



Doctorado en Ecología, Conservación y Restauración de Ecosistemas

**Dinámicas espacio-temporales en la distribución  
geográfica global de mamíferos terrestres y marinos:  
efectos ambientales y humanos a escala  
macroecológica**

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Que el trabajo descrito en la presente memoria, titulado “Dinámicas espacio-temporales en la distribución geográfica global de mamíferos terrestres y marinos: efectos ambientales y humanos a escala macroecológica”, ha sido realizado por D. Erik Joaquín Torres Romero dentro del Programa de Doctorado Ecología, Conservación y Restauración de Ecosistemas (D 330), reúne todos los requisitos necesarios para su aprobación como Tesis doctoral, por acuerdo del Consejo de Departamento celebrado el día de Junio 2015

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Móstoles, 28 de mayo de 2015

Miguel Ángel Olalla Tárraga

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## RESUMEN

En los dos últimos siglos, las presiones antrópicas junto con la variabilidad climática han aumentado de manera espectacular y se han convertido en uno de los principales motores de cambio de la biodiversidad, siendo ya perceptibles a muchos niveles. Por tanto, es primordial documentar la medida en que la distribución geográfica de las especies y sus rasgos biológicos están relacionados con ciertos parámetros ambientales y antrópicos, así como evaluar si estas relaciones muestran algún tipo de patrón, tal y como se esperaría de acuerdo con reglas ecogeográficas clásicas. La macroecología, como disciplina científica en auge en los últimos veinticinco, permite entender los patrones geográficos de organización y funcionamiento de los ensamblajes de especies a grandes escalas espaciales. En concreto, esta tesis doctoral pretende evaluar la validez de algunas de las reglas ecogeográficas que han provocado mayor interés dentro de la biogeografía y la macroecología y avanzar en el conocimiento sobre qué factores son los determinantes del gradiente latitudinal de riqueza de especies, tamaño corporal y tamaño de rango geográfico en faunas regionales y globales de mamíferos terrestres y marinos. A nivel metodológico se emplean Sistemas de Información Geográfica y herramientas estadísticas para realizar análisis interespecíficos de patrones macroecológicos (basados en ensamblaje y entre-especies). Asimismo, se aplican técnicas que controlan la autocorrelación espacial y filogenética en los datos y se implementa un innovador método de análisis de rutas filogenéticas. Nuestras conclusiones revelan que la evapotranspiración real es el principal motor de riqueza de especies de mamíferos terrestres a nivel global y que las zonas del planeta más accesibles para los humanos presentan una menor riqueza de especies. Por otra parte, en el Néartico y Paleártico Occidental las zonas que han permanecido climáticamente más inestables a lo largo de los últimos 20000 años, aunque albergan especies de amplia distribución geográfica, poseen igualmente una menor riqueza de especies de mamíferos terrestres. La inestabilidad climática tiene además un efecto sobre la distribución geográfica y el tamaño corporal de mamíferos terrestres de América del Norte, no así para la región Paleártica Occidental. En mamíferos marinos, de acuerdo con la hipótesis de conservación de calor, la temperatura del mar en superficie es fundamental para explicar los patrones globales de variación interespecífica en el tamaño corporal. Finalmente, a través de un novedoso análisis de rutas filogenéticas, identificamos el nicho climático de las especies de mamíferos como el principal factor determinante de sus rangos de distribución geográfico a escala global. El tamaño corporal, la amplitud de nicho trófico

o el impacto humano tuvieron una importancia secundaria sobre los rangos de distribución de mamíferos en su conjunto, pero fueron muy relevantes para explicar los patrones de ciertos órdenes taxonómicos.

**Palabras Clave:** Escala espacial, Impacto humano, Macroecología, Macroclimas, Mamíferos terrestres y marinos, Reglas ecogeográficas.

# Capítulo 1

## Introducción General

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## INTRODUCCIÓN

La macroecología es una de las más interesantes e importantes áreas de investigación dentro de las disciplinas de la biología y ecología y ha recibido una mayor atención por la comunidad científica en las últimas décadas. Hoy en día, la macroecología ha pasado de ser un tema de la periferia al centro del pensamiento ecológico, por lo menos así lo demuestra el número creciente de publicaciones, libros y reuniones que ponen de manifiesto a la macroecología como una disciplina en amplio crecimiento. Aunque sus raíces son más antiguas, sus orígenes se remontan a hace más de dos décadas desde que Brown y Maurer (1989) acuñaron por primera vez el término 'macroecología' en la revista *Science*. Posteriormente Brown amplió el término en su libro "Macroecology" (1995), para referirse a un programa de investigación emergente centrado a estudiar los patrones de la distribución y abundancia de los ensamblajes de especies a grandes escalas espaciales y temporales. En esencia la macroecología es una disciplina alternativa observacional y no experimental, que propone una nueva manera de ver y resolver los problemas de la ecología tradicional. En la actualidad el efecto del cambio climático, impacto humano, pérdida de hábitat y fragmentación son los

principales motores de cambio de la biodiversidad originando que un gran número de organismos se encuentren en peligro y otras estén extintas. Estos problemas de cambio fundamentalmente operan a escalas regionales y globales y no pueden ser enfrentados solamente por los experimentos ecológicos tradicionales. Por tanto, el interés actual en la macroecología podría radicar en tres razones. Primero, propone un enfoque innovador a nivel macroscópico lo que hace posible comprender qué factores (bióticos o abióticos, actuales o históricos) determinan las dinámicas espaciales y temporales en la composición, estructura y ensamblaje de las biotas regionales y continentales. Segundo, tiene la capacidad de forjar uniones con otras disciplinas como la biogeografía, paleobiología o macroevolución. Tercero, con el desarrollo de la tecnología entre la que destacan la Teledetección y los Sistemas de Información Geográfica (SIG), además de la disponibilidad de bases de datos sobre sus rasgos biológicos y distribución geográfica de las especies, han servido como complemento para entender cómo funcionan e interactúan las especies a grandes escalas espaciales y temporales. Es así como la macroecología ha contribuido a



mejorar nuestra comprensión sobre los patrones y procesos ecológicos de la biodiversidad convirtiéndola en una disciplina de investigación en auge (Olalla-Tárraga 2014).

### **Escala espacial y su importancia en el análisis**

En general, biogeógrafos y ecólogos reconocen que los procesos ecológicos actúan a diferentes escalas espaciales (Turner y Tjørve 2005), y por lo tanto los patrones detectados y sus procesos subyacentes normalmente serán dependientes de la escala de análisis (Willig et al. 2003). Además, la influencia de factores ambientales y/o antrópicos operan a diferentes escalas, lo que podría conducir a resultados diferentes. Esto es posible porque las variables predictoras son procesadas a distintas resoluciones espaciales, y por tanto los patrones detectados se ven afectados por la escala de estudio (Willig et al. 2003). El concepto de escala espacial se ha utilizado tradicionalmente en macroecología para referirse tanto a la resolución espacial (el tamaño de grano), como la extensión geográfica (área de estudio) (Rahbek 2005). El primero se refiere al tamaño de la unidad de muestreo (por ejemplo, las cuadrículas geográficas, transectos o tamaño del píxel), mientras que el segundo se refiere a la extensión definida como la dimensión

espacial máxima cubierta por la muestra (Wang et al. 2012). Irónicamente o inevitablemente, dependiendo de la perspectiva, la crítica más directa en macroecología ha sido el tamaño de la “escala espacial”. Sin embargo este debate ha sido en gran parte a través de estudios macroecológicos en dominios terrestres que argumentan que una resolución espacial de 0.5°, 1° ó 2° (aproximadamente 50 km x 50 km, 100 km x 100 km y 200 km x 200 km) es lo suficientemente fina como para capturar los detalles acerca de las variaciones de la diversidad, y lo suficientemente gruesa para no comprometer la fiabilidad de las medidas de la diversidad biológica (Hurlbert y Jetz 2007; Hortal 2008). Sin embargo, los estudios sobre la biodiversidad marina mundial se realizan en tamaños de grano más gruesos, por ejemplo 800 x 800 km (Tittensor et al. 2010). No obstante, los estudios macroecológicos con un tamaño de grano grande, y cubriendo una gran extensión espacial aún son escasos (Beck et al. 2012). Por tanto, no existen pautas universales para explorar y decidir sobre cuál es el mejor tamaño de grano para analizar diferentes tipos de datos a gran escala, más bien, depende del taxón de estudio, disponibilidad de bases de datos, recursos computacionales, propósito del estudio en cuestión, así

como la interpretación de los resultados obtenidos.

### **Reglas ecogeográficas**

Debido a que las especies tienden a presentar diferentes patrones de variación en sus rasgos biológicos a grandes escalas espaciales o regionales, documentar estos gradientes geográficos y sus posibles mecanismos subyacentes ha sido una prioridad para los científicos naturalistas desde el siglo XIX. Por ello, biogeógrafos y ecólogos han sugerido una serie de “reglas ecogeográficas” que tratan de encapsular las respuestas de la fauna y flora a las influencias de factores ambientales (McDowall 2008). Por ejemplo, la regla de Allen (1878) establece que en organismos endotérmicos los apéndices tienden a ser más cortos hacia climas más fríos, por otro lado la regla de Gloger (1833) propone que la pigmentación en los individuos es más oscura en ambientes más húmedos, mientras que la regla de Jordan (1892) describe que el número de vertebras en peces marinos aumenta con la latitud. Otras reglas de tipo evolutivo como la de Cope (1887) argumentan que los linajes de animales tienden a evolucionar hacia tamaños más grandes con el tiempo. Sin embargo, la regla del gradiente latitudinal de riqueza de especies, la regla de

Bergmann y la regla de Rapoport son las reglas ecogeográficas que, históricamente y a lo largo de los últimos años, han atraído una mayor atención de los investigadores y que han proporcionado avances fundamentales en nuestra comprensión de los patrones de variación geográfica y morfológica de las especies a grandes escalas. La primera establece que la riqueza de especies tiende a concentrarse en regiones tropicales y va decreciendo a medida que avanzamos hacia los polos. Este es con certeza el patrón más antiguo que se conoce en Ecología (Hawkins 2001; Turner 2004). Por otro lado, la regla de Bergmann fue propuesta para explicar un patrón general en el aumento de tamaño corporal al aumentar la latitud en comparación con las especies que viven en las regiones más cálidas y en altitudes más bajas (Bergmann 1847, Mayr 1956). Finalmente la regla de Rapoport describe una relación positiva entre el tamaño del área de distribución geográfica de las especies con el aumento de la latitud (Stevens, 1992). Sorprendentemente, la validez a gran escala de estas tres reglas ecogeográficas más estudiadas (gradiente latitudinal, regla de Bergmann o regla de Rapoport) y sus posibles procesos ecológicos y evolutivos subyacentes aún no han sido exploradas para la mayoría de los taxones de plantas y animales, sobre

todo a escala global. En este sentido, es necesario no sólo describir los patrones, sino profundizar nuestro conocimiento sobre las causas de la distribución geográfica de los ensamblajes de las especies a gran escala.

### **Objetivo general**

En los dos últimos siglos, las presiones antrópicas junto con la variabilidad climática han aumentado de manera espectacular y se han convertido en unos de los principales motores de cambio de la biodiversidad, siendo ya perceptibles a muchos niveles. Por tanto, se considera primordial documentar la medida en la que la distribución geográfica de las especies y sus rasgos biológicos están relacionados con ciertos parámetros ambientales y antrópicos, y si estas eventuales relaciones siguen algún tipo de patrón (como el esperado por las reglas ecogeográficas tradicionales). Estas reglas son relevantes para comprender y explicar los patrones de la distribución de las especies, así como describir los mecanismos subyacentes y las posibles respuestas a factores humanos y ambientales actuales e históricos, así como la historia evolutiva de los organismos. De esta forma el objetivo general de este trabajo es explorar la validez de las reglas ecogeográficas anteriormente

mencionadas en mamíferos terrestres y marinos a diferentes escalas espaciales. En concreto, se usará un enfoque metodológico comúnmente utilizado en macroecología (análisis de ensamblaje y entre-especies), y un posterior enfoque innovador basado en un análisis de rutas filogenéticas (Phylogenetic Path Analysis) combinado con el uso de diferentes modelos estadísticos y Sistemas de Información Geográfica (GIS), para evaluar algunas de las reglas ecogeográficas que han provocado mayor interés dentro de la macroecología (es decir, la riqueza de especies, el tamaño corporal y rango geográfico).

### **Objetivos específicos**

La presente Tesis Doctoral se encuentra estructurada en seis capítulos, un capítulo introductorio, seguido de cuatro capítulos en formato de artículos científicos en inglés con sus correspondientes secciones de introducción, material y métodos, resultados y discusión y, en el último capítulo se exponen las conclusiones generales de esta tesis doctoral. De los cuatro trabajos en formato de artículo, dos han sido ya aceptados en revistas internacionales con alto índice de impacto (*Journal of Animal Ecology*, *Global Change Biology*), mientras que los siguientes dos manuscritos han sido

enviados de igual manera a revistas internacionales con alto índice de impacto y se encuentran en proceso de revisión (*Global Ecology and*

*Biogeography, Basic and Applied Ecology*). La estructura de cada capítulo se expone a continuación.

	<b>Patrón de diversidad estudiado</b>	<b>Escala espacial</b>	<b>Grupo taxonómico</b>	<b>Resultados</b>
Capítulo 1	Introducción general			
Capítulo 2	Riqueza de especies	Global	Mamíferos terrestres	Torres-Romero & Olalla-Tárraga 2015 ( <i>Journal of Animal Ecology</i> )
Capítulo 3	Rasgos de historia de vida	Región Holártica	Mamíferos terrestres	Torres-Romero et al. 2015 ( <i>Basic Applied and Ecology</i> , en revisión)
Capítulo 4	Tamaño corporal	Global	Mamíferos marinos	Torres-Romero et al. 2015 ( <i>Global Ecology and Biogeography</i> , en revisión)
Capítulo 5	Rango geográfico	Global	Mamíferos terrestres	Olalla-Tárraga et al. 2015 ( <i>Global Change Biology</i> )
Capítulo 6	Conclusiones generales			

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## Capítulo 2

Desenredando los efectos humanos y ambientales sobre los gradientes geográficos de la riqueza de especies de mamíferos: una evaluación global y regional

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Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Torres-Romero E.J, Olalla-Tárraga M.A (2015) Untangling human and environmental effects on geographical gradients of mammal species richness: a global and regional evaluation. *Journal of Animal Ecology*, 84, 851–860.

