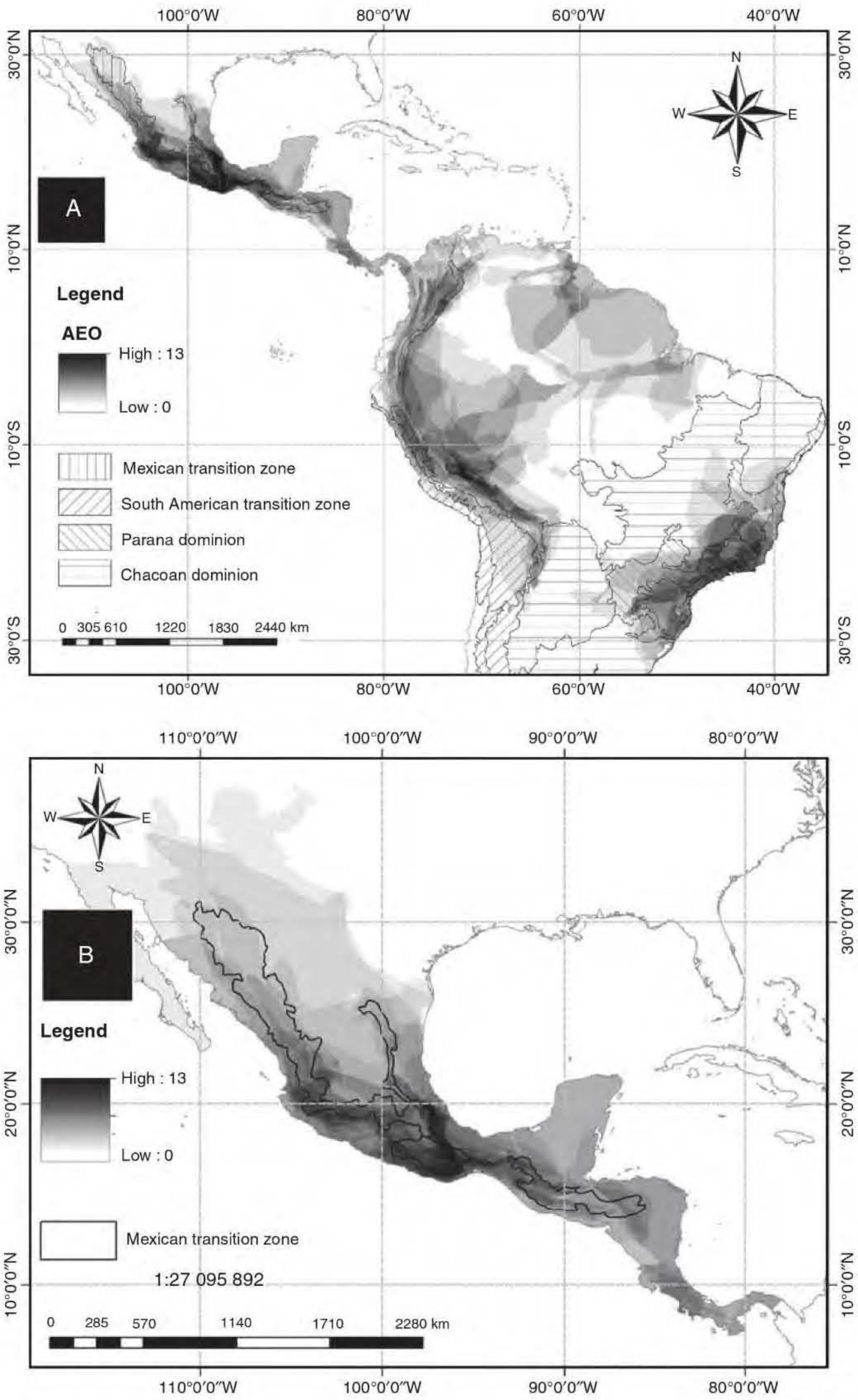

Fig. 1. Areas of endemism of the Neotropical mammals overlapping and the biogeographical transition zones defined in the present paper. A. Studied area, AEO (areas of endemism overlapping) and biogeographical units by Morrone (2014). B. Mexican transition zone. C. South American transition zone. D. Atlantic Forest integration zone. The scale indicates AEO from the lowest (light) to the highest (dark).

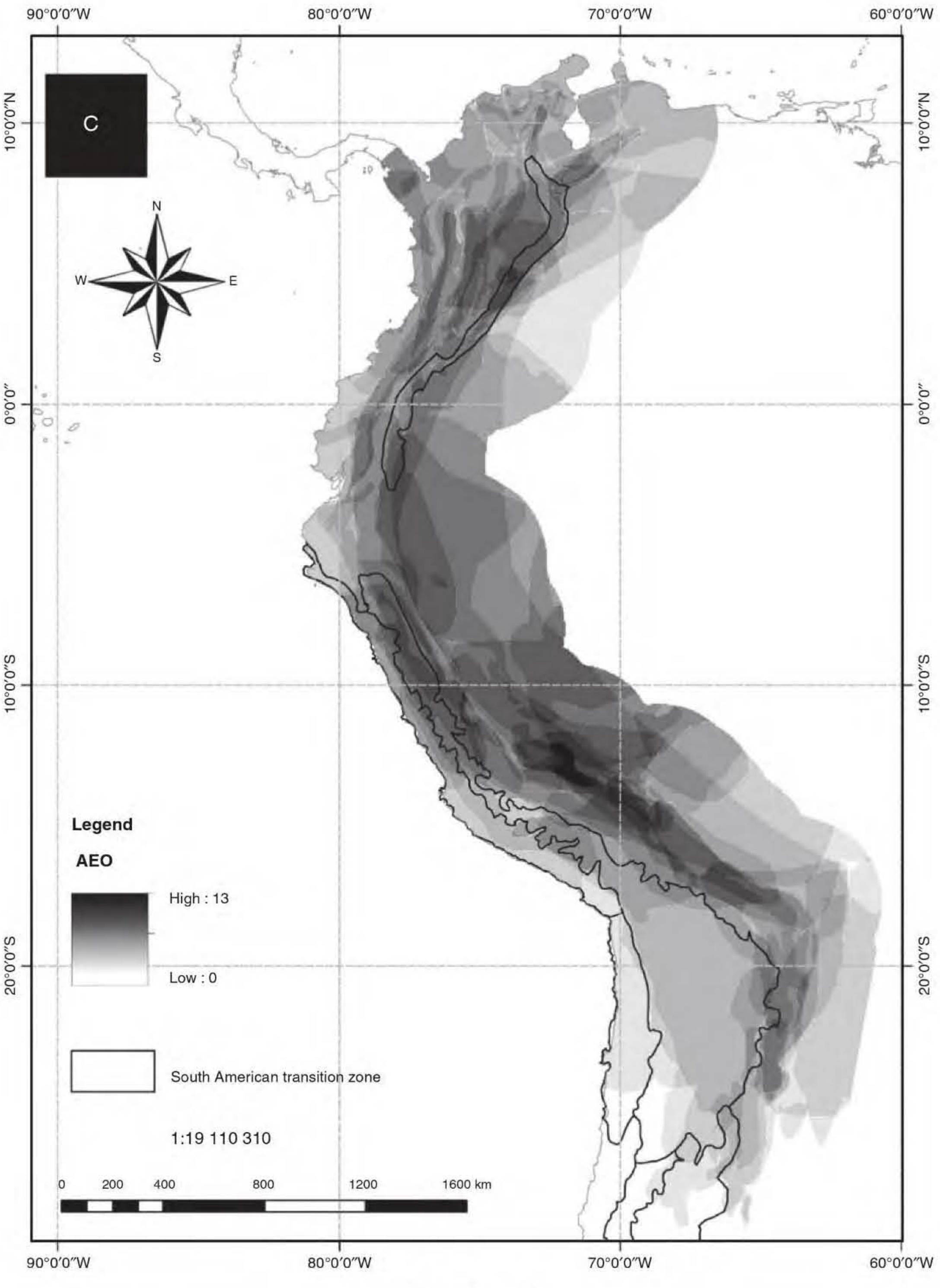

Fig. 1. (*continued*)