# Untangling human and environmental effects on geographical gradients of mammal species richness: a global and regional evaluation

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## Summary

1. Different hypotheses (geographical, ecological, evolutionary or a combination of them) have been suggested to account for the spatial variation in species richness. However, the relative importance of environment and human impacts in explaining these patterns, either globally or at the biogeographical region level, remains largely unexplored.

2. Here, we jointly evaluate how current environmental conditions and human impacts shape global and regional gradients of species richness in terrestrial mammals.

3. We processed IUCN global distributional data for 3939 mammal species and a set of seven environmental and two human impact variables at a spatial resolution of  $96.5 \times 96.5$  km. We used simple, multiple and partial regression techniques to evaluate environmental and human effects on species richness.

4. Actual evapotranspiration (AET) is the main driver of mammal species richness globally. Together with our results at the biogeographical realm level, this lends strong support for the water-energy hypothesis (i.e. global diversity gradients are best explained by the interaction of water and energy, with a latitudinal shift in the relative importance of ambient energy vs. water availability as we move from the poles to the equator).

5. While human effects on species richness are not easily detected at a global scale due to the large proportion of shared variance with the environment, these effects significantly emerge at the regional level. In the Nearctic, Palearctic and Oriental regions, the independent contribution of human impacts is almost as important as current environmental conditions in explaining richness patterns. The intersection of human impacts with climate drives the geographical variation in mammal species richness in the Palearctic, Nearctic and Oriental regions. Using a human accessibility variable, we show, for the first time, that the zones most accessible to humans are often those where we find lower mammal species richness.

**Key-words:** human accessibility, human footprint, macroclimate, macroecology, terrestrial vertebrates, water–energy dynamics

## Introduction

The spatial distribution of organisms is not stochastic, but the result of the complex interaction of ecological, geological and evolutionary processes that shape the structure of each community (Brown 1995; Rickart 2001). Thus, a central question in biogeography and macroecology is to understand the spatial patterns of species richness.

Richness, defined as the number of coexisting species in a community, is the most often used biodiversity indicator in these disciplines. Documenting species richness patterns and identifying possible underlying mechanisms has been a priority for natural scientists ever since the times of Von Humboldt in the 19th century (Hawkins 2001). A particular emphasis has been placed in understanding the causes of the latitudinal gradient of species diversity (i.e. the decrease in species numbers as we move polewards from the tropics). Complex diversity gradients have been documented at a global scale, and a number of ecological,

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geographical and evolutionary hypotheses have been adduced to account for the observed patterns (Hawkins *et al.* 2003a). Global species richness gradients have been documented for different terrestrial vertebrate taxa, including birds (Hawkins, Porter & Diniz-Filho 2003b; Jetz *et al.* 2012), mammals (Ceballos *et al.* 2005; Ceballos & Ehrlich 2006; Schipper *et al.* 2008; Davies *et al.* 2011), amphibians (Buckley & Jetz 2007; Gouveia *et al.* 2013) and reptiles (Terribile *et al.* 2009). Recently, Qian (2010) compared environment–richness relationships for these terrestrial vertebrate classes at regional to global scales using ecoregion level data. Similarly, Jetz & Fine (2012) have evaluated the relative importance of current and past climates in determining species richness of mammals, birds and amphibians in 32 bioregions world-wide. As a whole, mammal species richness patterns and their possible causes have been extensively studied at the biogeographical realm level, with studies available for the Western Palearctic (Whittaker, Nogués-Bravo & Araújo 2007; Flojgaard *et al.* 2011), Nearctic (Badgley & Fox 2000; Hawkins & Porter 2003) and Afrotropical (Andrews & O'Brien 2000) regions. Hypotheses related to climate (current and past), habitat heterogeneity, historical and evolutionary processes have all been identified as plausible explanations for broad-scale species richness gradients (Currie 1991; Andrews & O'Brien 2000; Hawkins *et al.* 2003a; Whittaker, Nogués-Bravo & Araújo 2007; Qian 2010; Jetz & Fine 2012; Gouveia *et al.* 2013). These macroecological investigations have greatly improved our understanding of the organization and functioning of species communities over large spatial scales.

On the other hand, several studies have used human population density as a proxy variable to incorporate the effects of human impacts on species richness patterns. At fine-grained spatial resolutions, most of these studies tend to detect a negative relationship between human impact and species richness, which is often mediated through habitat loss and competition for space (see e.g. Luck *et al.* 2004 for reptiles, Koh, Lee & Lin 2006 for birds or Pillsbury & Miller 2008 for anuran). McKinney (2008) documented negative human impacts on species richness for different taxa, including birds, mammals, reptiles, amphibians, plants and invertebrates. However, there is also some supporting evidence over the last decade for a positive correlation between human population density and species richness. Such a positive relationship does not seem to be region-specific, since it has been detected, for instance, in Africa (Balmford *et al.* 2001; Chown *et al.* 2003; Fjeldså & Burgess 2008), Asia (Lan & Dunbar 2000; Ding *et al.* 2006), Australia (Luck *et al.* 2004), Europe (Araújo 2003; Gaston & Evans 2004; Evans & Gaston 2005; Barbosa, Pautasso & Figueiredo 2013) or America (Real *et al.* 2003; Diniz-Filho *et al.* 2006; Vázquez & Gaston 2006). A classical explanation for these positive correlations is associated with historical human colonization patterns, primary productivity and habitat heterogeneity. The geographical overlap of species

richness hotspots and human settlements is usually mediated by the positive effects of climate diversity and primary productivity on species diversity, including humans (Vázquez & Gaston 2006). Although the human component should be considered an important factor when it comes to understanding geographical patterns of species distributions at large scales, as well as possible extinction events, the use of human impact variables in macroecological studies is still a challenge for two reasons. First, it is difficult to tease apart the independent effect of environmental and human variables (Araújo 2003). Secondly, and related to the above, the use of more complex variables beyond human population density is necessary to obtain more accurate assessments on the sign and magnitude of the relationships between humans and species richness. To overcome this limitation, some studies in macroecology (see e.g. Brooks *et al.* 2006; Nogués-Bravo *et al.* 2008) have assessed anthropogenic effects on species richness using a new variable: human footprint (Sanderson *et al.* 2002), a composite measure of human population density, land transformation, electrical power and road infrastructure. Nelson (2008) generated, through the combination of geographical information layers in GIS, a human accessibility variable that aims to synthesize the multidimensionality of human impacts. Human accessibility is computed using a cost-distance algorithm which calculates the travelling time between two locations on a regular raster grid. This variable is relevant at different spatial levels, from local development to global trade, and fills an important gap in our understanding of the spatial patterns of economic, physical and social connectivity (Nelson 2008). Its use in macroecological studies would contribute to complement the information provided by the human footprint and would be useful to more precisely characterize the relative roles of environment vs. humans as explanations of extant regional to global species richness patterns.

Here, we analyse mammal species richness gradients at the global and biogeographical realm levels to gain a better understanding on the relative importance of environmental variables and human impacts on the observed patterns. While mammals and birds are two groups that have received most of the attention in the macroecological literature, mainly due to the existence of readily available ecogeographical data for both taxa (Hawkins, Porter & Diniz-Filho 2003b; Ceballos *et al.* 2005; Ceballos & Ehrlich 2006; Schipper *et al.* 2008; Jetz *et al.* 2012), we still do not know the degree of generality of several biogeographical patterns globally and regionally, as well as the mechanisms responsible for these patterns. Our first goal is to determine, for both spatial scales, which are the main drivers of mammal species richness and, secondly, assess the combined effects and relative importance of climatic variables and human impact metrics (human footprint and accessibility). Globally, we expect a dominant contribution of the environment over human factors (Hawkins *et al.* 2003a). We predict, however, that human

effects on richness gradients will be more easily detectable as we descend to the biogeographical realm level (i.e. decrease the spatial extent of the analysis). Similarly, we anticipate the detection of inter-regional differences (Pearson & Dawson 2003; Belmaker & Jetz 2011) that would be highly informative to better predict possible biotic responses under global change scenarios.

## Materials and methods

### GEOGRAPHICAL DISTRIBUTION DATA FOR MAMMALS

Range maps were obtained from the IUCN Red List (<http://www.iucnredlist.org>, accessed in March 2012, Schipper *et al.* 2008). All islands, including Australia, were excluded to avoid possible island effects. Data were collected for a total of 3939 mammal species at the global level, whose distribution ranges were overlapped to obtain a global species richness map. We excluded marine mammals, as well as the polar bear (*Ursus maritimus*), sea otter (*Enhydra lutris*), introduced and extinct species from the analysis. The maps were processed using ARCGIS 10.0 to extract species richness values in a global grid comprising of  $96.5 \times 96.5$  km cells with an equal-area Berhmann projection (*c.*  $1^\circ$  at the equator). After excluding islands and coastal cells comprising <50% of continental surface, we analysed a total of 13 842 cells globally. Each of these cells was classified according to the mammal zoogeographical regions defined by Cox (2001).

IUCN distribution maps are depicted as range maps and obtained through a minimum convex polygon estimation procedure and represent extents of occurrence. While these maps are widely used in macroecological studies (see e.g. Ceballos *et al.* 2005; Schipper *et al.* 2008; Fløjgaard *et al.* 2011), they are of limited use at more local scales. At spatial resolutions above  $100 \times 100$  km, results based on range maps and point locality data tend to converge. This scale is fine enough to capture details about diversity variations, and coarse enough for not to compromise the reliability of derived biodiversity metrics such as species richness (Hurlbert & Jetz 2007; Hortal 2008). At this scale, results are likely to be qualitatively similar to those obtained at larger grain sizes, whereas performing analyses based on finer grain sizes (e.g. a resolution of  $10 \times 10$  km) would require more detailed information on local scale processes such as biotic interactions or disturbance regimes (see e.g. Hurlbert & Jetz 2007; Hortal 2008). So far, numerous studies on the relationship between human impacts and species richness have been conducted at a spatial resolution of  $100 \times 100$  km for different geographical extents (Balmford *et al.* 2001; Chown *et al.* 2003; Luck *et al.* 2004; Diniz-Filho *et al.* 2006; Hortal 2008). We feel that our grain size is therefore not only enough to provide a wide geographical coverage, but also to present a neat description of large-scale biodiversity gradients and their determinants.

### ENVIRONMENTAL AND HUMAN VARIABLES

We used nine explanatory variables, seven describing ecogeographical conditions and two of them as descriptors of human impacts. Environmental variables were selected on the basis of their importance for terrestrial vertebrate distributions, as found in previous macroecological and biogeographical studies (Currie 1991; Araújo 2003; Hawkins *et al.* 2003a; Whittaker,

Nogués-Bravo & Araújo 2007; Fløjgaard *et al.* 2011; Jetz & Fine 2012), and were grouped according to the following hypotheses that may account for the variation in species richness:

- 1 Energy: Species richness in terrestrial vertebrates has often been found to increase with environmental energy availability (Currie 1991; see Evans, Warren & Gaston 2005; for a detailed review on the underlying mechanisms to species richness–energy relationships). We tested this hypothesis using potential evapotranspiration (PET) and mean annual temperature, widely used indicators of ambient energy (Currie 1991; Hawkins *et al.* 2003a; Fisher, Whittaker & Malhi 2011). PET was obtained from a global resolution of  $0.5^\circ$  interpolated from weather station data for the period 1961–1990 (New, Hulme & Jones 1999), whereas temperature was obtained with a resolution of 5 arcmin ( $=0.083^\circ$ ) from World-Clim (Hijmans *et al.* 2005).
- 2 Water: Having access to water sources can be a major limiting factor for species, especially in warmer tropical climates (Hawkins *et al.* 2003a). We obtained annual precipitation (Bio12) with a resolution of 5 arcmin ( $=0.083^\circ$ ) from World-Clim (Hijmans *et al.* 2005).
- 3 Water–energy: We used annual AET, a joint descriptor of water and energy availability in the environment that has been found to be a primary driver of species richness gradients in plants (O'Brien 1993) and animals (Hawkins *et al.* 2003a). AET, complementary to PET, is best understood as a water balance variable that does not only reflect climatologic regimes, but partly other aspects of the environment such as soil and vegetation cover (Fisher, Whittaker & Malhi 2011). AET was obtained with a resolution of  $0.5^\circ$  interpolated from weather station data for the period 1961–1990 (New, Hulme & Jones 1999).
- 4 Topography: We used range in elevation within cells, which is often used as an estimate of climatic variation at the meso-scale in similar broad-scale studies (Whittaker, Nogués-Bravo & Araújo 2007). Range in elevation was calculated as the difference between maximum and minimum elevations in each cell using elevation data from GTOPO30, a global elevation model with a resolution of  $1 \text{ km}^2$  (available at <http://www1.gsi.go.jp/geowww/globalmapgsi/gtopo30/gtopo30.html>).
- 5 Primary productivity: Higher primary productivity levels can favour higher species richness (Hawkins *et al.* 2003a). We used a global vegetation index, annual NDVI calculated from monthly values for the period 1982–2000 with a resolution of 5 arcmin ( $=0.083^\circ$ ) (available at <http://edit.csic.es>), as a proxy variable for primary productivity. Annual integral values of NDVI are strongly correlated with net primary productivity (Schloss *et al.* 1999) and, hence, a commonly used surrogate for primary productivity in macroecological studies (see e.g. Cusens *et al.* 2012).
- 6 Human Impact: To account for human effects on species richness, we used the human footprint (Sanderson *et al.* 2002) and human accessibility (Nelson 2008) indices. The first one, with a resolution of 1 km, integrates human population density, land use and infrastructure (Sanderson *et al.* 2002, available at: <http://www.ciesin.columbia.edu/>). The second one represents the estimated travel time in hours via land or sea routes, and shows how accessible or isolated are different parts of the world (Nelson 2008).
- 7 Habitat diversity. Habitat diversity may contribute to increased species richness (Currie 1991) and was calculated here as the number of co-occurring ecoregions in a particular

cell. We used the Olson *et al.* (2001) classification of ecoregions.