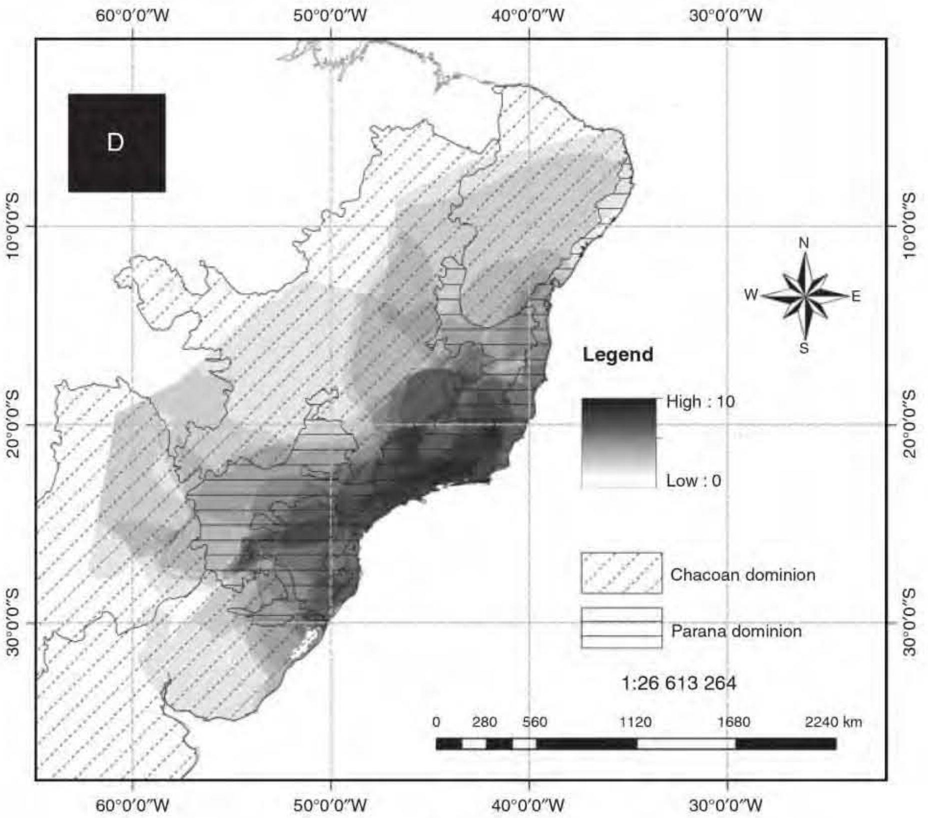

Fig. 1. (*continued*)

was present in all selected models, namely precipitation of the warmest quarter (bio18). The best explanatory variables according to standardised coefficient were precipitation of the warmest quarter (bio18) and climatic heterogeneity (Table 2).

Discussion

All the biogeographical divisions of earth imply the existence of transition zones between the divided units when contiguous. Biogeographical transitions are usually represented cartographically as sharp lines drawn on maps. However, rather than just static lines, transition zones involve areas containing gradients of biotic composition (Williams 1996; Ruggiero *et al.* 1998; Williams *et al.* 1999; Ruggiero and Ezcurra 2003). Such gradients in biotic composition should be mapped to identify places where major intergradations occur (Ferro and Morrone 2014). By measuring overlap between different mammalian areas of endemism we recovered three zones of substantial contact for the Neotropical region. Two of these zones coincide with the classical regional-level transition zones of the Neotropical region, namely the SATZ and the MTZ. However, whereas the location of MTZ defined by Morrone (2014) approximately coincided with our finding, the SATZ differed to some extent (Fig. 1). According to Morrone (2014), the SATZ in the tropical Andes includes the Paramos, and the western (dry) slopes of the Andes (Puna, Atacama, Prepuna and Monte biogeographical provinces). Our findings agreed with those of Morrone (2014) in that the Paramos (northern Andes) are part of the SATZ, but differed in the central Andes, where the transition zone was located at the eastern (humid) slopes of the Andes. The third prominent area identified in the present paper, the Atlantic Forest integration zone, is located between the Chacoan dominion and the Paraná dominion. This area has not been previously recognised as a strong continental transition zone and would require a formal definition. However, recent continental analysis of species turnover showed a high rate of replacement in this area for birds (Melo *et al.* 2009) and rodents (Maestri and Patterson 2016). Additionally, Costa (2003) reported incongruence of branching patterns among areas using cladistic approach for small mammal taxa occurring throughout Atlantic Forest, Amazon forests, Cerrado and Caatinga regions. Furthermore, the Atlantic Forest (Paraná Dominion) and Brazilian Cerrado (Chacoan Dominion) have been repeatedly recognised as a hotspot of endemism and biodiversity (Myers *et al.* 2000; Mittermeier *et al.* 2004, 2011). Thus, all this evidence suggests an existence of a prominent biogeographical transition zone in this region.

A commonality among the areas of biotic component mixture reported in the present paper is the presence of mountain areas associated with each one, including the central Andes in South America, the Sierras Madre in Mesoamerica and the Serra do Mar in eastern Brazil. This is important because

Table 1. Parameter estimates for best Neotropical transition-zone models selected according to Akaike weights (AICc w_i)
Bioclimatic variables (bio): 2, mean diurnal range in temperature; 3, isothermality; 8, mean temperature of wettest quarter; 12, mean annual precipitation; 15, precipitation seasonality; 18, precipitation of warmest quarter; 19, precipitation of coldest quarter. CH, climatic heterogeneity; TH, topographic heterogeneity; EF, eigenvector filter; Cond.Num., conditional number; AICc, corrected Akaike's information criterion; delta AICc, difference between AICi and the minimum AIC found for the set of models compared

Transition zone	Best model	Variable	r^2	Cond.Num.	AICc	Delta AICc	AICc w_i
Mexican transition zone	Mod #71	3, 8, 18, 19, TH, EF	0.937	3.449	2124.31	0	0.172
	Mod #74	3, 18, 19, TH, EF	0.937	3.449	2124.322	0.013	0.171
	Mod #8	3, 8, 15, 18, 19, TH, EF	0.937	3.526	2125.7	1.39	0.086
	Mod #70	3, 8, 18, 19, CH, TH, EF	0.937	3.504	2125.761	1.451	0.083
	Mod #73	3, 18, 19, CH, TH, EF	0.937	3.501	2125.811	1.501	0.081
	Mod #11	3, 15, 18, 19, TH, EF	0.937	3.522	2126.064	1.755	0.072
South American transition zone	Mod #85	3, 8, 18, CH, TH, EF	0.89	2.993	865.036	0	0.21
	Mod #22	3, 8, 15, 18, CH, TH, EF	0.89	3.3	866.099	1.063	0.12
	Mod #88	3, 18, CH, TH, EF	0.889	2.794	866.168	1.132	0.12
	Mod #70	3, 8, 18, 19, CH, TH, EF	0.89	3.222	867.029	1.994	0.078
Atlantic Forest integration zone	Mod #79	2, 18, CH, EF	0.959	2.075	1977.847	0	0.049
	Mod #16	2, 12, 18, CH, EF	0.96	2.761	1977.857	0.01	0.049
	Mod #3	2, 12, 18, EF	0.959	2.63	1978.624	0.777	0.034
	Mod #66	2, 18, EF	0.959	1.914	1978.717	0.87	0.032
	Mod #94	18, CH, EF	0.959	1.962	1978.749	0.902	0.031
	Mod #13	2, 8, 12, 18, CH, EF	0.96	3.088	1979.158	1.311	0.026
	Mod #9	2, 3, 12, 18, CH, EF	0.96	2.84	1979.331	1.484	0.024
	Mod #17	2, 12, 18, CH, TH, EF	0.96	3.01	1979.404	1.557	0.023
	Mod #18	2, 12, 18, TH, EF	0.959	2.822	1979.436	1.589	0.022
	Mod #31	12, 18, CH, EF	0.959	2.573	1979.597	1.75	0.021
	Mod #80	2, 6, 18, TH, EF	0.959	2.361	1979.598	1.751	0.021
	Mod #72	2, 3, 18, CH, EF	0.959	2.2	1979.615	1.768	0.02
	Mod #12	2, 8, 12, 18, EF	0.959	2.947	1979.641	1.794	0.02
	Mod #76	2, 5, 18, CH, EF	0.959	2.203	1979.764	1.918	0.019

differences in elevation entails strong environmental changes that certainly affect the distribution of organisms, imposing biotic limitation and promoting differentiation among biota. Indeed, β diversity as a measure of the difference in species composition has proved to be useful for detection of transition zones between biogeographical regions (Williams 1996; Ruggiero *et al.* 1998; Ferro 2013, Ferro *et al.* 2017). An assessment of environmental drivers for β-diversity at continental scales has shown that topographic heterogeneity is the best predictor for turnover patterns of birds and mammals in the American continent (Melo *et al.* 2009, Maestri and Patterson 2016). Additionally, even within ecoregions, variability in elevation is a good predictor for β diversity in birds (Veech and Crist 2007).

All selected models included shared variables with strong explanatory power. Particularly, for the SATZ and the MTZ, the following three of the four selected variables for each best model were shared: topographic heterogeneity, isothermality and precipitation of the warmest quarter (Table 1). For the Atlantic Forest integration zone, the following two variables were consistently selected: precipitation of the warmest quarter, also selected for models in the other two transitions zones recognised in the present paper, and climatic heterogeneity, also selected for all best models of the SATZ. The presence of a similar set of variables with strong explanatory power in different transition zones suggests the existence of a general process shaping this phenomenon, but the difference in the explanatory power of these variables in different models also indicates some singularities for each region.