#### DATA ANALYSIS

We used simple and multiple regressions to examine the relationship between species richness and explanatory variables. In the presence of spatial autocorrelation, and to obtain unbiased estimates of the levels of significance in simple regressions, we used the modified *t*-test of Dutilleul (1993), which calculates the geographically effective degrees of freedom using spatial correlograms. We then evaluated the relative support for each hypothesis using OLS multiple regressions. This is a commonly used linear regression method in geographical ecology that provides unbiased estimates of regression slopes in the presence of spatial autocorrelation (Hawkins 2012). However, following Bini *et al.* (2009), we compared standardized regression coefficients between spatial and non-spatial (OLS) models to assess possible rank shifts. The former models were built using spatial eigenvector mapping (SEVM), an efficient technique to reduce residual autocorrelation in multiple regression models and remove spatial trends in a response variable (see Diniz-Filho & Bini 2005; Dormann *et al.* 2007 for further details). We calculated spatial filters according to the methods described in Diniz-Filho & Bini (2005) and Dormann *et al.* (2007) and selected them using the criterion defined by Griffith & Peres-Neto (2006) of selecting eigenvectors that minimize Moran's *I* in regression residuals (with a threshold of 0.05). We calculated filters separately for each biogeographical region, except for the Palearctic, which we divided into Occidental and Oriental for computational reasons.

Given the number of variables in our multiple regression models, we calculated variance inflation factors (VIF) to assess potential multicollinearity problems. A VIF value lower than 10 indicates that collinearity does not represent a major concern in the analysis (Olalla-Tárraga *et al.* 2009). We used an AIC-based information-theoretic approach to compare the fits of all possible combinations of explanatory variables and select the best-fit models (Burnham & Anderson 2002). It should be noted that such model-building strategy relies on a well-defined priori set of scientific hypotheses, so that data dredging is not an issue here. Since models other than just the estimated best model often contain valuable information, we used Burnham & Anderson's (2002) rule of thumb to identify those models with  $\Delta\text{AIC} < 2$ , which also have substantial support and should receive consideration in making statistical inferences. For these regression models, we estimated the  $R^2$  to evaluate their explanatory power, as well as Akaike weighting factors ( $w_i$ ) as evidence of the relative degree of support for each of them. We used standardized regression coefficients, instead of  $w_i$  values, to rank the importance of each predictor in regression models. When all predictors are present in the best set of models, it is virtually impossible to discern their relative influences using  $w_i$  values (Olalla-Tárraga, Rodríguez & Hawkins 2006; Diniz-Filho, Rangel & Bini 2008). A model averaging strategy produced quantitatively and qualitatively similar results on the relative importance of each predictor (results not shown).

We then run partial regression analyses using species richness as the response variable and two sets of explanatory variables (the best environmental predictor for each of our best models, on one hand, and human impacts on the other). This method allowed us to estimate how much of the variation in species richness is jointly explained by both data sets and the variance that

can be exclusively attributed to either environmental factors or human impacts (see Legendre & Legendre 1998 for a detailed description of this variation partitioning method). All statistical analyses were conducted at the global scale and for each biogeographical realm and performed using SAM 4.0 (Spatial Analysis in Macroecology; Rangel, Diniz-Filho & Bini 2010), R 2.15 (R Development Core Team 2012) and Geospatial Modelling Environment (GME; Beyer 2012).

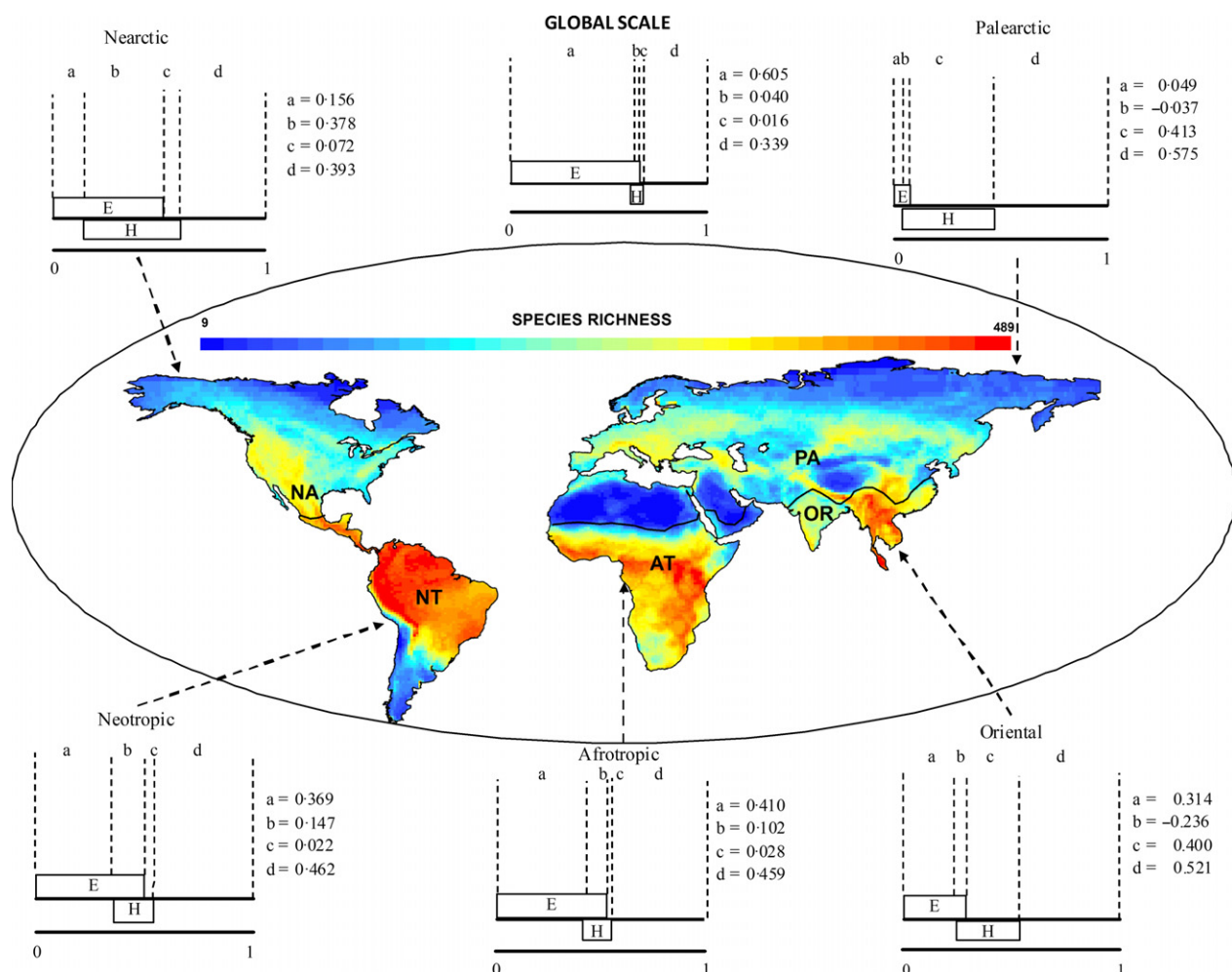
#### Results

The largest concentration of mammal species is located in the tropics, with a high diversity of species in most of South America, the Amazon basin, oriental slope of the Andes of Bolivia, Peru and Ecuador, as well as oriental Africa and Southeast Asia (Fig. 1). All simple correlations that were significant according to the Dutilleul's (1993) modified *t*-test show a positive association between species richness and environmental variables (Table 1, Appendix S1, Supporting information). For human impact variables, significant associations were found only in the Palearctic, Nearctic and Afrotropics, but with opposite signs for human footprint and human accessibility (positive and negative respectively). Correlation coefficients were also computed for human population density (obtained from <http://sedac.ciesin.columbia.edu/data/collection/gpw-v3>), but revealed very weak associations of this variable with mammal richness (Appendix S2, Supporting information) and, hence, this human impact metric was not retained for further analyses.

Overall, our multiple regression models with spatial filters do not show significant rank shifts in standardized regression coefficients and, hence, do not affect the interpretation based on OLS models (see Appendix S3, Supporting information). In multiple regression models at the global scale and for tropical regions (Neotropics and Afrotropics), the variable that best explained the variation in richness was AET. This finding is further supported by the joint importance of precipitation, temperature and elevation as secondary variables in the tropics and globally (Table 2). AET was significantly the most important variable in explaining richness. In the Nearctic and Palearctic regions, potential evapotranspiration (PET) became the most important variable, while range in elevation and AET were identified as of secondary importance. Our division of the Palearctic to run spatial models interestingly detected that PET and elevation explained most of the variance in the Occidental region, whereas AET and elevation accounted for most of the variation in species richness in the eastern half. Finally, in the Oriental region, human footprint was identified as the most important variable with a negative sign and NDVI as secondary variable.

Our best models according to the AIC criterion explained in all cases proportions of variance between 59% for the Oriental region and 79% for the Nearctic, and received strong support as shown by  $w_i$  values (Table 2). All in all, these models provide strong evidence





**Fig. 1.** Richness patterns of terrestrial mammal species at the global scale. Abbreviations for biogeographical realms are: Afrotropic (AT), Nearctic (NA), Neotropic (NT), Palearctic (PA) and Oriental (OR). Results of partial regression analyses at the global and biogeographical realm levels, using species richness as response variable and the best environmental predictor (E) and human footprint and accessibility (H) as explanatory variables for Global, AET; Afrotropic, AET; Oriental, NDVI; Nearctic, PET; Neotropic, AET; and Palearctic, PET. In each case, (a) represents the independent contribution of environmental variables, (b) shows the variation shared between human and environmental variables, (c) the independent contribution of human impact, and (d) is the unexplained variance. Abbreviations as in Table 1.

**Table 1.** Pearson correlation coefficients of environmental and human variables against species richness at the global and biogeographical realm level

Region	Variables								
	AET	PET	PREC	TEMP	NDVI	ELEV	ECOR	ACCES	F-PRINT
Global	0.803*	0.559*	0.742*	0.484*	0.491*	0.129	0.318*	-0.169	0.233*
Afrotropic	0.716*	0.168	0.665*	-0.278	0.533*	0.203	0.255*	-0.206*	0.361*
Nearctic	0.367	0.731*	0.128	0.683*	0.475*	0.502*	0.322*	-0.664*	0.489*
Neotropic	0.718*	0.634*	0.687*	0.683*	0.410*	-0.096	0.343*	0.409	-0.179
Oriental	0.441	0.066	0.475	-0.174	0.280	0.402*	0.251*	0.302	-0.350
Palearctic	0.663*	-0.111	0.552*	-0.098	0.387*	0.417	0.345*	-0.447*	0.602*

AET, annual actual evapotranspiration; PET, annual potential evapotranspiration; PREC, annual precipitation; TEMP, mean annual temperature; NDVI, primary productivity; ELEV, range in elevation; ECOR, ecoregions; ACCESS, accessibility human; F-PRINT, human footprint.

Significance levels are corrected for spatial autocorrelation using the modified *t*-test developed by Dutilleul (1993).

\*Identify significant regressions ( $P < 0.05$ ) after the modified *t*-test of Dutilleul.

**Table 2.** Multiple regression models for species richness against environmental and human variables. The models are ranked in each case by the AIC of the best settings, and only the best models ( $\Delta\text{AIC} < 2$ ) with their corresponding coefficients of determination ( $R^2$ ) and the standardized regression coefficients of the predictors included in the model are shown. Abbreviations as in Table 1

Region	Model	Predictor in model									$\Delta$ AIC	Wi	$R^2$
		AET	PET	PREC	TEMP	NDVI	ELEV	ECOR	ACCES	F-PRINT			
Global	1	0.611		0.255	0.147	-0.076	0.125	0.106	-0.080	-0.113	0	0.598	0.750
	2	0.614	-0.012	0.252	0.156	-0.073	0.126	0.106	-0.078	-0.113	0.794	0.402	0.750
Afrotropic	1	0.454	-0.051	0.282	-0.136	0.060	0.067	0.134	-0.126		0	0.361	0.647
	2	0.453	-0.049	0.281	-0.135	0.068	0.070	0.134	-0.137	-0.019	1.1	0.208	0.647
Nearctic	1	-0.322	0.517	-0.030	0.113	0.147	0.332	0.033	-0.255	0.083	0	0.838	0.791
Neotropic	1	0.482	0.043	0.203	0.437	-0.136	0.255	0.112	-0.025	-0.077	0	0.404	0.773
	2	0.476	0.043	0.197	0.442	-0.141	0.254	0.110		-0.064	0.845	0.265	0.773
	3	0.500		0.200	0.450	-0.117	0.265	0.112	-0.026	-0.080	1.368	0.204	0.733
Oriental	1	0.275	-0.120	0.167	0.220	0.445	0.330		-0.093	-0.588	0	0.628	0.590
	2	0.276	-0.120	0.166	0.217	0.446	0.324	0.008	-0.095	-0.590	1.972	0.234	0.590
Palearctic	1	0.346	-0.370	0.040	0.211	0.044	0.318	0.070	-0.198	0.158	0	0.964	0.620

that the variables analysed here largely explain the variation in mammal species richness both regionally and globally. In both simple and multiple regressions, the relationship between species richness and human accessibility had a negative sign. By contrast, human footprint is positively correlated with richness in the Palearctic, Nearctic and Afrotropics. In multiple regression models for the Oriental region, as a result of the combined effect with environmental variables, the human footprint variable shows a negative sign. Partial regression analyses allowed us to explore in more detail the independent contributions of environment vs. human impact to explaining the variation in richness. This analysis confirms the dominance of water–energy dynamics, as measured by AET, as a predictor of richness. Human influence variables, however, had a significant impact within some biogeographical regions (Fig. 1). While the independent contribution of human effects is minimal globally and in the tropics (Neotropics and Afrotropics), these variables increase their relative importance in the Oriental, Nearctic and Palearctic regions (Fig. 1). In these three biogeographical realms, the variance that can be exclusively explained by human impact is similar or even higher than that one independently explained by the environment. In the Palearctic, these proportions are higher, representing 41.3% (human effect) and 4.9% (environment) of the variation in species richness, respectively (Fig. 1). As in the Palearctic there is no shared variance (the [b] component is negative) in the Oriental region, and the independent contributions of both groups of variables are higher and over 30% of variance in both cases. Note that our finding of a negative [b] component indicates that environment and human impact variables together explain the variation in species richness better than the sum of their individual effects (Legendre & Legendre 1998). Finally, in the Nearctic, the proportion of variance that can be independently assigned to human effects is about half of the independent contribution of the environment, with 7.2% and 15.6%, respectively.

## Discussion

Our results support the hypothesis that current climate plays a leading role in determining global gradients in mammal species richness and suggest that AET, PET and precipitation are the most important environmental drivers. The combination of water–energy alone, measured by AET, can explain almost 60% of the variation in richness globally and in the tropics (Afrotropics & Neotropics). In temperate macroclimates, Palearctic and Nearctic, PET (a measure of energy inputs in the environment) was the best explanatory variable. In these regions, a secondary topographic effect (more pronounced in the case of the Nearctic region) was detected. All together, these findings suggest that species richness gradients in mammals are being driven primarily by direct effects of climate. We show that the spatial dynamics in water and energy available in the environment play a major role in the geographical distribution of mammal species richness. In particular, energy availability is a key limiting factor in temperate climates, whereas water availability becomes particularly important in tropical regions. Hence, as previously found for other vertebrate classes (Evans & Gaston 2005; Whittaker, Nogués-Bravo & Araújo 2007; Qian 2010), our results confirm the validity of the conjecture of Hawkins *et al.* (2003a) for mammals (see also Davies *et al.* 2011).

A recent meta-analysis for a diversity of animal taxa, including mammals, in different terrestrial and freshwater ecosystems found that primary productivity and species richness tend to be positively associated at all spatial scales and resolutions (Cusens *et al.* 2012). In accordance with these results, our Pearson correlation coefficients show positive relationships between NDVI and species richness in all cases. Similarly, part of the explanatory power of AET could actually be attributed to primary productivity since aspects of the environment, such as soil and vegetation cover, other than the energy and water regimes are measured by this variable (Fisher, Whittaker

& Malhi 2011). Therefore, we cannot discard the role of primary productivity and food availability on the observed gradients. The different responses of mammal trophic guilds to environmental variation may have also contributed to obscure the response of species richness to NDVI. Sandom *et al.* (2013) recently found that richness in predator mammalian species mostly depends on prey availability, whereas productivity and climate prevailed to explain richness in prey species.

While the water–energy combination represents a well-supported explanation for gradients observed globally, the importance of human impacts emerges when disaggregating the analysis by biogeographical region. Interestingly, we found that the Oriental, Palearctic and Nearctic regions are those where the independent effect of humans is as important as the environment to explain richness patterns. These results suggest that the observed anthropogenic effects on mammal richness do not only depend on the disturbance levels that currently take place in each region, but are also mediated through patterns of intensive land use in the past and the historical location of human settlements. Humans have historically preferred to settle in areas of high energy and resource availability and reach higher population densities when occupying the most productive and diverse habitats, more conducive to population growth. Both primary productivity and early settlements turn out to be important determinants of current population distribution that affect the geographical variation of species richness (Luck 2007). Since the late Pleistocene, humans have transformed terrestrial ecosystems worldwide for hunting, foraging, land clearing and agriculture, a capacity that has largely affected the geographical distribution of species, among others. In the Palearctic and Oriental regions, the early presence of intensive land-use technologies has resulted in long-term impacts from forest clearing, increased fire frequencies, megafaunal extinctions, species invasions and soil erosion (Ellis *et al.* 2013). Contrarily to the tropics, where the historical imprint of human activities is lower, the Palearctic and Oriental regions (and more recently the Nearctic) have traditionally demanded high agricultural productivities to sustain densely settled areas. In the Oriental, Palearctic and Nearctic regions, the geographical distribution of human footprint is in fact spatially structured across environmental gradients (Appendix S4, Supporting information). That is, human population density, land transformation, electrical power and road infrastructure (the basic components of the human footprint index) are altogether predictably dependent on broad-scale environmental conditions that operate across these three biogeographical realms. The environmental covariation of human footprint and mammal richness likely accounts for most of the spatial congruence (and positive association) between both variables in the Palearctic and Nearctic. In agreement with this finding, similar coarse-grained studies have also reported a positive correlation between human density and extant species richness in these regions (Ara-

újo 2003; Luck *et al.* 2004; Barbosa, Pautasso & Figueiredo 2013). Our results are also coincident with previous region-specific analyses that point towards the importance of productivity–diversity relationships to explain the geographical coincidence of high human pressure areas with biodiversity hotspots (Waide *et al.* 1999; Araújo 2003). The intermediate disturbance hypothesis (Huston 1994) does not seem to be supported by our data, since we would expect a unimodal relationship between diversity and disturbance and, hence, the highest concentration of species richness at intermediate levels of human impacts. It is also possible that humans may have historically acted as major extinction filters, so that present-day biodiversity in these regions could be biased towards species that are generally more tolerant of humans (Araújo 2003; Barbosa, Pautasso & Figueiredo 2013). According to this hypothesis, only the more tolerant species might have been able to persist under high human pressures. Although we cannot fully discard this scenario, selective extinctions of the most intolerant species to humans appear to be insufficient to explain why species richness is lower in less disturbed areas, especially if we consider that human-tolerant habitat generalists should be widespread. This question remains unsolved and begs for further research in the future.

Despite the high proportions of shared variance between humans and environment in explaining richness, our partial regression analyses were able to clearly detect the independent contribution of human impacts on the distribution of mammal species in the Oriental, Palearctic and Nearctic regions. Here, we simultaneously used, for the first time, two variables combined to assess human impacts on global and regional richness patterns, namely human footprint (Sanderson *et al.* 2002) and human accessibility (Nelson 2008). The joint use of two human impact metrics did not only allow identifying those biogeographical regions where anthropogenic effects on mammal diversity are more evident, but also gain further insights into possible underlying mechanisms. Over large spatial scales, habitat loss and fragmentation are believed to be the major drivers of the ongoing human-caused environmental change, and the use of human footprint as a single metric of human impact may not always be sufficient to detect such landscape level change processes. Our study shows the usefulness of incorporating a human accessibility variable to macroecological analyses. Human accessibility, highly dependent on the global road network, could be interpreted as a crude proxy variable of habitat unsuitability for native animals and plants in large-scale ecological studies. Those areas more accessible to humans may offer less suitable habitat for mammals as a result of higher fragmentation and hunting pressures.

Contrarily to human footprint, human accessibility was negatively correlated with species richness in every biogeographical realm where we detected a significant independent contribution of human impacts (Oriental, Palearctic and Nearctic regions). Only in the former case,

human footprint was also negatively correlated with species richness. Rondinini *et al.* (2011) indeed recently pointed out that extinction risk for mammals in the Oriental region could be underestimated compared to other biogeographical realms. They found that Indomalayan mammals, as a result of extensive land-cover changes, only have a low proportion of suitable habitat available within their geographical ranges. On the opposite side, Nearctic mammals occupy a much higher proportion of suitable habitat within their distribution ranges. Their results suggest that the IUCN expert-drawn range maps used for the purpose of our analyses can be closer to the area of occupancy (AOO) or the extent of occurrence (EOO) depending on the biogeographical realms. Such differences do not affect our ability to detect human impacts in both regions, but may partially account for the high proportion of variance in mammal species richness that can be exclusively attributed to humans in the Oriental region.

In general, areas where human populations are more dependent on the exploitation of natural resources for their livelihoods frequently show a negative relationship between human impacts and species richness (see, e.g. Luck *et al.* 2004; Koh, Lee & Lin 2006; Pautasso 2007; McKinney 2008). In densely populated regions, species extinction rates are higher, which results in decreases of species richness, a scenario supported by the widespread disappearance of mammal populations in regions with high human density (Luck 2007). The detrimental effects on biodiversity of excessive landscape changes often become more evident at local scales. This is the case, for instance, of highly urbanized and industrialized areas in Europe (see e.g. Araújo 2003). Our large-scale analyses are not able to fully capture the complex range of socio-economic and cultural factors inherent to the relationship between human impacts and biodiversity (Huston 2005). When interpreting our results, we should bear in mind the coarse grain size of our analyses and that correlation does not imply causation. While we were not able to detect an influence of human impacts on mammal species richness in the tropics at the spatial resolution of our analyses, it is worth mentioning that fine-grained studies often reveal that human impacts also exist in these regions but are only detectable at more local scales (see, e.g. Koh, Lee & Lin 2006; Pautasso 2007). Disentangling human effects on species richness still represent a significant challenge to set up conservation goals in high population density areas (Fjeldså & Rahbek 1998; Luck *et al.* 2004; Araújo & Rahbek 2007).

Along these lines, our findings achieve special relevance in understanding patterns of mammal population decline as well. Quite interestingly, our best predictors of species richness are also considered to be the most important extrinsic factors to predict mammal population declines nowadays (Collen *et al.* 2011). For example, Cardillo *et al.* (2004, 2005, 2008) suggested that a higher human population density within the range of a species means more competition for resources and more opportunity for

conflict and exploitation and, therefore, a greater extinction risk for mammals. This extrinsic factor is associated with habitat degradation, fragmentation and destruction, events that occur more frequently in densely populated localities. Cardillo *et al.* (2008) and Price & Gittleman (2007) demonstrated that low AET values are typically associated with a high extinction risk of mammals. Fisher, Blomberg & Owens (2003) and Cardillo *et al.* (2008) also suggested that precipitation, along with temperature, plays a complex role in their effect on mammal population size. Thus, under drought periods and in areas of low productivity or resource scarcity, mammal populations are more vulnerable to extinction processes.

In conclusion, we found that the joint availability of energy–water in the environment can influence the geographical distribution of mammal species and humans, which have historically inhabited high energy areas (where the increased availability of resources may have promoted population growth). Overall, the intersection of human impacts with climatic variation drives the geographical variation in mammal species richness in the Palearctic, Nearctic and Oriental regions. Using a human accessibility variable, we show, for the first time, that the zones most accessible to humans are often those where we find lower mammal species richness. These results suggest the need to conduct similar additional studies for other taxa and assess its implications for the design of actions for species conservation under ongoing global change processes.

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## Data accessibility

Data available from the Dryad Digital Repository, doi:10.5061/dryad.qc700 (Torres-Romero & Olalla-Tárraga 2015).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Corrected significance levels using geographically effective degrees of freedoms in simple regressions of environmental variables against species richness of mammals at the global scale and biogeographical realm level.

**Appendix S2.** Pearson correlation coefficients of human population density (HPD) against species richness at the global and biogeographical realm level.

**Appendix S3.** Standardized regression coefficients of each predictor in multiple regressions between species richness against environmental and human variables after using spatial filtering for each biogeographical realm.

**Appendix S4.** Coefficients of determination ( $R^2$ ) of multiple regressions between human population density (HPD) and human footprint (HF) as response variables, and the full set of environmental variables at the global and biogeographical realm levels.

## **Supporting Information**

### **Untangling human and environmental effects on geographic gradients of mammal species richness: a global and regional evaluation**

Erik Joaquín Torres-Romero, Miguel Á. Olalla-Tárraga

**Appendix S1.** Corrected significance levels using geographically effective degrees of freedoms in simple regressions of environmental variables against species richness of mammals at the global scale and biogeographic realm level. The modified t-test developed by Dutilleul (1993) was used for these calculations. Abbreviations: AET (annual actual evapotranspiration), PET (annual potential evapotranspiration), PREC (annual precipitation), TEMP (mean annual temperature), NDVI (primary productivity), ELEV (range in elevation), ECOR (ecoregions), ACCESS (accessibility human), F-PRINT (human footprint), HPD (human population density)

Region	Variable	Probabilities
		Corrected (d.f)
Global	ACCES	0.090 (98.81)
	AET	0 (33.64)
	TEMP	0.019 (20.89)
	ELEV	0.142 (129.04)
	NDVI	0 (99.59)
	PET	0.002 (24.42)
	ECOR	0 (240.68)
	PREC	0 (37.94)
	F-PRINT	0.016 (104.19)
	HPD	0.580(199.32)

Region	Variable	Probabilities
		Corrected (d.f)
Afrotropic	ACCES	0.020 (125.27)
	AET	<0.001(18.73)
	TEMP	0.156(25.39)
	ELEV	0.104(62.90)
	NDVI	<0.001(35.21)
	PET	0.193(59.62)
	ECOR	<0.001(163.54)
	PREC	<0.001(21.66)
	F-PRINT	0(119.23)
	HPD	0.033(251.04)

Region	Variable	Probabilities
		Corrected (d.f)
Nearctic	ACCES	0.007(12.75)
	AET	0.154(14.49)
	TEMP	0.030(7.95)
	ELEV	0.036(15.60)
	NDVI	0.003(34.34)
	PET	0.015(8.05)
	ECOR	0.005(69.79)
	PREC	0.520(24.64)
	F-PRINT	0.050(13.71)
	HPD	0.065(162.68)

Region	Probabilities	
	Variable	Corrected (d.f)
Neotropic	ACCES	0.126(13.26)
	AET	0.003(12.07)
	TEMP	0.015(9.83)
	ELEV	0.576(34.55)
	NDVI	0.019(30.26)
	PET	0.012(12.67)
	ECOR	0.025(40.33)
	PREC	0.010(10.67)
	F-PRINT	0.442(18.63)
	HPD	0.445(398.31)

Region	Probabilities	
	Variable	Corrected (d.f)
Oriental	ACCES	0.078(33.03)
	AET	0.072(15.45)
	TEMP	0.413(22.13)
	ELEV	0.021(30.29)
	NDVI	0.082(37.50)
	PET	0.544(83.66)
	ECOR	0.041(63.96)
	PREC	0.094(11.38)
	F-PRINT	0.166(15.11)
	HPD	0.014(52.09)

Region	Probabilities	
	Variable	Corrected (d.f)
Palearctic	ACCES	0(123.57)
	AET	0(99.58)
	TEMP	0.440(62.62)
	ELEV	0(165.29)
	NDVI	0(229.38)
	PET	0.353(69.50)
	ECOR	0(415.52)
	PREC	0(96.53)
	F-PRINT	0(92.47)
	HPD	0(303.18)

**Appendix S2.** Pearson correlation coefficients of human population density (HPD) against species richness at the global and biogeographic realm level. For comparison purposes correlations for human footprint (F-PRINT) and human accessibility (ACCESS) are also reported. Significance levels are corrected for spatial autocorrelation using the modified t-test developed by Dutilleul (1993). Asterisks (\*) identify significant regression ( $p < 0.05$ ) after the modified t-test of Dutilleul

Human impact variables			
Region	HPD	F-PRINT	ACCES
Global	0.039	0.233*	-0.169
Afrotropic	0.133*	0.361*	-0.206*
Nearctic	0.143	0.489*	-0.664*
Neotropic	-0.038	-0.179	0.409
Oriental	-0.331*	-0.350	0.302
Palearctic	0.232*	0.602*	-0.447*

**Appendix S3.** Standardized regression coefficients of each predictor in multiple regressions between species richness against environmental and human variables after using spatial filtering for each biogeographic realm. Abbreviations as in Appendix S1

Region	Predictor in model									R <sup>2</sup>
	AET	PET	PREC	TEMP	NDVI	ELEV	ECOR	ACCES	F-PRINT	
Afrotropic	0.065	0.025	0.212	0.010	0.043	0.064	0.024	-0.052	0.006	0.973
Nearctic	0.015	0.054	0.079	0.143	0.075	0.168	0.033	-0.130	0.038	0.943
Neotropic	0.251	-0.064	0.207	0.339	0.061	0.201	0.094	-0.055	-0.022	0.882
Oriental	-0.153	0.005	0.086	0.007	0.252	0.067	0.099	-0.088	-0.042	0.941
Palearctic-Occidental	-0.030	0.078	0.059	<.001	-0.026	0.078	0.032	-0.053	0.017	0.763
Palearctic-Oriental	0.108	-0.060	0.086	0.098	0.081	0.174	0.050	-0.068	-0.004	0.923

**Appendix S4.** Coefficients of determination ( $R^2$ ) of multiple regressions between human population density (HPD) and human footprint (HF) as response variables, and the full set of environmental variables at the global and biogeographic realm levels

Region	$R^2$	
	HPD	HF
Global	0.077	0.303
Afrotropic	0.109	0.292
Nearctic	0.072	0.679
Neotropic	0.050	0.271
Oriental	0.180	0.548
Paleartic	0.233	0.552

References used for Appendix S2:

Dutilleul, P. (1993) Modifying the t-test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.