Topographic heterogeneity quantifies the variation among pixel values of an elevation layer. This variable yielded the greatest explanatory power for the SATZ, where the elevation gradient is notoriously abrupt (more than 3500 m in a few dozen linear kilometres), and it was the second most important one, considering its explanatory power, for the MTZ. As discussed above, differences in altitude and the correlated temperature variations are surrogates for habitat differentiation and are related to biological diversity. However, heterogeneous topography can also play a role in the intermingle of biotic components, favoured by non-extreme climatic conditions. As a consequence of topographic heterogeneity, microclimatic conditions frequently vary within small geographical areas. For instance, solar radiation depends on slope orientation, moist capture is higher on ridges, whereas adjacent valleys are frequently dryer (Sarmiento 1986). These microclimatic conditions generate a network of vegetation patches with an associated distinctive fauna (Ferro and Barquez 2009). Thus, the interacting influences of climate, topography and soil on a mounting side may be important determinants of species distributional range-limit integration at a local scale. Although mountain ranges are present in the Atlantic forest integration zone, the topographic heterogeneity was not a relevant variable in this region, being present only in 4 of 14 selected modes (Table 1) and with a low explanatory power (Table 2). This was probably due to the short elevation gradient, with only isolated peaks being higher than 2000 m (Safford 1999). However, the topography, together with the decreased rainfall away from the

Table 2. Summary of the parameter estimates for variables averaged across 127 spatial ordinary least squares (OLS) for Neotropical transition zones
Numbers indicate bioclimatic variables (bio; see Table 1). CH, climatic heterogeneity; TH, topographic heterogeneity; PF, predicted by filter; coeff., coefficient; s.d. coeff., standardised coefficients; s.e., standard error and *t*, *t*-values associated to standardised coefficients

Transition zone	Variable	Importance	Coeff.	s.d. coeff.	s.e.	*t*	95% lower	95% upper
Mexican transition zone	Constant	–	–0.8	0	0.209	–3.822	–1.21	–0.39
	3	0.999	0.014	0.053	0.003	4.113	0.007	0.02
	8	0.543	0.001	0.013	0.001	2.816	0.001	0.001
	15	0.314	0.001	–0.005	0.001	–1.726	–0.001	0.001
	18	0.801	0.001	0.025	0.001	2.726	0.001	0.001
	19	0.878	0.001	–0.026	0.001	–2.725	0.001	0.001
	CH	0.337	–0.003	–0.008	0.001	–2.412	–0.005	0.001
	TH	1	0.875	0.045	0.202	4.327	0.479	1.271
	EF	1	0.936	0.905	0.014	67.292	0.909	0.964
South American transition zone	Constant	–	0.001	0	0.009	0.001	–0.018	0.018
	3	0.91	0.031	0.031	0.011	2.863	0.01	0.053
	8	0.709	–0.025	–0.025	0.009	–2.697	–0.043	–0.007
	15	0.374	–0.013	–0.013	0.005	–2.423	–0.023	–0.002
	18	0.99	0.041	0.041	0.012	3.376	0.017	0.065
	19	0.289	0.001	0.001	0.004	0.005	–0.008	0.008
	CH	0.748	–0.025	–0.025	0.009	–2.722	–0.043	–0.007
	TH	0.987	0.05	0.05	0.016	3.102	0.018	0.081
	EF	1	0.954	0.898	0.013	72.771	0.928	0.979
Atlantic Forest integration zone	Constant	–	0.12	0	0.153	0.785	–0.18	0.42
	2	0.602	–0.001	–0.009	0.001	–2.756	–0.003	0.001
	3	0.353	–0.001	–0.005	0.001	–2.393	–0.003	0.001
	8	0.318	0.001	–0.004	0.001	–1.903	0.001	0.001
	12	0.486	0.001	–0.009	0.001	–2.607	0.001	0.001
	18	0.844	0.001	0.017	0.001	2.54	0.001	0.001
	CH	0.603	0.004	0.01	0.001	2.775	0.001	0.007
	TH	0.366	0.173	0.006	0.07	2.47	0.036	0.311
	EF	1	0.989	0.969	0.007	133.264	0.974	1.004

coasts, creates a complex mosaic of vegetation types (rain forest, *Araucaria* forests, seasonal deciduous and semideciduous forest, and the Cerrado), accounted for in our analysis by climatic heterogeneity, which certainly affects mammals distributions and has affected their evolution in this region (Costa and Leite 2012, Machado *et al.* 2013, Leite *et al.* 2016).

Another observed recurrent explanatory variable is isothermality (bio 3), which was the variable with greatest explanatory power for the MTZ (mean = 60%). This variable quantifies thermal variability as a quotient between diurnal temperature oscillations relative to the annual temperature range. The higher the value, the more similar the diurnal and annual temperature ranges are. Thus, in isothermal regions, temperature remains fairly constant year-round, with the seasonal variation in temperature regime being similar to the day–night variation. Because biogeographical transition zones are areas where marginal distributional ranges of species overlap, populations inhabiting the transition zones are at, or near, their limits of physiological tolerance. Therefore, high isothermal regions would prevent extreme cooling or heating events, favouring the persistence of species belonging to different biotic components with different historical settings. In fact, high rates of mortality in marginal populations occur after extreme environmental events (Gaston 2009 and reference therein).

The third pervasive variable is precipitation of the warmest quarter (bio 18), which was present in the best models for the three transition zones here identified (mean MTZ = 635 mm, SATZ = 919 mm, AF = 570 mm). High temperatures and water availability have been repeatedly mentioned as direct key climatic determinants of species richness across the world (see revision in Hawkins *et al.* 2003). However, although obviously related to water supply, this variable can be interpreted as a temperature buffer, preventing heat stress in the framework of transition zones. Mammals, as endotherms, can better tolerate low temperatures than high temperatures by daily torpor or increased food consumption to maintain energy balance. Indeed, high temperatures and the resulting heat stress have large effects on most aspects of reproductive function in mammals (Heldmaier *et al.* 2004). The evaporative cooling effect of rainfall during the warmest period of the year can enhance the thermoregulatory demand of mammals, reducing the deleterious effects of heat stress (Hansen 2009). Thus, rainfall in the warmest quarter probably facilitates the coexistence of a set of mammal species with different distributional ranges, and presumably with different thermal requirements, in a given geographical area.

Our results have demonstrated the existence of a similar set of related environmental variables for all the transition zones, with the variables being almost the same for the MTZ and SATZ, but different for the Atlantic Forest integration zone. Despite their differences, some commonalities could be found. The most apparent one was the heterogeneity component, being topographic for the SATZ and MTZ but climatic for the Atlantic Forest. The precipitation of the warmest quarter, which is the variable with the greatest explanatory power for the Atlantic

Forest integration zone, and the second-greatest for the SATZ, is interpreted as thermal buffer. Whereas precipitation variable had low explanatory power for the MTZ, the variable with the highest explanatory power for this zone was isothermality, which is related to thermal stability throughout the year. Therefore, we found some support for our hypothesis of the existence of general processes shaping biogeographical transition zones. However, the contribution of these variables to all models was small, suggesting that additional factors may enhance our understanding of the processes in biogeographical transition zones. Particularly, historical factors such as orogeny, river dynamics, history of glacial cycles, sea-level changes, climatic changes favouring the formation of refuges, and ecological factors such as guild composition and niche differentiation among biotic components would return a more complete picture of the integration of biotic components in biogeographical transition zones (Leite *et al.* 2016; Ficetola *et al.* 2017). Nonetheless, as a first approach to assess the climatic and environmental properties of biogeographical transition zones, our findings suggest a general trend in predictors as transition-promoting factors related to heterogeneity (topographic and climatic) and non-extreme thermal conditions (precipitation of the warmest quarter and isothermality). So as to confirm or reject the generality of our results, further investigation should evaluate transition zones at different spatial and hierarchical scales, as well as from different regions around the world.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

Thanks go to the editors of this special issue. This work was developed during the visit of EANU to the 'Programa de Investigaciones de Biodiversidad Argentina' (PIDBA) – Universidad Nacional de Tucumán and 'Instituto de Eco-regiones Andinas' (INECOA) – 'Consejo Nacional de Investigaciones Científicas y Técnicas' (CONICET) – Universidad Nacional de Jujuy-Argentina. E. A. Noguera-Urbano thanks all people at both institutions for their hospitality during his visit. Special thanks go to the 'Becas Mixtas 2016 MZO 2017 Movilidad en el extranjero (291062); to Programa de Apoyos a Estudiantes de Posgrado (PAEP), Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México (UNAM); and the Consejo Nacional de Ciencia y Tecnología of México' (CONACyT) (Doctoral scholarship 262582) for financial support.