## Capítulo 3

### Inestabilidad climática desde el Último Glacial Máximo y la redistribución de las faunas de mamíferos: una comparación Neártica vs. Paleártico occidental

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Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

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## **Climatic instability since the Last Glacial Maximum and the redistribution of mammal faunas: a Nearctic vs. Western Palearctic comparison**

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### **Abstract**

Climate now and in the past has played a key role in shaping the geographic patterns of biodiversity. The imprint of Quaternary climatic fluctuations is particularly evident on the geographic distribution of Holarctic faunas, which dramatically shifted their ranges following the alternation of glacial-interglacial cycles during the Pleistocene. Here, we evaluate the existence of differences between climatically stable and unstable regions (defined in terms of temperature anomalies since the Last Glacial Maximum) in the geographic distribution of several biological attributes of extant terrestrial mammals of the



Nearctic and Western Palearctic. Specifically, we use a macroecological approach to assess the dissimilarities in species richness, range size, body size, longevity and litter size of species that inhabit regions with contrasting histories of climatic stability. While several studies have documented how the distributional ranges of animals can be affected by long-term historic climatic fluctuations, there is less evidence on the species-specific traits that determine their responsiveness under such climatic instability. We find that climatically unstable areas have more widespread species and lower mammal richness than stable regions in both continents. We detected stronger signatures of historical climatic instability on the geographic distribution of body size in North American mammals, possibly reflecting lagged responses to recolonize deglaciated regions. However, the way that animals respond to climatic fluctuations varies widely among species and we were unable to find a relationship between climatic instability and other mammal life-history traits (longevity and litter size) in any of the two biogeographic realms. We, therefore, conclude that beyond some biological traits typical of macroecological analyses such as geographic range size and body size it is difficult to infer the responsiveness of species distributions to climate change solely based on particular life-history traits.

**Keywords:** Quaternary climatic fluctuation, terrestrial mammals, Holarctic region, climatically stable areas, life-history traits, vulnerability, climate change.

## INTRODUCTION

Climate, now and in the past, has played a key role in shaping current biodiversity patterns (see e.g. Currie 1991; Hawkins et al. 2003; Araujo et al. 2008). Distinguishing the relative importance of past and present climates on the geographic ranges of species is a central research question in the field of biogeography. While numerous studies have found a strong association of current climatic gradients with broad-scale patterns in species richness for different taxonomic groups and regions (Hawkins et al. 2003; Whittaker et al. 2007; Qian 2010; Torres-Romero & Olalla-Tárraga 2014), the imprint of past climates remains little explored. Several workers have shown the relevance of climatic oscillations during the Pleistocene and the alternation of glacial-interglacial cycles throughout this geological epoch as a crucial factor to understand the geographic distribution of species nowadays (Hawkins & Porter 2003; Rodríguez et al. 2006; Araújo et al. 2008; Nogués-Bravo et al. 2010; Hortal et al. 2011). In particular, most of the Holarctic region was covered by ice during the Last Glacial Maximum (LGM, 21 000 years ago), which caused dramatic changes in the distribution of organisms. The exposure of large areas to the LGM ice-sheets heavily impacted

the climatically suitable areas for many species of terrestrial mammals in this biogeographic region, thus reducing their geographical ranges and increasing their vulnerability to extinction (Nogués-Bravo et al. 2010).

Overall, Pleistocenic glaciations left a legacy of high extinction rates and impoverished faunas, with those species highly sensitive to rapid climate variations either shifting their geographic ranges or catastrophically collapsing (Johnson 2002; Thuiller et al. 2005; Sandel et al. 2011). However, the end of this glacial period and the retreat of Pleistocenic ice sheets generated newly habitable land that became available to be recolonized (Varela et al. 2014). According to the post-glacial recolonization hypothesis (Hewitt 1999, Araújo et al. 2008), highly vagile species would have been able to more rapidly spread northwards and recolonize these newly exposed areas, whereas geographic range expansions for the majority of species would have been slower. This scenario is also coincident with the observation that climatic stability over time in the Holarctic tends to be associated with higher species diversity in mammals and birds (Hawkins & Porter 2003) or reptiles and amphibians (Araújo et al. 2008).

The climatic stability hypothesis predicts that climatically stable areas, compared

to unstable regions, are associated with high levels of richness, endemism and intraspecific genetic diversity (Fjeldsa & Lovett 1997; Jansson 2003; Barrientos et al. 2014). While climate stability favors species persistence and speciation, climatically unstable areas increase extinction risk and species adaptability becomes essential to predict population declines and assess their vulnerability (Dynesius & Jansson 2000; Sandel et al. 2011). Many studies have explored how the distributional ranges of plants and animals may be affected by long-term historic climatic fluctuations (see. e.g. Araújo et al. 2008; Griswold et al. 2008; Lima-Ribeiro et al. 2010; Rodríguez-Robles et al. 2010; Werneck et al. 2012; Terrence et al. 2012; Varela et al. 2014). Nonetheless, there is less evidence on the specific life-history traits (such as body size, geographic range size, litter size and a suite of reproductive traits) that determine the responsiveness of species to survive under such climatic variability scenarios (but see. e.g. Isaac 2009; Tafani et al. 2013; Chessman 2013; Gonzalez & Revilla 2013). Possible individual responses of species to better cope with climate change go from the ability to survive longer, changes in migration patterns or expansions of geographic ranges, to simple behavioral changes to enter hibernation, torpor,

aestivation, latency, and use of burrows (see e. g. Cardillo et al. 2003; Morris et al. 2008; Davidson et al. 2009; Ozgul et al. 2010; Turbill et al. 2011). Understanding the adaptive value of these life-history traits is fundamental to gain a better knowledge on the ability and response of species against climate change globally. Indeed, the extent to which a life-history trait mitigates the impact of environmental fluctuation stress on fitness is perhaps the most robust gauge of its adaptive value (Stahler et al. 2013). Here, we evaluate whether any differences exist or not between climatically stable and unstable areas (defined in terms of temperature anomalies since the LGM) in the geographic distribution of a number of certain biological attributes of extant terrestrial mammal faunas in the Holarctic. Specifically, we use a broad-scale macroecological approach to assess the dissimilarities in species richness, range size, body size, longevity and litter size of extant mammal species that inhabit regions with contrasting histories of climatic stability (since the LGM). Typically, ecogeographical ‘rules’ have been used to encapsulate the responses of the Earth’s faunas and floras to the influences of environmental factors in a patterned way (McDowall 2008). Beyond the well-known latitudinal

diversity gradient that refers to the general decrease in species richness as we move towards more seasonal macroclimatic regimes (Hawkins et al. 2003), some other ecogeographical rules also predict varying biological traits between climatically stable and unstable regions. For instance, Rapoport's rule describes a positive relationship between the geographic range size of species with increasing latitude and elevation (Stevens 1992; Gaston et al. 2008; Whitton et al. 2011), whereas Bergmann's rule refers to a general pattern of increasing body size with decreasing temperature (Bergman 1847; Diniz-Filho et al. 2008; Rodriguez et al. 2008). Accordingly, we expect to find that climatically unstable areas will be inhabited by less species, which overall will have broader geographic distributions, larger body sizes, and greater longevities and litter sizes than those that occur in less seasonal environments. In the latter case, we anticipate that mammal faunal assemblages will be dominated by range-restricted, small-bodied and short-lived species (Araujo et al. 2008; Graham et al. 2010; Lyons et al. 2010). We similarly aim to identify differences between mammalian orders and biogeographic realm (i.e. Nearctic vs. Palearctic) and conduct separate analyses in each case.

If Quaternary climatic fluctuations have had a significant effect on the geographic distribution of terrestrial mammals, these should mostly be evident in the Holarctic (Davies et al. 2009).

## **MATERIALS AND METHODS**

### Distributional, life-history traits and climatic data

Mammal range maps were compiled from the IUCN Red List (<http://www.iucnredlist.org>, accessed in June 2013). All islands were excluded to avoid possible island effects. Overall, we compiled information for a total of 563 and 259 mammal species (with 15 species shared in both regions) that occur in the Nearctic and Western Palearctic (until the Ural Mountains) region respectively. We used ArcGIS 10.0 to calculate geographical range sizes (in hectares) for each species.

We gathered information on four life-history traits that are commonly used as predictors of extinction risk in terrestrial mammals (Cardillo et al. 2004; Collen et al. 2011; Murray et al. 2011; Gonzalez & Revilla 2013): geographic range area, adult body size, longevity and litter size. Data were primarily obtained from "Pantheria" (Jones et al. 2009), which contains more than 5416 species records, complemented with "AnAge" (online

database, <http://genomics.senescence.info/species/>-maintained by J. P. de Magalhães) and "MoM v4.1" data (Smith et al, 2003). We followed Wilson & Reeder's (2005) taxonomy. Body size and longevity records were log 10 transformed.

Following Jansson (2003) and Araujo et al. (2008), we used the geographical pattern in mean annual surface-air temperature change between the LGM and the present as a proxy variable for long term climate stability. We built climate stability layers subtracting LGM temperatures to current temperatures and calculating absolute values (for details see Hijmans & Graham, 2006) in R 2.15 (R Development Core Team, 2012). Both climate variables (present and LGM bio1 data) were downloaded from World-Clim (Hijmans et al. 2005) and have a spatial resolution of 2.5 arc-min resolution. We then defined consensus maps (i.e. testing different temperature ranges) of stable and unstable areas in each biogeographic region using a temperature anomaly threshold of 15° C. This temperature threshold renders approximately equal areas of stable and unstable climates for both biogeographic regions, so that we can discard that our results are an artifact of species-area effects. Finally, we assigned species to each region based

on the overlap between their species distributional ranges and climate stability maps using GME (Geospatial Modelling Environment; Beyer 2012). Species richness was calculated as the sum of overlapping ranges with each climatic region in each biogeographic realm.

### Data Analysis

For each biogeographic realm separately, we compared stable vs. unstable regions using Wilcoxon paired-sample tests, with a threshold of  $P \leq 0.05$  to detect possible level of significance. Specifically, we explored if stable and unstable parts of both continents differed in terms of species richness, geographic range size, body size, longevity and litter size of their mammal faunas. To assess the potential influence of the varying overlap of species ranges with each of the two regions (stable and unstable), we also calculated which proportion of the extent of occurrence of each species overlay with each region and use these measurements as weighting factors when testing the significance by Wilcoxon tests. However, the results obtained using weighted analyses (not shown) were qualitatively and quantitatively similar to those based on simple overlap metrics and hence will not be further discussed. All statistical analyses were performed using Statistica (StatSoft, Inc. 2013).

## RESULTS

The largest concentration of terrestrial mammals is located in climatically stable regions of both the Nearctic and Palearctic, with lower species richness values in unstable regions (Fig. 1). A total of 403 mammal species are found in climatically stable areas of the Nearctic, whereas 160 species occur in unstable areas. Additionally, we found 147 species whose geographic ranges overlap both stable and unstable areas. Rodentia, Carnivora and Eulipotyphla were the taxa with more representatives at the level of order, family and species in the Nearctic (Table 1). In the Western Palearctic results are similar, with more species in stable than unstable areas (i.e. 163 vs. 96) and a total of 91 species that occur in both parts. In this biogeographic region, the best represented taxonomic orders in terms of species richness are coincident with those in the Nearctic (Table 2).

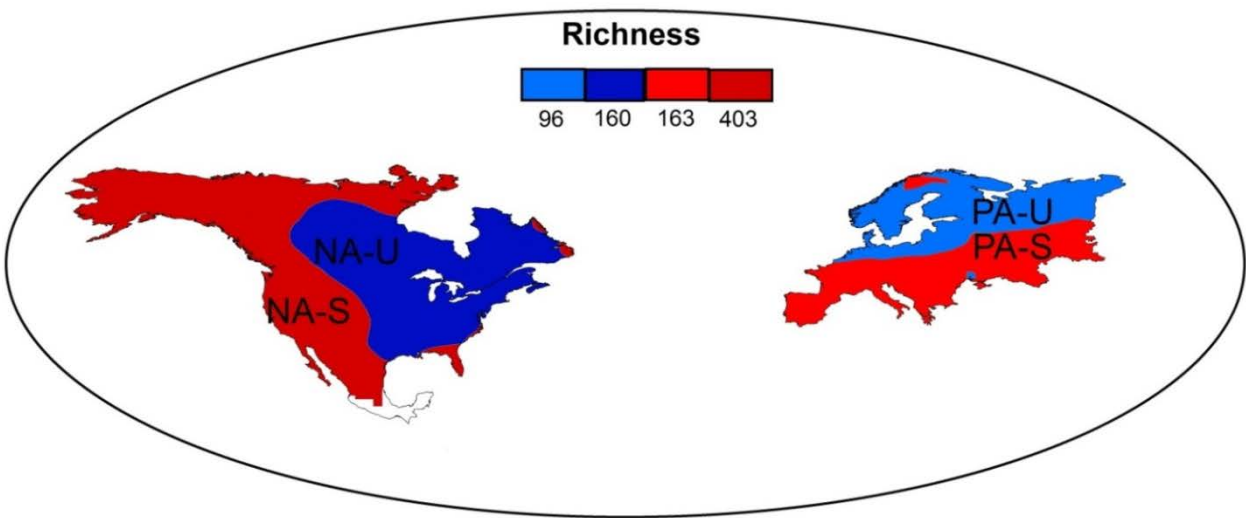
For both the Nearctic and Western Palearctic, we found that there are significant differences ( $p < 0.05$ ) between climatically unstable and stable regions in terms of range size, so that species that occur in the former regions have larger geographical ranges (Tables 1 and 2). In the Nearctic, this pattern also holds for Rodentia, Eulipotyphla and Didelphimorphia, but the remaining mammal orders do not show significant

differences in range sizes between unstable and stable regions. In the Western Palearctic, only Rodentia shows significant differences in range size between both regions when we disaggregate the analysis at the level of taxonomic order.

Species body sizes were also significantly different between unstable and stable parts of the Nearctic, with large-bodied species dominating in more unstable environments. However, none of our analyses at the level of taxonomic order detected such differences. Unstable and stable parts of the Western Palearctic do not display significant changes in the body sizes of species. Neither the overall comparisons nor the taxonomic-level analyses identified significant differences between unstable and stable regions for longevity and litter size of species (Tables 1 and 2).

## DISCUSSION

During the Late Pleistocene, mammal species of the Nearctic and Palearctic continuously shifted their distributional ranges in response to the expansions and contractions of glaciers associated with glacial-interglacial cycles (Lyons et al. 2010). As documented by the fossil record, Quaternary climatic changes had



**Figure 1.** Comparison of terrestrial mammal species richness between climatically unstable (U) and stable (S) regions of the Nearctic (NA) and Western Palearctic (PA). See main text for details on how climatically unstable and stable regions were depicted.

dramatic effects on the distribution of terrestrial mammals and contributed to the severe extinction events that specially affected mammalian megafaunas (Graham et al. 1996; Lima-Ribeiro et al. 2012; Lima-Ribeiro et al. 2014). Here we have assessed the role of historical climatic instability on the geographic distribution of extant mammal species in the Holarctic. In accordance with the climatic stability and post-glacial recolonization hypotheses, we find that the imprint of past climatic fluctuations is still evident on the geographic ranges of mammalian faunas in the Nearctic and western Palearctic. In both biogeographic

realms, those regions that have remained more climatically stable since the Last Glacial Maximum (21 000 years ago) harbor the largest concentration of species. This finding concurs with previous studies that have detected a signal of the most recent Pleistocenic Ice Age on contemporary species richness gradients for terrestrial vertebrate taxa in Europe and North America (Hawkins & Porter, 2003, Jansson 2003, Araujo et al. 2008).

**Table 1.** Comparisons of different life-history traits between climatically stable (s) and unstable (u) parts of the Nearctic. In each case P in bold represent the level statistically significant.

Order	Nearctic														
	Richness		Shared	Range		P	Body size		P	Longevity		P	Litter size		P
	s	u		s	u		s	u		s	u		s	u	
Total	403	160	147	154.181	437.904	<b>&lt;0.05</b>	2.202	2.465	<b>&lt;0.05</b>	1.948	1.963	>0.05	3.936	4.079	>0.05
Carnivora	43	30	30	526.85	785.433	>0.05	3.679	3.651	>0.05	2.327	2.317	>0.05	3.53	3.926	>0.05
Cetartiodactyla	13	11	11	338.436	351.703	>0.05	5.069	5.089	>0.05	2.418	2.430	>0.05	1.378	1.392	>0.05
Cingulata	1	1	1	60.422	208.248	>0.05	3.596	3.596	>0.05	2.255	2.255	>0.05	3.96	3.96	>0.05
Didelphimrphia	5	1	1	29.070	478.539	<b>&lt;0.05</b>	2.465	3.388	>0.05	1.747	1.778	>0.05	7.788	8.62	>0.05
Eulipotyphla	47	22	16	126.841	392.309	<b>&lt;0.05</b>	0.92	0.949	>0.05	1.394	1.418	>0.05	5.041	5.137	>0.05
Lagomorpha	20	13	10	148.95	219.493	>0.05	3.089	3.089	>0.05	1.950	1.986	>0.05	3.599	3.678	>0.05
Rodentia	272	82	78	95.343	371.487	<b>&lt;0.05</b>	1.911	1.906	>0.05	1.807	1.778	>0.05	4.005	4.262	>0.05
Pilosa	1	0													
Primates	1	0													

Despite the difficulties involved in disentangling current vs. historical climatic conditions as explanations for these patterns, there is increasing evidence on the role that climatic extinction filtering during the LGM and subsequent post-glacial recolonization processes have played. Contemporary species-poor mammal assemblages are coincident with regions that have remained climatically unstable over the past 21 kya and only recently became available for colonization after the glacial retreat following the LGM.

As climate warmed and ice-sheets retreated, some pioneer highly-vagile species were able to leave ice age refugia and expand their ranges (see e.g.

Hewitt, 1999 for a depiction of possible post-glacial expansion routes of different mammal species in Europe). Compared to the more vagile birds, mammals (as well as amphibians and reptiles) are considered to have slower dispersal abilities and hence, their broad-scale species richness patterns tend to show stronger signatures of historical climatic instability likely as a reflect of lagged responses to recolonize deglaciated regions (Hawkins & Porter, 2003, Lawes et al. 2007, Araujo et al. 2008).

Over large spatial scales, species richness is measured by overlapping the geographic ranges of species that co-occur in a particular region (Simpson, 1964). One of the fundamental ecological



**Table 2.** Comparisons of different life-history traits between climatically stable (s) and unstable (u) parts of the Western Palearctic. In each case P in bold represent the level statistically significant.

Order	Western-Palearctic														
	Richness		Shared	Range		P	Body size		P	Longevity		P	Litter size		P
	s	u		s	u		s	u		s	u		s	u	
Total	163	96	91	296.327	508.397	<b>&lt;0.05</b>	1.827	1.746	>0.05	1.792	1.728	>0.05	4.722	5.022	>0.05
Carnivora	25	20	19	469.077	728.985	>0.05	3.478	3.585	>0.05	2.291	2.308	>0.05	4.376	4.445	>0.05
Cetartiodactyla	13	7	7	271.926	481.258	>0.05	4.905	5.136	>0.05	2.399	2.443	>0.05	1.647	1.807	>0.05
Eulipotyphla	32	18	18	298.222	502.592	>0.05	1.366	1.189	>0.05	1.583	1.517	>0.05	5.305	5.767	>0.05
Lagomorpha	7	4	3	288.304	542.904	>0.05	3.208	3.089	>0.05	2.127	2.219	>0.05	3.757	3.39	>0.05
Rodentia	86	47	44	249.745	417.858	<b>&lt;0.05</b>	1.827	1.746	>0.05	1.792	1.728	>0.05	4.722	5.022	>0.05

and evolutionary characteristics of a species is geographic range size, an emergent species-level trait (Jablonski, 2005) with profound consequences for their persistence and extinction risk under changing environmental conditions (Gaston 2003). Our analyses have also identified significant differences in the geographic range sizes of species that occupy climatically stable and unstable regions of the Nearctic and Western Palearctic. While range-restricted species dominate mammal assemblages in climatically stable parts of both biogeographic realms, climatically unstable regions harbor more widespread species. This finding is again consistent with a specific prediction of the climatic stability and post-glacial recolonization

hypotheses, namely that the limited colonization abilities of narrow-ranging species make them to preferentially occur in areas that remained favorable during the last glacial period (Araujo et al. 2008). Widespread species, on the contrary, have better abilities to track climate changes and more rapidly recolonize newly available climatically-suitable habitats after glacial retreat (see also Jansson 2003). Using sister species contrasts for 296 pairs of mammal species, Davies et al. (2009) found that temperature change since the LGM is the best single predictor of range size, with large-ranged species more likely occurring in regions that have experienced large postglacial warming. They suggested that Quaternary

temperature oscillations may have shaped the contemporary distribution of range sizes through range contractions and extinctions of small-ranged species during glacial expansion and rapid recolonization by good dispersers after glacial retreats.

The observed patterns in species richness and range size are undoubtedly a product of intrinsic biological traits of species (e.g. dispersal abilities) and extrinsic environmental factors (e.g. climatic history). Indeed, depending on their specific autoecological characteristics such as dispersal abilities, body size and a suite of other life-history traits, species may respond differently to changing climates. However, the relationship between species-specific ecological traits and range shifts as a response to past climate changes in mammals remains very little explored (but see Lyons et al. 2010).

Out of the three organismic-level traits that we explored (body size, longevity and litter size), we only find significant differences in body size between climatically unstable and stable regions in the Nearctic. Mammal species that occur in the most unstable environments of the Nearctic are overall larger-bodied than their counterparts in zones that have

remained more climatically stable over the last 21 kya. This finding is possibly related to the better dispersal abilities of the largest species compared to the smaller ones (Whitmee & Orme 2013), which may have allowed them to more rapidly recolonize deglaciated landscapes and expand their ranges as temperatures warmed. In agreement with this result, Lyons et al. (2010) found a highly significant positive correlation between body size of Late Pleistocene mammals in North America and their range shifts in response to climate change. These authors also detected that Carnivora consistently had larger range shifts than Rodentia. It is likely that the existence of range size differences between climatically unstable and stable regions for Rodentia and its lack for Carnivora in our analyses for both biogeographic realms similarly reflect contrasting dispersal rates. In general, Carnivora daily range over wider areas than Rodentia (Carbone et al. 2005) and have higher maximum dispersal (Whitmee & Orme 2013). In other words, large-bodied more vagile carnivores may have been able to more rapidly spread and recolonize deglaciated regions, whereas rodents will need more time to colonize climatically suitable habitats that were affected by Quaternary climatic fluctuations.

Why do we observe body size differences between unstable and stable climates in the Nearctic but not in the Western Palearctic? Although we can only speculate on possible explanations, it is tempting to suggest that the differing responses have to do with the spatial extension of ice sheet and the temporal patterns of glacial retreat in each realm. Hawkins & Porter (2003) argued that North American mammals have had less time to recolonize deglaciated parts of the continent after the ice sheets melted compared to European species. Moreover, the geographical extension of glaciated areas in the Nearctic were larger than in the Palearctic, so that Eurasian organisms generally had to cover less distance to recolonize previously glaciated latitudes and have had more time to do it (Hawkins & Porter 2003). Consequently they expected stronger signal of past climates on North American than in European (especially those with more limited dispersal abilities) faunas.

Independently of body size, several studies have shown that other life-history traits such as lower reproductive capacity, greater food requirements and/or longer longevity are predictors of extinction risk in mammals (see e.g. Purvis et al. 2000; Cardillo et al. 2005).

However, our analyses do not detect significant differences in longevity and litter size between climatically unstable and stable regions in any of the continents. Johnson & Gaines (1990) suggested that if species have a higher capacity of movement, then individuals must possess the physical ability to disperse and survive to the dispersal process, but should also be able to successfully reproduce upon arrival in a climatically suitable environment. Perhaps the coarse grained nature of our study did not allow the detection of potential differences in these two life-history traits between unstable and stable parts of the Nearctic and Western Palearctic. We do not feel, however, that these results are an artifact of our analytical approach. Lyons et al. (2010) explored the relationship between range size and maximum lifespan and litter size of North American mammals over the last 40 kya and did not find significant correlations for any of the three different time slices they analyzed (Pre-Glacial to Glacial, Glacial to Holocene, Holocene to modern). Only when they analyzed the correlation between both life-history traits and shifts in distributional range centroids they were able to observe significant, albeit weakly explanatory, relationships. This may simply be reflecting the relationship between body size and range

shifts (Lyons et al. 2010). Bearing in mind our results, we agree with Lyons et al. (2010) that “the different orders of mammals do not have suites of traits that predetermine a particular type or magnitude of range shift in response to climate change and are consistent with the claim that species range shifts are individualistic”. Beyond geographic range size and body size it is difficult to infer the responsiveness of species distributions to climate change solely based on particular life-history traits. Species range shifts are a function of multiple extrinsic and intrinsic factors.

In conclusion, we found that climatically unstable areas over time have more widespread species and lower mammal species richness than stable regions in both continents. These findings are in agreement with the climatic stability and postglacial recolonization hypotheses and likely emerge from the interplay of intrinsic biological traits of species (dispersal abilities) with extrinsic environmental factors (climatic history). We detected stronger signatures of historical climatic instability on North American mammals possibly as a reflect of lagged responses to recolonize deglaciated regions (i.e. species in this region may have had less time to disperse after Pleistocenic glacial retreats

and the geographical extension of ice-sheets was larger than in Eurasia). However, we are unable to find a relationship between long-term climatic stability and other life-history traits (longevity and litter size) in any of the two biogeographic realms. We, therefore, conclude that beyond some biological traits typical of macroecological analyses such as geographic range size and body size it is difficult to infer the responsiveness of species distributions to climate change solely based on particular life-history traits.

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## Capítulo 4

Regla de Bergmann en los  
océanos? Temperatura determina patrones interespecíficos globales  
del tamaño corporal en mamíferos marinos

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Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Torres-Romero E.J., Morales-Castilla I., Olalla-Tárraga M.A (2015) Bergmann's rule in the oceans? Temperature determines global interspecific patterns of body size in marine mammals. *Global Ecology and Biogeography*.

# **Bergmann's rule in the oceans? Temperature determines global interspecific patterns of body size in marine mammals**

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## **Abstract**

**Aim** Bergmann's rule remains unexplored in marine mammals. We first examine at a global extent if these organisms show the same pattern reported for terrestrial mammals and then evaluate the influence of current environmental conditions and human impacts on the observed patterns.