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Handling editor: Tania Escalante

Australian Systematic Botany, 2017, **30**, 485–494
doi:10.1071/SB16055_AC

Supplementary material

Environmental factors related to biogeographical transition zones of areas of endemism of Neotropical mammals

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Table S1. Summary of the principal-component analysis (PCA) on the climatic variables used to build the climatic heterogeneity layer for the transition zones

Bioclimatic variables included in the PCA (bio). Number of principal components (PC), eigenvalue (λ), percentage of eigenvalues (%λ) and accumulative of eigenvalues (Aλ)

Transition zone	Variable (bio)	PC	λ	%λ	Aλ
Mexican transition zone	1, 2, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 16, 17	1	1 294 044	94.3752	94.3752
		2	74 923	5.4642	99.8394
		3	2202	0.1606	100
South American transition zone	1, 2, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 16, 17	1	777 336	80.1007	80.1007
		2	184 065	18.9671	99.0678
		3	9046	0.9322	100
Atlantic Forest integration zone	1, 4, 5, 6, 7, 9, 10, 11, 13, 14, 15, 16, 17, 19	1	560 598	96.4898	96.4898
		2	11 974	2.061	98.5509
		3	8419	1.4491	100

Systematics and Biodiversity (2016), **14(2)**: 131–139

Perspective

Areas of endemism: travelling through space and the unexplored dimension

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(Received 23 June 2015; accepted 5 November 2015)

The current concept of areas of endemism assumes that they are geographic areas where there is spatial congruence of at least two endemic taxa. When this congruence is non-random, areas of endemism are explained by historical and ecological factors. Space has been the main dimension of analysis of areas of endemism, and the role of the time dimension in areas of endemism remains unclear. Phylogenetic information is a source of temporal information to explore the structure of the areas of endemism. I review the concept of areas of endemism and discuss their conceptual models (structure and boundaries). I propose four scenarios about the structural integration of endemic taxa in the space-time dimensions into areas of endemism. A better understanding of how to interpret areas of endemism can be analysed using phylogenetic information from endemic taxa to test simultaneous divergence and to propose temporal strata. Although the evolutionary relationships of the space and time dimensions have rarely been characterized in areas of endemism, I used this conceptual framework to interpret the Andean area of endemism and its evolution.

Keywords: Andean mammals, areas of endemism, biogeography, phylogenies, spatial congruence

Introduction

The concept of 'endemism' has had several meanings and applications in the biogeographic, ecological, and conservation literature. Frequently, endemism refers to a restricted geographic distribution, or when a taxon occurs only in a specific, restricted area (Anderson, 1994; Peterson & Dawson, 1998; Polunin, 1960). Under both of these definitions it is accepted that organisms' distributional areas provide information about the complex relationships between their physical environment and their biological features (link between earth history and the history of life: Brown, Stevens, & Kaufman, 1996; Pigot & Tobias, 2013).

The identification of areas of endemism is an important and basic question in the study of biogeography (Henderson, 1991). The 'congruence of distributional areas' criterion is more or less accepted as a conceptual foundation for identifying areas of endemism and endemic taxa. Endemism has historical and ecological significance in evolutionary biogeography in that it is diagnostic of geographic zones where taxa are spatiotemporally integrated (Morrone, 2009; Nelson & Platnick, 1981). This fundamental assumption of areas of endemism was summarized by Linder (2001): 'An implicit assumption in any area of endemism is that its biota has a single history and consequently that the biogeographical relationships of all the elements in the biota should be the same' (p. 892).

While space is an essential dimension of analysis of areas of endemism (Anderson, 1994; Cracraft, 1985; Haffer, 1978; Linder, 2001; Morrone, 1994; Müller, 1973; Platnick, 1991; Szumik, Cuezzo, Goloboff, & Chalup, 2002), evolution operates in three dimensions: space, time, and form (Croizat, 1964). Some techniques have been proposed to test the relationship between areas of endemism using the phylogenetic relationship among taxa (e.g., Cladistic biogeography methods; Humphries & Parenti, 1999; Nelson & Platnick, 1981). However, the phylogenetic relationships among endemic taxa that characterize areas of endemism have been poorly explored in biogeographic studies. As a first step, biogeographers should focus on the space and time dimensions of areas of endemism, or the space-time relationship of the endemic taxa. My objectives are to review the concept of area of endemism, to examine its conceptual model (structure and boundaries), and to propose four scenarios to explain the integration of endemic taxa in space-time.

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ISSN 1477-2000 print / 1478-0933 online

http://dx.doi.org/10.1080/14772000.2015.1135196

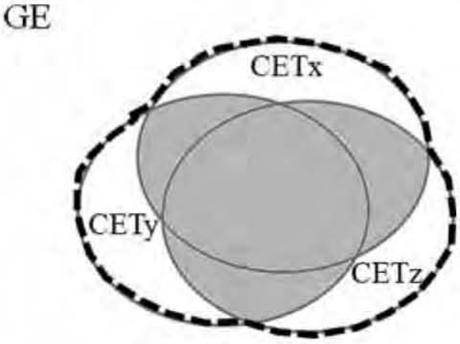

Fig. 1. Diagrammatic representation of an area of endemism (AoE) supported by three *congruent endemic taxa* (CET: x−y−z). Dotted line indicates the area of endemism boundaries and the geographic environment (GE) is the zones outside of the area of endemism.

One dimension (space)

Evolution operates in three dimensions: space, time, and form (Croizat, 1964), and biogeography focuses on the space and time dimensions or spatiotemporal relationship (Morrone, 2009). In the identification of areas of endemism, only the space dimension is analysed (Anderson, 1994; Cracraft, 1985; Haffer, 1978; Linder, 2001; Morrone, 1994; Müller, 1973; Platnick, 1991; Szumik et al. 2002) and spatial congruence has complete preeminence (Fig. 1). Currently, it is partially accepted that an area of endemism is a hypothetical historical unit in geographic space influenced by multiple processes, which is defined by at least two non-random congruent distributional areas (Espinosa, Aguilar, & Escalante, 2001; Linder, 2001; Morrone, 1994; Parenti & Ebach, 2009; Platnick, 1991; Fig. 1).

Although the identification of areas of endemism would be straightforward by the application of the above criterion, the estimation of the degree of spatial congruence might still be problematic. The spatial congruence between two taxa is rarely perfect due to the biological attributes of the species (ages, ecologies, or dispersal abilities; Cracraft, 1985). Henderson (1991) pointed out that while the degree of congruence is critical in the identification of areas of endemism, it is also vague and difficult to measure. This problem is a persistent one, although there are some operative assumptions and methods for remedying it (Table 1).

Abstractions about space can be influenced by extrinsic factors such as the taxonomic validity of the taxon, the method used to estimate maps of the distributional areas and the method of analysis. Also, the geographic space of the areas of endemism can be affected directly by intrinsic factors related to the nature of the distributional areas (physical and climate barriers, interspecific interactions, population dynamics, genetics and phylogenetics, and the simultaneous effect of both historical and ecological processes). Therefore it is necessary to process and analyse as much information as possible about the areas of endemism (Harold & Mooi, 1994) and their congruent endemic taxa to avoid interpretation errors.

Two dimensions (space−time)

Areas of endemism can be defined by the congruence of phylogenetically unrelated (Fig. 2) or related taxa (Fig. 3). In general, an area of endemism emerges from a vicariant event in the case of related taxa (Harold & Moi, 1994), while vicariance and other processes (e.g., geodispersal, extinction) affect and define an area of endemism of unrelated taxa. In areas of endemism composed of unrelated taxa, phylogenetic information is only incorporated to analyse the 'historical relationship' between areas (Nelson & Platnick, 1981), without considering the divergence time of the congruent endemic taxa.

The congruence of phylogenetic patterns between unrelated taxa has been employed to test areas of endemism (e.g., Cladistic biogeography; Morrone, 2009; Nelson & Platnick, 1981), but not to explain the spatial congruence of endemic taxa. Although geological or physiographic information can be introduced to recognize areas of endemism (Harold & Moi, 1994), that information represents indirect data about the space and time of the congruent endemic taxa. Other, more direct information is necessary, for example from fossils, phylogeography, and molecular clocks, to validate areas of endemism, their historical relationships (Morrone, 2009), and their structure.

A conceptual model of the stages of biotic evolution indicates that the interaction between space (distributional areas), and time/form (through phylogenies) is possible (Morrone, 2009). Phylogenetic information facilitates the understanding of the causes, process, and interactions of the dynamic integration of different taxa (Cardillo & Meijaard, 2010; Emerson & Gillespie, 2008; Webb, Ackerly, McPeek, & Donoghue, 2002), and phylogenies provide acceptable inferences about time and divergence of the taxa (Kumar, 2005; Svennblad, 2008).

Considering the necessity of incorporating divergence time to explain areas of endemism, I suggest four scenarios that would serve as theoretical frameworks for analysing the structural nature of areas of endemism and their congruent endemic taxa:

1. (1) An area of endemism composed of asynchronous taxa (different temporal strata). The model $AoE1 = X \cup Y$ is supported by at least two related or unrelated taxa with different divergence times (Fig. 2).
2. (2) An area of endemism with synchronous taxa (one temporal stratus). The area is defined by at least two taxa with similar divergence time. In the model $AoE2 = \{W,X\}$, two sister taxa have geographic congruence. When two or more non-sister taxa have geographic congruence the model is $AoE2' = \{W,Y\}$ (Fig. 3).

Table 1. Comparison of methods used in the identification of areas of endemism.