**Location** Global

**Methods** We used range maps to document interspecific body size gradients and examined six environmental and human-based hypotheses. We analyzed the data using a comparative cross-species method and a spatially explicit assemblage approach at three different grain sizes (200 x 200 km, 400 x 400 km and 800 x 800 km). The associations between hypothesis-linked predictors and body size were analyzed through simple and multiple regressions that controlled for both spatial and phylogenetic autocorrelation.

**Results** We globally detected clear latitudinal body size gradients, following a Bergmannian pattern (i.e. increasing size polewards). Consistently across methodological approaches (cross-species and assemblage analyses) and grain sizes, sea surface temperature is the main driver of this pattern. Spatially, the role of temperature is most evident in the southern than in the northern hemisphere. Taxonomically, pinniped body sizes are critically constrained by temperature worldwide whereas cetacean size clines show a weaker, albeit dominant, association with temperature. In the northern hemisphere, salinity and primary productivity mostly determine body size variation in cetaceans. The secondary effect of human impacts on body size detected by OLS cross-species regressions is phylogenetically structured (i.e. mostly affects large-bodied species) and disappears once the evolutionary history of the clades is considered in PGLS regressions.

**Main conclusions** As in terrestrial mammals, our findings support heat conservation as an explanation for interspecific body size patterns in marine mammals worldwide. Pinnipeds, compared to cetaceans, have relatively larger surface to volume ratios and, hence, lower heat retention capacities which may explain why their body size distributions are more strongly associated with temperature variation.

**Keywords:** Bergmann's rule, Body size gradients, Heat conservation hypothesis, Human impact, Marine mammals, Macroecology, Spatial scales.

## INTRODUCTION

Understanding the geographic variation of species traits across latitudinal gradients is a central question in macroecology. A number of “ecogeographical rules” have been described to explain spatial patterns in the variation of morphological features of species across large-scale climatic gradients (Gaston *et al.*, 2008). Bergmann's rule, arguably the best-known ecogeographical rule, states that the body sizes of endothermic species in cold regions are larger than those of species that live in warmer regions (Bergmann, 1847). This rule was originally conceived, and is usually interpreted, as an adaptation of endothermic species and suggests that large-bodied species may be favored in colder climates due to the better body-heat retention resulting from their reduced surface-to-volume ratios (i.e. the heat conservation hypothesis).

Bergmann's rule was initially formulated as an interspecific geographic trend in endothermic vertebrates (Bergmann, 1847), but subsequent research on body size gradients has focused on two different levels of the biological organization: intra- and inter-specific. Interspecifically, Bergmann's rule has been studied following two approaches: the classical cross-species method and a more recent assemblage-based approach (Gaston *et al.*, 2008). The congruence between results produced

by both methods and the extent to which method selection can affect our perception of patterns and interpretation of possible underlying processes remains largely unexplored (but see Olalla-Tárraga *et al.*, 2010). Cross-species models treat each single species as a data point and inspect the relationships between body size and explanatory variables through bivariate plots, while controlling for phylogenetic non-independence. The assemblage-based approach uses spatial units of analysis and examines the geographic variation in average body size of co-occurring species within grid-cells (while controlling for spatial autocorrelation effects). The strengths and weaknesses of each approach have been discussed in detail in Olalla-Tárraga *et al.* (2010).

In endotherms, several studies have found support for the rule at the intraspecific level (Ashton, 2002; Meiri & Dayan, 2003). Similarly, interspecific patterns consistent with Bergmann's rule have been detected for both mammals (see. e.g. Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2008; Morales-Castilla *et al.*, 2012a) and birds (see e.g. Olson *et al.*, 2009; Morales-Castilla *et al.*, 2012b). Rodríguez *et al.* (2008) used a spatially explicit assemblage-based approach to document the existence of body size gradients in non-volant terrestrial mammals of the New World.

Interestingly, these authors found non-linear responses of body size to temperature, with a clear Bergmann-like pattern associated with temperature gradients in colder macroclimates (over most of the Nearctic), but not in warmer areas in the Neotropics. More recently, Clauss *et al.* (2013) conducted a worldwide cross-species analysis and documented an overall significant correlation between body mass and latitude in mammals.

Apart from the classical heat conservation hypothesis originally suggested by Bergmann (1847) as an explanation of the pattern, alternative hypotheses suggest that factors other than temperature may impose constraints to mammalian body size. Several abiotic and biotic features of the environment have been identified as potential drivers of size clines, including primary productivity, habitat and water availability, predation, competition or human impacts (see Gaston *et al.*, 2008; Olalla-Tárraga *et al.*, 2009; Diniz-Filho *et al.*, 2009). However, most studies on Bergmann's rule have simply examined the relationship between latitude or temperature with body size and have neglected the possible role played by this set of alternative hypotheses. Human impacts are a paradigmatic example. Now and in the past, humans have played a principal role in determining biodiversity changes and

have driven many mammal species, especially large-sized ones, to extinction (see e.g. Ceballos & Ehrlich, 2002). In the oceans, dolphins and whales have been exposed to human pressures for centuries, including illegal hunting activities for meat and body parts used in traditional medicine, thus showing high extinction rates at local, regional and global scales (Turvey *et al.*, 2007; Harkonen *et al.*, 2012). Despite the link between hunting pressures and increasing human population densities with the decline and extinction of large-bodied mammal species, studies on Bergmann's rule rarely take into account human impact variables among the set of possible explanatory variables (but see Diniz-Filho *et al.*, 2009).

The detection of large-scale body size patterns and their linkage with underlying ecological processes can be further confounded by scale-dependent issues. The concept of spatial scale has been traditionally applied in macroecology in two ways: spatial resolution (which refers to the size of minimum sampling unit or grid cells, also termed as grain size) and geographical extent (which refers to the extension of the study area and is defined as the maximum spatial dimension covered by the sample) (Rahbek, 2005). While the effect of spatial scale on geographical patterns of species richness has been widely

recognized in macroecology (Rahbek , 2005), its influence on body size gradients has been poorly elucidated. Both the perception of pattern and the explanatory power of independent variables are directly dependent on the scale of analysis (Rahbek & Graves, 2000), but there are no universal guidelines about which is the best grain size to analyze different kinds of data over coarse spatial scales. Hortal (2008) suggested that a spatial resolution of 100 km x 100 km is adequately fine to capture details about diversity variations, and coarse enough not to compromise the reliability of derived biodiversity measures. Similarly, Hurlbert & Jetz (2007) argued that analyses at scales of 200 km x 200 km or higher may be appropriate for less known taxa as amphibians or insects. Most continental and global-scale studies on terrestrial realms have relied on these two spatial resolutions. However, studies on global marine biodiversity have also been conducted at even larger grain sizes, such as 800 x 800 km (Tittensor *et al.*, 2010). Our main goal is to gain a better understanding on the determinants of large-scale body size gradients, by conducting the first global study of geographical interspecific patterns in body size for marine mammals and investigating the degree of support for several hypotheses that have been proposed to explain Bergmann's rule.

Marine mammals represent a suitable model group to test Bergmann's rule and examine the role of abiotic and biotic factors on latitudinal body size gradients. If the same processes determining body size variation in terrestrial mammals operate for marine mammals, then size clines in marine mammals should be strongly correlated with temperature (here operating across bathymetric and latitudinal gradients). Because of the different physical characteristics of marine and terrestrial environments, marine mammals have evolved a wide range of morphological and physiological adaptations for dealing with life in a medium with greater density, higher thermal conductance and capacity and lower oxygen concentration. Marine mammals do not have to spend the same amount of energy than their terrestrial relatives to maintain anatomical support structures, but have tended to select streamlined body shapes and a reduced number of body projections in order to aid movement and minimize inertial drag. A fusiform body shape with small appendages enhances locomotion through the dense aquatic medium and reduces heat loss (i.e. decreases the surface-to-volume ratios). Similarly, some marine mammals have a counter current heat exchange mechanism and/or layers of fur or blubber to better conserve heat. Nonetheless, we surprisingly do not



know yet if Bergmann's rule holds for this group of endotherms in the sea, much less the mechanisms responsible for such spatial variation (if any). As we are interested in the detection of global interspecific patterns in body size of marine mammals, we will compare the outcomes of two methods: cross-species and assemblage-based. Secondly, we aim to assess the congruence across three spatial resolutions (i.e. grain sizes) of the mechanisms explaining broad-scale body size gradients in the oceans. Finally, to better understand body size responses to abiotic and biotic features of the environment, we deconstruct our analyses by taxonomic group (cetaceans and pinnipeds), and hemisphere (Northern and Southern) respectively.

## MATERIALS AND METHODS

### Species data

Distribution maps of marine mammals were obtained from the IUCN Red List (<http://www.iucnredlist.org>, accessed in July 2014). The maps were processed using ARCGIS 10.0 to extract presences-absences of each species and map them onto an equal-area global grid at three different spatial resolutions (200 x 200 km, 400 x 400 km and 800 x 800 km, which approximately represent 2°, 4° and 8° at the Equator and constituted the different grain sizes in our study). We

excluded from the analysis those species that were outside of the marine realm as well as recently extinct species. This left a total of 115 species (33 pinnipeds, 79 cetaceans and 3 sirenians) for analysis. After excluding grid cells containing >10% of continental surface, we analyzed a total of 11015, 2878 and 799 cells for each grain size, respectively.

Body size data of adults (in grams) were extracted from the Pantheria database (Jones *et al.*, 2009). Data for species not included in Pantheria were completed from the literature. To conduct assemblage-based analyses, we obtained "mean body size" within each cell as our response variable, for which raw data was first log<sub>10</sub>-transformed to minimize the effects of the typically right-skewed distribution of body sizes (Rodríguez *et al.*, 2008).

### Environmental and human predictors

We used marine global coverage environmental layers from AquaMaps (Kaschner *et al.*, 2013) at a resolution of 0.5° to generate six explanatory environmental variables (see below). We also extracted data on human impacts on marine ecosystems (Halpern *et al.*, 2008). The values of the predictors were summarized for both the cross-species and the assemblage-based analyses. For the former, mean values of each predictor were

computed for each grid-cell at each of the grain sizes considered. For the latter, an average of the values of each predictor was calculated within each species geographic range. These variables could explain large-scale gradients in body size based on the following hypotheses:

1) Energy: we used sea surface temperature (SST) to test the heat conservation hypothesis, which predicts that large-bodied species are better adapted to cold climates due to the reduction of the surface area-to-volume ratio, which would be advantageous for their thermoregulation in cold environments (Bergmann, 1847).

2) Salinity: To survive in a hyperosmotic environment, marine mammals have to conserve freshwater and avoid dehydration. Unlike terrestrial mammals, marine mammals possess reniculate kidneys that allow them to maintain water and electrolyte homeostasis during prolonged periods of complete water and food abstinence and, hence, to occupy habitats with a broad range of salinity (Ortiz, 2001). Since reniculate kidneys of cetaceans and pinnipeds have likely evolved in response to their body sizes and diving abilities (Vardy & Bryden, 1981), we hypothesize that large body size may confer a better osmoregulatory capacity which would result in a positive association between size and environmental salinity (SAL).

3) Resource availability: Areas with higher productivity provide more food supply, which would be necessary to maintain species with large body size (Rosenzweig, 1968; Roman & McCarthy, 2010). We tested this hypothesis using net primary productivity (NPP).

4) Habitat preferences: We included distance to land (LD) as an indicator of habitat preference given that some marine species (i.e. pinnipeds) are restricted to areas fairly close to their terrestrial resting sites. Distance to resting sites can also be associated with the reproductive capacity or simply the ability to have pups (Boyd, 1998).

5) Habitat availability: This hypothesis has been proposed by Rodríguez *et al.* (2008) to explain body size gradients of terrestrial mammals in the Neotropical region (i.e. the occurrence of small species in highlands and large species in lowlands). We calculated the interaction between sea surface temperature and depth range (SST X DEPTH) to capture possible climatic effects on body size at the mesoscale.

6) Human impacts: This hypothesis predicts more severe human impacts on large-bodied species (i.e. cetaceans) and lower ones for the smaller ones (i.e. pinnipeds). We incorporated a metric of anthropogenic impacts (HIM) on marine ecosystems (Halpern *et al.*, 2008) to test the

importance of human pressures on body size.

### **Assemblage-based approach**

First, we calculated Pearson correlation coefficients to explore associations between explanatory variables and mean body size of marine mammals, while controlling for spatial autocorrelation using a modified Dutilleul's t-test (results provided in Appendix S1). We then used ordinary least squares multiple regression (OLS) to generate models with different combinations of predictors. We used an AIC-based approach to compare all possible combinations of explanatory variables and select the best-fit models (Burnham & Anderson, 2002). Specifically, we selected those models that contained valuable information (i.e. with  $\Delta AIC \leq 2$ ) which also have substantial support and should receive consideration in making statistical inferences. We estimated the coefficients of determination ( $R^2$ ) to evaluate the explanatory power of each regression model. Additionally, we used  $\Delta AIC$  values to calculate the Akaike weighting ( $w_i$ ) of each model which can be interpreted as the probability that the model is actually the best explanatory model. To identify possible collinearity among predictors, we calculated variance inflation factors (VIF) in our models, considering that VIF values lower than 10 indicate that collinearity is

not an issue (Olalla-Tárraga *et al.*, 2009). On the other hand, we also used spatial eigenvector mapping (SEVM) to evaluate the robustness of OLS standardized regression coefficients to spatial autocorrelation. This technique allows introducing the spatial structure of the data in multiple regression models, thus reducing spatial autocorrelation in the residuals (see Griffith & Peres-Neto, 2006 for more details of this method). We calculated spatial filters and minimized spatial autocorrelation in model residuals by selecting spatial filters until residual Moran's  $I$  coefficients were lower than 0.05 (Griffith & Peres-Neto, 2006). For computational reasons, spatial filters were only computed at the grain sizes of 400 km x 400 km and 800 km x 800 km. Also, following Meiri & Thomas (2007), we adjusted mean body size within grid cells by the number of species, using species richness values (SR) as weighting factors in OLS regressions. We conducted global, as well as separate analyses for the northern and southern hemispheres.