Method	Convention	Unit of comparation	Criterion	Results	Author
Parsimony Analysis of Endemicity	PAE	Geographic areas or localities of occurrence	Count of species	Clades of areas or localities	Rosen and Smith (1988)
Parsimony Analysis of Endemicity	PAE	Grid cells	Count of species	Clades of grid cells	Morrone (1994, 2014b)
Criteria for recognition of areas of endemism	?	Distributional areas and phylogenies	Identification of at least two monophyletic taxa with phylogenetic congruence	Groups of areas	Harold and Mooi (1994)
Optimality criteria for evaluating competing sets of areas of endemism	?	Grid cells	Congruence index of at least two species (con) and Congruence of areas (CON)	Clusters of grid cells associated by similarity or parsimony	Linder (2001)
Analysis of Endemicity or Optimality Criterion	AE	Grid cells or localities of occurrence	Index of endemicity	Sets of cells or localities of at least two species or areas of endemism maps	Szumik et al. (2002); Szumik and Goloboff (2004)
SIGnificant Co-Occurrence of Taxa	Sigcot	Grid cells	Evaluation of the significant spatial congruence using nulls models	Groups of grid cells	Mast and Nyffeler (2003)
Combination of SIGnificant Co-Occurrence of Taxa and PAE	?	Grid cells	Evaluation of the significant spatial congruence using nulls models and clusters from an analysis of parsimony	Groups of grid cells	Giokas and Sfenthourakis (2008)
Nested Areas of Endemism Analysis	NAEA	Cladogram or minimal spanning network of geographic areas or grid cells, for example results of PAE	Values of within-clade distance (DC) and the nested clade distance (DN)	Clades of grid cells or areas	Deo and DeSalle (2006).
Network Analysis Method	NAM	Localities of occurrence	Identification and removal of intermediary species to segregate units of co-occurrence, using betweenness measure and clustering coefficient	Groups of localities and co-occurrence units	Dos Santos, Fernández, Cuezzo, and Domínguez (2008)
Geographic Interpolation of Endemism	GIE	Localities of occurrence	A Kernel index is indicator of the degree of species distribution overlap	Maps of kernel index density	Oliveira, Brescovit, and Santos (2015)
A grid-based protocol for delimiting AoEs using alternative criteria for the recognition of areas of endemism	?	Grid cells	Grid cells method combined with six qualitative criteria based on congruence	Cells and hypotheses of events	Da Silva, Pinto-da-Rocha, and DeSouza (2015)

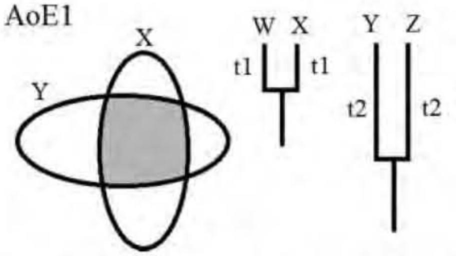

Fig. 2. An area of endemism defined by asynchronous and unrelated taxa (X–Y), with divergence times *t1* and *t2*, $\mathrm{AoE1} = X \cup Y$.

(3) An area of endemism with related synchronous taxa and unrelated synchronous taxa. The area is structured by at least four taxa with similar divergence time between pairs, such that they all form a single temporal stratus. Each pair is composed of sister taxa in the model $\mathrm{AoE3} = \{W,X\} \cup \{Y,Z\}$ or are composed of non-sister taxa in the model $\mathrm{AoE3}' = R \cup T \cup W \cup Z$ (Fig. 4).

(4) An area of endemism composed of one or more synchronous congruent endemic taxa and one or more asynchronous congruent endemic taxa. This model integrates at least three taxa; the synchronous subset is composed of sister taxa $\mathrm{AoE4} = \{W,X\} \cup Y$ or non-sister taxa $\mathrm{AoE4}' = T \cup X \cup Y$ (Fig. 5). This model explains the conformation of an area of endemism with multiple temporal strata.

In the literature there are several processes proposed to affect areas of endemism and their congruent endemic

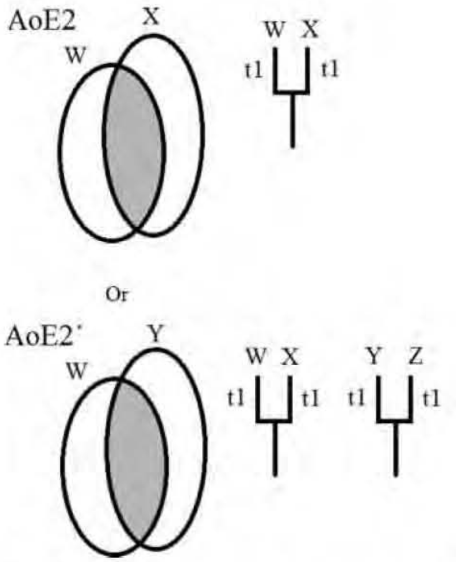

Fig. 3. Areas of endemism supported by synchronous related taxa (W–X) or synchronous unrelated taxa (W–Y). All of them have similar divergence time *t1*, $\mathrm{AoE2} = \{W,X\}$ or $\mathrm{AoE2}' = \{W,Y\}$.

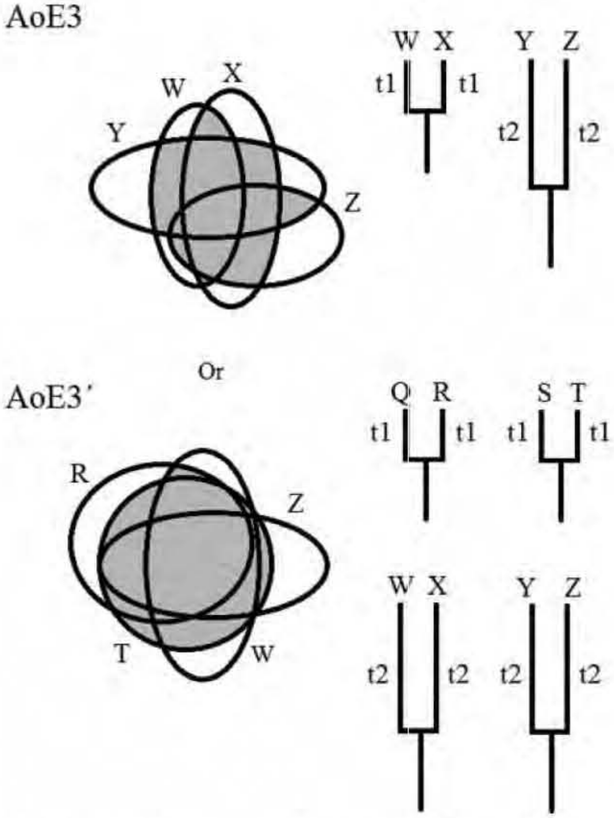

Fig. 4. Areas of endemism defined by related synchronous taxa and unrelated synchronous taxa, with divergence times *t1* and *t2*, $\mathrm{AoE3} = \{W,X\} \cup \{Y,Z\}$ or $\mathrm{AoE3}' = R \cup T \cup W \cup Z$.

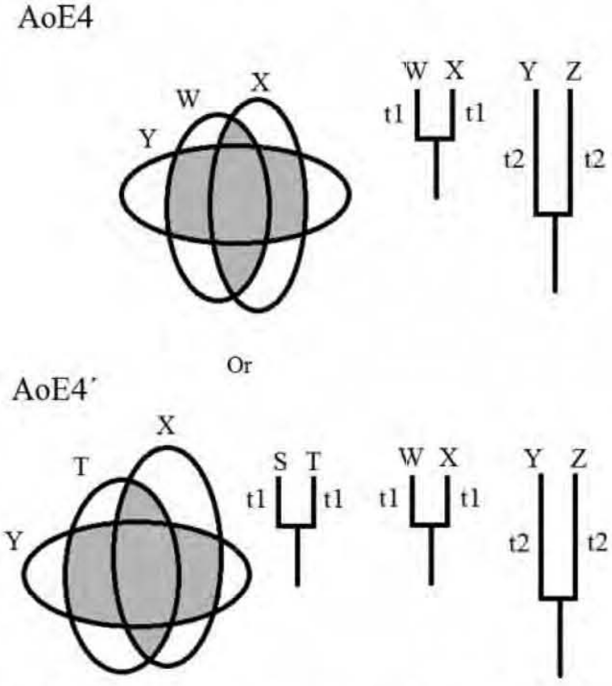

Fig. 5. Areas of endemism supported by one or more synchronous congruent endemic taxon and one or more asynchronous congruent endemic taxon, with divergence times *t1* and *t2*, $\mathrm{AoE4} = \{X,W\} \cup Y$ or $\mathrm{AoE4}' = T \cup X \cup Y$.

taxa. The dispersal of populations could cause a breakdown of the taxonomic composition (synchronous or asynchronous) and modify the shape of the areas of endemism (Fig. 2). Vicariance events (geological and/or ecological) could cause areas of endemism defined by synchronous taxa (Fig. 3). The process that explain the models detailed above are as follows: (i) the number and shape of areas of endemism may change due to the divergence of one species in an area; (ii) the percentage of spatial congruence may decrease due to the expansion of the distributional area of one or more of the congruent endemic taxa; (iii) the spatial congruence may decrease due to the contraction of the distributional area of a species whose range initially extended beyond the area; (iv) the area of endemism may shrink or disappear due to the extinction of an endemic species; and (v) the area of endemism may expand or contract due to the extinction within a specified area of one taxon that allows the expansion of a congruent endemic taxon (Anderson, 1994).

The simultaneous divergence and phylogeographic processes (migration, colonization, expansion) of the congruent endemic taxa in the above models can be tested, for example, employing Approximate Bayesian Computation (e.g., Chan, Brown, & Yoder, 2011). This method estimates divergence time based on the variation in effective population size among related and/or unrelated species pairs (Chan et al., 2011). Indeed, comparing divergence times using any statistical method would be a method for generating preliminary hypotheses about the historical integration of the congruent endemic taxa.

In general, areas of endemism are evolutionary entities. They evolve following the stages of their congruent endemic taxa (Fig. 2), and can be in a stable stage, a stage of expansion or contraction, of breaking off by vicariance, or geodispersal and extension of their endemic taxa. Moreover, the congruent endemic taxa form asynchronous or synchronous subsets (Temporal strata) and define the structure and nature of the areas of endemism.

Areas of endemism: boundaries and structure

Most areas of endemism are demarcated by physiographic barriers such as rivers (Cracraft, 1985; Haffer, 1978) and mountains (Müller, 1973). However, their boundaries are fuzzy due to the relationship between the distributional areas and the evolution of their taxa (Anderson, 1994; Cracraft, 1985; Harold & Mooi, 1994; Henderson, 1991).

Cracraft (1985), Haffer (1978), and Müller (1973) tackled the problem of the representation of areas of endemism in a practical way by merging distributional areas of the taxa and considering the zone of maximum overlap or congruence zones (distributional cores) as the boundaries of the pattern. Alternatively, the area can be defined as the distributional area of all of the congruent endemic taxa (Carine, Humphries, Guma, Reyes–Betancort, & Santos, 2009; Szumik et al., 2002). I consider that the distributional cores (Cracraft, 1985; Haffer, 1978; Müller, 1973), represent high congruence zones or high richness of congruent endemic taxa, and the zones outside of the congruence cores represent the dynamism of endemism (e.g., conceptual models; Anderson, 1994; Da Silva, Pinto-da-Rocha & DeSouza, 2015).

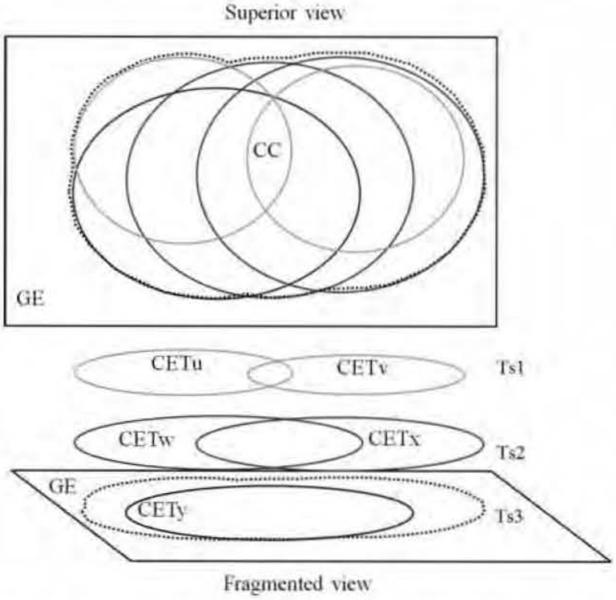

Fig. 6. Schematic overview of the structure and boundaries of an area of endemism defined by five congruent endemics taxa (CET: u, v, w, x, y). Fragmented view indicate how the congruent endemic species integrate three temporal stratus (ts). Dotted line indicates the area of endemism boundaries, congruence core (CC) is the zone with the highest congruence, and temporal stratus (Ts) are subsets of one or more synchronous endemic species. GE = geographic environment.

Therefore, the incorporation of the temporal dimension into the analysis of areas of endemism allows the redefinition of their structure as follows (Fig. 6): (i) hypothetical boundaries of the area of endemism or geographic environment composed by the merging of the distributional areas with one or more temporal strata (Ts), with spatial congruence and with or without synchrony; (ii) two or more synchronous or asynchronous congruent endemic taxa; and (iii) congruence core representing the high richness of congruent endemic taxa. The structure and boundaries of the area of endemism are hypotheses (Espinosa et al., 2001; Morrone, 2001; Nelson & Platnick, 1981), which must be tested with new data (Harold & Mooi, 1994), analysed with different methodological approaches, and generalized through comparisons against areas of endemism of other taxa (Morrone, 1994).

Andean Cordillera: an area of endemism and its temporal strata of mammals

The aim of the analyses presented here was to explore the structure of the Andean area of endemism (Aae) in mammals. The Aae is an important area of endemism and an interesting test of the framework proposed here because the development of the Andes has marked the divergence of many Neotropical and Andean mammals. The Andes have been the scene of diversification of mammals in the Neotropics due to their role as a distributional barrier and geodispersal path (Paterson, Solari, & Velazco, 2012). Uplift in the Central and Northern Andes was a process caused by plate tectonic readjustments. Plate subduction in the Pacific margin caused uplift in the Central Andes (Paleogene [~65 to 34 Ma]; Hoorn et al., 2010), and the subsequent collision of the Pacific plate (Neogene [~23 Ma]) with the South American and Caribbean plates resulted in intensified mountain building in the Northern Andes (Hoorn et al., 2010). Andean uplift affected the regional climate and the Neotropical landscape by reconfiguring drainage systems in South America, which are related with the evolution of Andean mammals.

I begin by extracting divergence time for Andean endemic species. I then describe the structure of the area of endemism comparing the divergence times of endemic taxa. Finally, I explore some models (Figs 2–5) of the possible evolutionary scenarios of the Aae to illustrate a straightforward example of the internal structure of areas of endemism.

Methods. I used Aae as described by Noguera-Urbano and Escalante (2015 [Ae14: northern South American transition zone]) as the biogeographic unit. The Aae was defined as the Central and Northern Andes, from the cordilleras of Venezuela and Colombia to southeastern Bolivia. The Aae was characterized by five endemic species, two rodents (Mountain Paca: *Cuniculus taczanowskii* [Stolzmann, 1885]; Golden Oldfield Mouse: *Thomasomys aureus* [Tomes, 1860]) and three marsupials (Andean White-eared Opossum: *Didelphis pernigra* J. A. Allen, 1900, Andean Slender Mouse Opossum: *Marmosops impavidus* Tschudi, 1845 and Sepia Short-tailed Opossum: *Monodelphis adusta* Thomas, 1897). I extracted the minimal, supported and maximal divergence times from ultrametric phylogenies of each endemic mammal (Table 2), which were drawn in a box plot to visualize the range of the divergence time and identify temporal strata.

The five endemic species of the Aae had historical and spatial congruence, since all of them evolved in South America (Table 2). Aae is composed of five asynchronous congruent endemic taxa (Fig. 7), which are non-sister species. This area of endemism agrees with the fourth model (see Fig. 5), indicating an area of endemism structured by multiple temporal strata. The boxplot indicated four temporal strata in the Aae (Fig. 7) that correspond with geological epochs (Ts1 = Pleistocene; Ts2 = Pliocene; Ts3 = Upper Miocene; Ts4 = Lower Miocene). Although the five endemic mammals are associated with the Andean Cordillera, the temporal strata correspond to several episodes in the evolution of the Andes (Fig. 7). Ts1 and Ts2 evolved during intensified mountain building in the Eastern Cordillera (Fig. 7), Ts3 evolved when the Eastern Cordillera mountain building had just begun. Ts4 evolved when the Northern Andes were younger, at the same time as the Central Andes were undergoing intensified mountain building. Three temporal strata (Ts1, Ts2, Ts3) correspond with the most intense peaks of Andean mountain building during the late middle Miocene (~12 Ma) and early Pliocene (~4.5 Ma) (Hoorn et al., 2010).

With respect to the endemic species, *M. impavidus* (Ts1) inhabits Andean forest and probably evolved in the South American moist forest by parapatric speciation (Jansa, Barker, & Voss, 2013). It might have colonized Andean lands during the late Pleistocene by accumulating genetic changes through climatic oscillations. In another hand, *T. aureus* and *C. taczanowskii* (Ts2) evolved at a similar time (Fig. 7, Table 2) and are restricted to the Andes. While at present *T. aureus* occupies the middle and higher altitude Andean lands, its ancestral distribution

Table 2. Phylogenetic information of the endemic congruent taxa that compose the Andean area of endemism. Ma is million years before present.

Divergence time (Ma.)	*Thomasomys aureus*	*Cuniculus taczanowskii*	*Didelphis pernigra*	*Marmosops impavidus*	*Monodelphis adusta*
Maximal	3.8	6	19.8	0	28
Supported	3.1	3.8	10.3	2.5	20.5
Minimal	2.2	2	9	0	14
Hypothetical ancestral area	South America	Andes- Amazonia	South America	South America	South America
Reference	Parada, D'Elía, and Palma (2015)	Upham and Patterson (2012)	Lim (2012)	Jansa, Barker, and Voss (2013)	Vilela, de Oliveira, and de Moraes (2015).

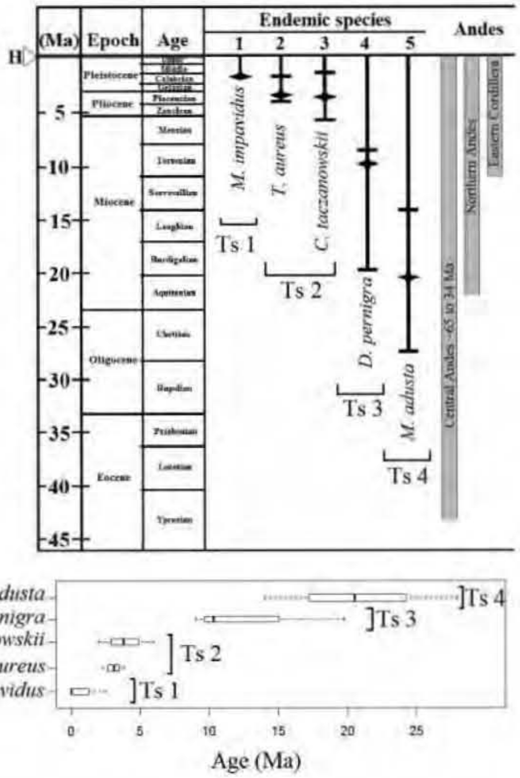

Fig. 7. Timescale of Andean area of endemism (Aae) and their endemic mammal summarizing the timespans, Andes uplift, their temporal structure (Temporal strata is Ts) and a boxplot used to define the Ts. H = Holocene.

may be the Andes lowlands (Parada, D'Elía, & Palma, 2015). Considering that *T. ladewi*, which is the sister species to *T. aureus*, is restricted to the Andean highlands of northwest Bolivia, this indicates that *T. aureus* evolved by parapatric speciation in the Andean ecosystems. In contrast, the hypothetical ancestral area of *C. taczanowskii* is the Amazonia region (Upham & Patterson, 2012). This suggests a dispersal event from the lowlands to the Andes, as has occurred in other taxa (Lim, 2012). Finally, at least two dispersal events probably occurred in the Aae: *M. adusta* (Ts3) migrated from the Central Andes to Northern Andes, and *D. pernigra* from the Central Cordillera (Northern Andes) to the Eastern Cordillera. Likely dispersal routes would include Andean vegetation along the Ecuador and Colombia Mountains, which in some periods of the Middle and Late Miocene would have formed a widespread forest (Simpson, 1975).

The evolution of the Andes (Andean uplift and orogeny, climatic variations) has produced renewed accommodation space and spatial integration of species. Thus, the five species of mammals have been integrated within a biogeographic unit named Aae in four temporal strata. Apparently, the processes that produced the spatial integration of mammals within Aae were parapatric speciation followed by dispersal events (colonization of new geographic areas) through the Andes.

Conclusions

Areas of endemism are primary biogeographic homology hypotheses. This means that they are a conjecture about the history of taxa that are spatiotemporally integrated in an evolutionary unit (i.e., biotic components, Morrone, 2001; or biotas, Morrone, 2014a). Therefore the structure and boundaries of the areas of endemism must be explained and tested.

The current conceptual framework of areas of endemism is based on spatial congruence, and the temporal relationship of the endemic congruent taxa was explored. In general, a better understanding of how to interpret areas of endemism could be gained by exploring the relationship of endemic species in the space and time dimensions, with phylogenetic information and identification of temporal strata. By applying this revised framework to explain the geographic integration in the Andean area of endemism, I conclude that within Aae the integration of species was due to parapatric speciation, followed by dispersal events through the Andes. Further study of this framework should contribute both to increased understanding of the processes that generate and maintain areas of endemism, and propose evolutionary scenarios of biodiversity.

Acknowledgements

I am profoundly grateful to David Espinosa Organista, Tania Escalante, Fernando Cervantes and Octavio Rojas for insightful comments that greatly helped me to improve this review. This paper constitutes a partial fulfilment of the requirements to obtain a doctoral degree from Posgrado en Ciencias Biológicas of the National Autonomous University of México (UNAM). I am also grateful to the Associate Editor and two anonymous reviewers for valuable comments on the manuscript. Special thanks to Lynna Kiere for reviewing the English writing of this manuscript.

Disclosure statement

No potential conflict of interest was reported by the author.

Funding

Funding was provided by the Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM) and the Consejo Nacional de Ciencia y Tecnología from México (CONACyT) (Doctoral scholarship 262582).

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Associate Editor: Sven Buerki

DISCUSIÓN GENERAL

El "*endemismo*" es un concepto ampliamente usado en variadas disciplinas de la ciencia, por ejemplo, en medicina, botánica, zoología, ecología, biología de la conservación y biogeografía. Este concepto generalmente se lo relaciona con exclusividad de un taxón a un área geográfica (Noguera-Urbano, 2017; Capítulo 1). Sin embargo, las propuestas prácticas u operativas del concepto han llevado a diferenciar variados enfoques (Noguera-Urbano, 2017; Capítulo 1). Lo cual ha llevado a la ambigüedad en la definición de las áreas de endemismo (AE), principalmente porque el endemismo se cuantifica con base en las áreas de distribución y en un único contexto temporal (Noguera-Urbano, 2017; Capítulo 1).

Al considerar que las AE son hipótesis o conjeturas sobre una historia biogeográfica común entre taxones (Morrone 2001), se debe asumir que hay otros factores que intervienen en su estructuración (Murray & Crother 2016). Dentro de los factores ecológicos se encuentran las variaciones de los regímenes climáticos, las cuales han afectado a las AE en el pasado (Gámez et al. 2014, Noguera-Urbano et al. Enviado; Capítulo 1). Ahora, si se consideran a las AE como comunidades debido a la integración de especies pertenecientes a múltiples linajes, la ecología de cada especie también puede afectar a las áreas de endemismo (Murray & Crother 2016, Noguera-Urbano et al. Enviado; Capítulo 1). Es decir, la dispersión o extinción de una o más especies endémicas puede ocasionar que la composición de las áreas de endemismo cambie y en consecuencia se alteren las dimensiones de las áreas de endemismo (Noguera-Urbano et al. Enviado; Capítulo 1).

Los factores históricos que afectan los cambios en el tamaño de las AE son: la edad del área de endemismo, la diversidad de atributos funcionales, representado en el número de especies y ordenes taxonómicos, y la diversidad filogenética (Noguera-Urbano et al. Enviado; Capítulo 1). Esto indica que las áreas de endemismo son altamente susceptibles a la integración de múltiples y asincrónicos linajes adaptados a condiciones ambientales o barreras geográficas similares (Cracraft 1985). Algunas tendencias encontradas en el análisis de factores históricos, como por ejemplo, la relación inversa entre el número de especies endémicas, edad y el tamaño del área, podrían indicar que la integración de especies es diferencial con respecto al a nivel biogeográfico (Noguera-Urbano et al. Enviado; Capítulo 1). A niveles jerárquicos mayores, como en subregiones y dominios, ocurre una integración de un número más alto de especies y con mayor edad que a nivel de provincia.

Por otra parte, se ha propuesto que las áreas de endemismo se estructuran por efecto de la posible respuesta simultánea y paralela de los taxones que las integran a factores históricos y ecológicos (Rosen 1988, Morrone 1994, Espinosa et al. 2001, Szumik et al. 2002). Esto resulta en AE que han persistido en el tiempo (Gámez et al. 2014, Noguera-Urbano et al. Enviado; Capítulo 1). Es decir, la integración de algunas especies endémicas perdura como patrón biogeográfico a pesar de las variaciones climáticas y muy posiblemente de otros fenómenos relacionados con la evolución de la tierra (Graham et al. 1996). Tal es el caso de las áreas de endemismos de los mamíferos neotropicales, las cuales posiblemente han cambiado de forma y tamaño a lo largo del tiempo, pero han persistido al menos desde el último periodo interglaciar. Por otra parte, los cambios de las AE han sido proporcionales a su tamaño. Es decir, AE pequeñas (provincias), tienden a tener menores pérdidas de área geográfica que aquellas de mayor tamaño (subregión, dominio) (Noguera-Urbano et al. Enviado; Capítulo 1). Esto probablemente se deba a que las AE de menor tamaño funcionen como refugios climáticos. En ellos el clima local está desacoplado del clima regional, así los hábitats conservan condiciones estrechamente relacionados con la topografía y los microclimas que son favorables para algunas especies (Keppel et al. 2012). Mientras, las AE de mayor tamaño, posiblemente presentan altas tasas de reducción de área por efecto del clima regional.

La respuesta a las variaciones del clima, de las especies en conjunto que conforman a las AE, las soporta como ensamblajes integrados en el espacio. Sin embargo, cuando se analizan posibles agrupamientos filogenéticos, las áreas de endemismo en su mayoría parecen que no siguen ninguna tendencia. Tan solo dos áreas de endemismo (Provincias del Bosque Magallánico y el sur de la Puna), presentaron especies altamente relacionadas en la filogenia. Esto se explica por la composición de cada una de las áreas de endemismo, ya que en ambas, las especies que las soportan son murciélagos y roedores que evolucionaron en el Neotrópico. Esto indica que en algunos casos, la integración de especies endémicas transciende al espacio, llegando a compartir una historia evolutiva común. Por otra parte, la ausencia de patrones de agrupamiento filogenético en la mayoría de áreas de endemismo, soporta la idea de que las especies endémicas representan linajes variados con múltiples adaptaciones que les permiten coexistir (Cracraft 1985).

Las AE están afectadas también por factores históricos y ecológicos a nivel regional. En el caso de la región Neotropical, los taxones endémicos (familias, géneros y especies), se integran conformando diferentes AE anidadas dentro de la región. Nueve AE componen a la región Neotropical, las cuales pueden ser diferenciadas por su composición de taxones y tamaño. En general parece ser que los límites de la región varían de acuerdo con la heterogeneidad del ambiente. Esto es evidente en el patrón de superposición de AE descrito en el Capítulo II, el cual indica que el tamaño de la región Neotropical tiende a reducirse al entrar en contacto con la región Neártica (norte) y la región Andina (sur). En los límites de la región Neotropical existen áreas de hibridación biótica o zonas de transición (Hershkovitz 1958, Morrone 2004), las cuales actúan como barreras a la dispersión de especies neotropicales. En el caso de la Zona de Transición Sudamericana, algunos análisis sobre la forma y extensión de las áreas de distribución de especies de mamíferos muestran que la topografía, las variaciones de la temperatura y la resistencia ambiental, pueden actuar como barreras a la dispersión de las especies neotropicales (Ruggiero et al. 1998). Por otra parte, hay una tendencia a la reducción del endemismo Neotropical desde el norte y sur del continente, encontrándose una mayor concentración sobre la línea Ecuatorial. Este patrón macroecológico es similar al que se ha descrito para correlacionar la riqueza de especies o diversidad filogenética con la latitud (Capítulo II). Algunas explicaciones para dicho patrón son altas tasas de especiación, bajas tasas de extinción, múltiples eventos de dispersión, y alta estabilidad climática de los mamíferos y otros grupos en zonas tropicales (Pianka 1966, Rolland et al. 2014).

Con respecto a los factores históricos que explican la estructuración de la región Neotropical con base en AE de mamíferos, la integración de los taxones es diferencial al igual que en áreas de menor escala (ej. Provincias, Capítulo I). Es decir, las especies endémicas representan linajes que evolucionaron asincrónicamente. A nivel regional, los murciélagos nuevamente representan el mayor número de especies endémicas, y esto produce que la estructura filogenética de la región Neotropical se presente como un patrón de agrupamiento (especies cercanamente emparentadas), debido a procesos como especiación *in situ* y conservadurismo de nicho, como se ha propuesto para otros grupos de mamíferos (ej. Cardillo & Mijaard 2010, Cardillo 2011). En consecuencia, los mamíferos endémicos de la región Neotropical se encuentran espacialmente y filogenéticamente integrados. El agrupamiento filogenético de las especies endémicas también podría indicar que ellas se han expandido rápidamente desde su proceso de especiación (Cardillo 2011, Cantalapiedra et al. 2014), como lo sugieren múltiples eventos de dispersión de mamíferos a lo largo de los Andes y otras zonas de América del Sur (Parada et al. 2015; Rojas et al. 2016). Además, la descripción de cinco cenocrones (Americano, Antillano, Centroamericano, Norteamericano y Norte-Centroamericano), soportan la idea de que las especies endémicas se han integrado espacio-temporalmente como en una unidad evolutiva (región Neotropical), como ha sido sugerido por Hershkovitz (1969) y Webb (1991).

Al avanzar en la interpretación de las tendencias generales de las asociaciones entre AE, los resultados del Capítulo III en su primera parte, indican que las AE tienen una conglomeración espacial, relacionada principalmente con lugares de alta heterogeneidad ambiental y topográfica. Dos de ellos se encuentran cercanos o sobre las Zonas de Transición Mexicana y Suramericana, mientras que un sector con un elevado número de áreas de endemismo se describe como zona de integración del Bosque Atlántico (Brasil). Como se mencionó en el Capítulo I, hay tendencias generales del efecto del clima sobre áreas de endemismo menores, lo que se puede generalizar también a nivel regional, ya que algunos parámetros climáticos como la isotermalidad, la heterogeneidad topográfica y la precipitación en la época más caliente, afectan de una manera equivalente tanto a la Zona de Transición Sudamericana como a la Mexicana. En la zona de integración del Bosque Atlántico la heterogeneidad climática y la precipitación en la época más caliente presentan el mayor efecto. Los resultados demuestran la existencia de un grupo similar de variables ambientales relacionadas con la concentración de AE. Sin embargo, la heterogeneidad topográfica tiene mayor efecto sobre las dos zonas de transición, mientras que la zona de integración del Bosque Atlántico es altamente dominada por variables climáticas.

Finalmente, las AE representan unidades ecológicas y evolutivas que son dinámicas, sin importar el tamaño que ellas presenten. Aunque los límites o su relación con otras áreas de endemismo cambien por influencia por ejemplo del clima (Capítulos I y II) o el efecto de la evolución de las especies y la tierra (Capítulos I, II y II), las AE tienen a conservar un núcleo, que definí como zona de máxima superposición, compuesto por la intersección del mayor número de áreas de distribución, el cual tiende a persistir en el tiempo. Tradicionalmente, el análisis de la dimensión espacial en las áreas de endemismo ha llevado a que se descuide el análisis de las otras dimensiones como el tiempo y la forma. Sin embargo, en el presente documento de tesis se comprueba que las áreas de endemismo pueden ser el resultado de la integración filogenética y temporal de las especies endémicas.

Con respecto a la integración temporal, múltiples grupos de especies endémicas pueden representar múltiples estratos temporales, algunos de ellos son sincrónicos mientras que otros son asincrónicos y con relaciones filogenéticas lejanas (Capítulo III). La divergencia simultánea y los procesos filogeográficos (migración, colonización, expansión) de las especies endémicas en los modelos propuestos en el Capítulo III, requieren ser explorados a una escala de poblaciones, con el fin de incrementar evidencias sobre la integración y dinámica de las especies endémicas. Por ejemplo, en el AE correspondiente a los Andes del norte y centro (Venezuela hasta el sureste de Bolivia; Noguera & Escalante 2015), las especies endémicas se encuentran actualmente integradas en el espacio, pero sus edades demuestran que evolucionaron de manera independiente en un intervalo temporal compuesto por al menos cuatro épocas (Oligoceno, Mioceno, Plioceno, Pleistoceno), con tan solo dos especies (*Thomasomys aureus* y *Cuniculus taczanowskii*) que probablemente evolucionaron en la misma época (Plioceno). Sin embargo, los análisis independientes de los eventos evolutivos de cada especie endémica, demuestran que el levantamiento de los Andes ha ocasionado un reacomodamiento del espacio y también la integración de las especies en el área de endemismo andina. En este caso los posibles eventos que produjeron la integración se relacionan con especiación parapátrida seguida por eventos de dispersión en los Andes (Capítulo III).

CONCLUSIONES GENERALES

- El término *área de endemismo* se refiere a un patrón de distribución geográfica que involucra restricción, integración temporal de los taxones y una historia evolutiva común. Sin embargo, la dinámica de las distribuciones geográficas de las especies y los métodos con que se estimen pueden producir sesgos en la identificación e interpretación de los patrones de endemismo.
- Las respuestas individuales de las especies endémicas a factores históricos y ecológicos hacen que las áreas de endemismo sean dinámicas a cualquier nivel biogeográfico, pero como generalidad persisten a lo largo del tiempo.
- Las áreas de endemismo de los mamíferos neotropicales a nivel biogeográfico, están afectadas en su forma, tamaño y estructura por atributos como: el número de especies que las caracteriza, la edad de esas especies, el número de órdenes taxonómicos, la heterogeneidad topográfica, la heterogeneidad climática y la latitud.
- La generalidad de las áreas de endemismo a escala de subregión y provincia es la ausencia de agrupamientos filogenéticos entre especies endémicas. Lo cual indica que ellas representan linajes distantes entre sí, cuya integración puede ser sincrónica o asincrónica de diversos linajes.
- La región Neotropical presentó agrupamiento filogenético, debido a que muchas de las especies endémicas pertenecen a linajes que evolucionaron en América.
- El espacio ha sido la dimensión principal de análisis en las áreas de endemismo. Por lo tanto, se propuso que el tiempo puede ser otra dimensión que permita caracterizarlas. Al incluir el tiempo, se pone en evidencia que las especies endémicas pueden presentar diferentes tiempos de integración. Ya que los procesos evolutivos y biogeográficos producidos por la unión de los continentes (ej. Gran Intercambio Biótico Americano), levantamiento de montañas (ej. formación de los Andes), formación de ríos, etc. influyeron diferencialmente en las especies endémicas y su dinámica espacial.
- Las áreas de endemismo están afectadas tanto por factores biológicos, ecológicos y filogenéticos, a cualquier nivel dentro de la jerarquía biogeográfica. Por lo tanto, las áreas de endemismo persisten en el tiempo, pero son dinámicas y evolucionan con la tierra.

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