### **Cross-Species approach**

We run species-level analyses in order to assess whether the main drivers of body size variation were consistent across two different interspecific methods. In the cross-species approach, analysis units cannot be considered independent due to

phylogenetic autocorrelation (Felsenstein, 1985), but spatial autocorrelation is not of direct concern. That is, species that are closer in the phylogeny will tend to show more similar values of body size than expected at random (Blomberg *et al.*, 2003), which would inflate degrees of freedom of classical statistical tests. To evaluate the impacts of phylogenetic autocorrelation in our models, we compared OLS regressions with phylogenetic generalized least squares (PGLS). The latter method accounts for phylogenetic co-variation among species and yields unbiased regression coefficients and significance levels (Freckleton *et al.*, 2002). PGLS fits a linear model while adjusting a value of parameter  $\lambda$  (Pagel, 1999), which ranges from 0 to 1, with values close to 1 indicating that the response variable strongly fits a Brownian Motion model of evolution.

For phylogenetic analyses we utilized the super-tree from Fritz *et al.* (2009) because it provides an almost complete phylogeny of mammal species and because the whole tree is assembled following a systematic methodology. Additional phylogenetic hypotheses are available in the literature for Pinnipeds (Nyakatura *et al.*, 2012) and Cetaceans (Steeman *et al.*, 2009), and were utilized for the separate analyses of each of these taxonomic groups. Cross-species analyses were constrained to

include only species for which we had data on distributions, body size and phylogeny. Consequently, phylogenetic trees were pruned to only include those species meeting this requisite. After conforming our data to the taxonomy of Wilson & Reader (2005) to avoid taxonomic discrepancies, our cross-species analyses encompassed a total of 97 species (of which 68 species were cetaceans and 29 were pinnipeds). We excluded all sirenians from these analyses as they comprise a clade with too few species to perform a phylogenetic analysis.

## RESULTS

Mean body size shows a clear geographical gradient globally, exhibiting a marked latitudinal Bergmann's rule pattern, with the largest sizes found towards the poles and the smallest sizes towards the equator (Fig. 1). Our best OLS models at the assemblage level (i.e. those with  $\Delta AIC \leq 2$ ) produced qualitatively similar results across the three grain sizes (Table 1), so hereafter we will specifically refer to those obtained at a spatial resolution of 200 x 200 km. Global analyses for all species identified the dominant role of sea surface temperature (SST), salinity (SAL) and net primary productivity (NPP) in accounting for the spatial variation in body size (Table 1). Standardized regression coefficients

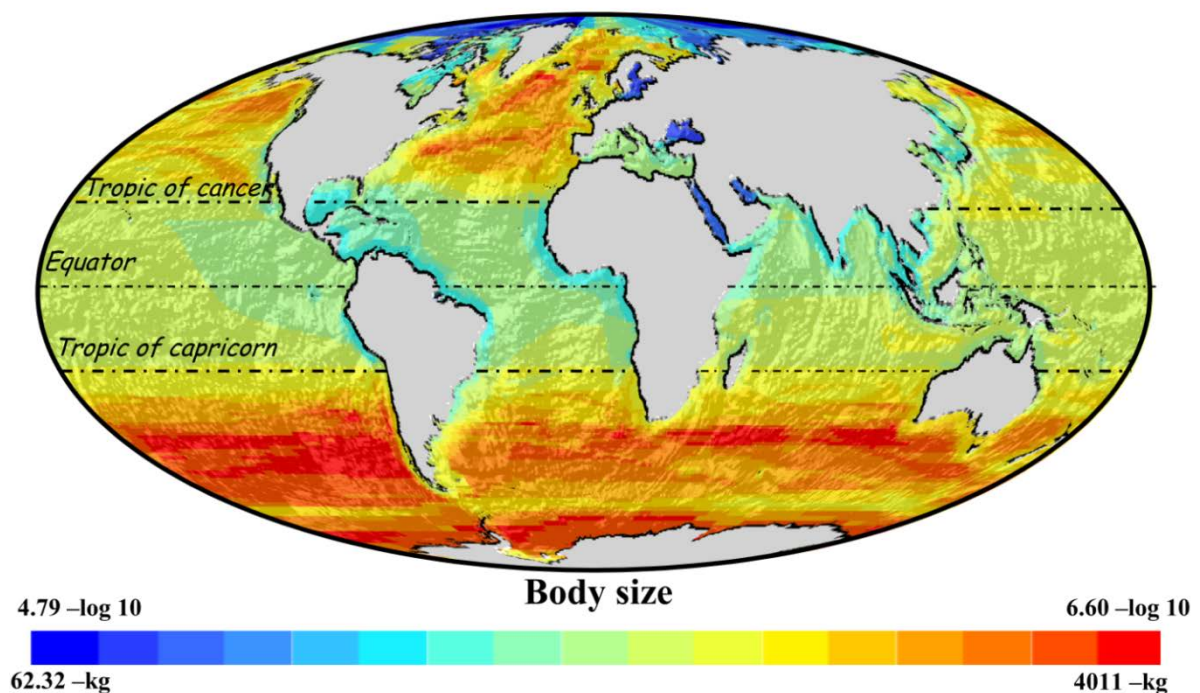
indicated that SST is the strongest predictor in the southern hemisphere and SAL in the northern hemisphere. Analyses for pinnipeds clearly identified SST as the most important driver of body size variation in all cases, either globally or for each hemisphere separately (Table 1). In cetaceans, however, SST only becomes the strongest predictor in the southern, but not the northern hemisphere. At the global scale and in the northern hemisphere, NPP and SAL better explained the variation in cetacean mean body size. Multiple regression models accounted for large proportions of variance in all cases but had higher explanatory power (between 60.9 and 82.6%) in the southern hemisphere (Table 1). SEVM models were able to substantially reduce residual autocorrelation and presented higher coefficients of determination (Table 1) but did not alter the sign and ranks of the standardized regression coefficients obtained through non-spatial OLS models (results not shown). Furthermore, these relationships remained robust after accounting for potential effects of species richness (Appendix S2).

In global OLS cross-species models, land distance and human impacts ranked first and second, respectively, as predictors of body size variation (Table 2). However, when phylogenetic relationships were accounted for in

PGLS models, SST emerged as the only variable significantly associated to body size variation. For pinnipeds, SST was consistently the only significant predictor of body size variation regardless of whether phylogenetic relationships were accounted for or not (Table 2). PGLS analyses for cetaceans also detected SST as major driver of body size, with a secondary role of NPP (Table 2). Interestingly, increasing body size with decreasing temperature remained as the main predictor after phylogenetic relatedness was considered, in all cases. It is to note that body size had a strong phylogenetic signal for all three groups as indicated by  $\lambda = 1$ .

## DISCUSSION

Our results reveal a strong cline in species' body size increasing from the equator towards the poles. Both cross-species and assemblage-based analyses show congruent responses and confirm that interspecific body size patterns are mostly associated with the variation in sea surface temperature, even after controlling for phylogenetic and spatial non-independence. The association of sea surface temperature with body size gradients is stronger for pinnipeds than for cetaceans, but both taxonomic groups show a negative temperature-size relationship regardless whether we disaggregate by



**Figure 1.** Geographic distribution patterns of body size in marine mammals of the world. Numbers included in the legend of the map are represented using averages of log10-transformed body masses and units are in kilograms.

hemispheres or consider the whole world. This spatial pattern and the importance of temperature as primary driver is robustly the same across the three grain sizes that we examined (200 x 200 km, 400 x 400 km and 800 x 800 km). Altogether, these results provide evidence strongly supporting Bergmann's rule in marine mammals at the global scale.

Our findings agree with most empirical evidence in terrestrial environments, where temperature and potential evapotranspiration are typically the most important environmental drivers of

mammal body size patterns, either in the Western Hemisphere (Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2008; Morales-Castilla *et al.*, 2012a) or in Europe (Rodríguez *et al.*, 2006). In marine realms, despite the limited number of studies on Bergmann's rule, several authors have detected a relationship between temperature or energy availability and body size variation for marine fishes (Lindsey, 1966), bivalves (Berke *et al.*, 2013), crabs (Defeo & Cardoso, 2002) and copepods (Lonsdale & Levinton, 1985).

**Table 1.** Multiple regression models for body size against environmental and human variables. For each model predictor we report standardized partial regression coefficients in OLS regression. Coefficients of determination ( $R^2$ ) of OLS and SEVM models are also provided. Abbreviations: HIM (human impact), SST (sea surface temperature), SAL (salinity), NPP (net productivity primary), LD (land distance), SSTxDEPTH (interaction between sea surface temperature and depth range).

		Predictor in model							R <sup>2</sup>		
Taxonomic level	Region	HIM	SST	SAL	NPP	LD	SST X DEPTH	Wi	OLS	SEVM	
200 km x 200 km											
Global	Both hemispheres	0.059	-0.373	0.524	0.209	0.278	0.075	1	0.341		
	Northern hemisphere	0.321	-0.072	0.331	0.258	0.155	0.082	0.999	0.454		
	Southern hemisphere	0.167	-0.806	0.062	-0.049	0.206	-0.018	0.533	0.609		
Pinnipeds	Both hemispheres	0.035	-0.943	0.042	0.149	0.021	0.044	0.999	0.743		
	Northern hemisphere	0.107	-0.954	-0.017	0.086	0.005	0.039	0.501	0.763		
	Southern hemisphere	0.052	-0.944	0.031	0.201	-0.01	0.025	0.501	0.751		
Cetaceans	Both hemispheres	0.024	-0.204	0.382	0.256	0.082	0.041	0.806	0.165		
	Northern hemisphere	0.164	0.011	0.211	0.296	0.023	0.040	0.402	0.241		
	Southern hemisphere	-0.065	-0.861	0.041	-0.121	-0.077	-0.007	0.649	0.826		
Sirenians	Both hemispheres	-0.151	0.275	-0.015	0.196	-0.188	0.119	0.558	0.196		
400 km x 400 km											
Global	Both hemispheres	0.029	-0.426	0.535	0.194	0.277	0.111	0.538	0.361	0.527	
	Northern hemisphere	0.285	-0.179	0.377	0.257	0.151	0.127	0.995	0.431	0.828	
	Southern hemisphere	0.141	-0.793	0.034	-0.067	0.214	-0.011	0.365	0.609	0.871	
Pinnipeds	Both hemispheres	0.028	-0.958	0.042	0.174	0.026	0.059	0.761	0.738	0.752	
	Northern hemisphere	0.108	-0.985	-0.004	0.104	0.008	0.067	0.494	0.751	0.848	
	Southern hemisphere	0.034	-0.899	-0.013	0.227	-0.002	0.013	0.265	0.752	0.877	
Cetaceans	Both hemispheres	0.004	-0.247	0.382	0.223	0.057	0.041	0.352	0.156	0.185	
	Northern hemisphere	0.124	-0.067	0.246	0.269	0.003	0.041	0.292	0.189	0.667	
	Southern hemisphere	-0.089	-0.852	0.031	-0.134	-0.065	0.016	0.438	0.826	0.949	
Sirenians	Both hemispheres	-0.136	0.405	-0.006	0.125	-0.268	0.054	0.494	0.251	0.255	
800 km x 800 km											
Global	Both hemispheres	0.271	-0.345	0.452	0.125	0.158	-0.027	0.707	0.322	0.691	
	Northern hemisphere	0.536	-0.135	0.272	0.153	0.025	-0.051	0.331	0.463	0.681	
	Southern hemisphere	0.118	-0.776	0.043	-0.164	0.179	-0.028	0.412	0.664	0.748	
Pinnipeds	Both hemispheres	0.062	-0.984	0.017	0.184	0.038	0.075	0.296	0.714	0.775	
	Northern hemisphere	0.176	-1	-0.03	0.091	0.033	0.095	0.229	0.706	0.762	
	Southern hemisphere	0.044	-0.992	0.068	0.268	0.001	0.023	0.192	0.751	0.793	
Cetaceans	Both hemispheres	0.222	-0.192	0.321	0.147	-0.052	-0.087	0.351	0.171	0.407	
	Northern hemisphere	0.327	-0.035	0.189	0.159	-0.116	-0.101	0.371	0.232	0.411	
	Southern hemisphere	-0.108	-0.815	0.015	-0.179	-0.043	0.035	0.366	0.834	0.871	
Sirenians	Both hemispheres	-0.172	0.271	-0.014	0.085	-0.242	0.374	0.651	0.382	0.388	

Sea surface temperature has also been found to be the predictor that better explains geographical gradients of species diversity across 13 different marine taxa at the global level (Tittensor *et al.*, 2010).

Of the six hypotheses that we examined, the heat conservation hypothesis received the strongest support, suggesting that large-bodied species are favored in colder environments because their reduced surface-to volume ratios allows them for better heat retention than smaller species. However, the observed spatial patterns of interspecific variation in body size in marine mammals are also partially driven by other environmental factors. The prevailing effect of sea surface temperature on body size changes depends on the spatial and taxonomic scale of analysis. Spatially, the role of surface temperature is most evident in the southern than in the northern hemisphere, an asymmetry already noted by Clarke (2009) as essential to account for macroecological and macrophysiological patterns in marine organisms. Taxonomically, pinniped body sizes are critically constrained by sea surface temperature worldwide whereas cetacean size clines show a weaker, albeit dominant, association

with temperature. In the northern hemisphere, salinity and primary productivity mostly determine body size variation in cetaceans. Pinnipeds, compared to cetaceans, have relatively larger surface to volume ratios and, hence, lower heat retention capacities which may explain why their body size distributions are more strongly associated with temperature variation. In addition to this, the observed temperature-size relationships may be in part mediated by latitudinal changes of upper trophic structure in the oceans. Pinnipeds are top predators in cold regions, but their difficulty of capturing fish prey and increasing vulnerability to predation by large ectothermic and partially endothermic sharks displaces them as leading predators in the tropics and subtropics (Cairns *et al.*, 2008). On the contrary, toothed whales can occupy all ocean temperature zones and are unaffected by such temperature dependent predation success (Cairns *et al.*, 2008). To some degree, this may also account for the contrasting responses of pinnipeds and cetaceans to primary productivity. However, the variable best accounting for body size variation in cetaceans worldwide and in the northern hemisphere is salinity.



**Table 2.** Model outputs for ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) regressions for the relationship between body size and predictor variables. Asterisks (\*) identify significance level ( $p < 0.05$ ). Abbreviations as in Table 1.

	Predictor in model						$\lambda$	$R^2$	LogLik
	HIM	SST	SAL	NPP	LD	SST X DEPTH			
Global	0.259*	-0.110	-0.031	-0.142	0.510*	-0.052	0.000	0.311	-119.082
Global PGLS	-0.038	-0.182*	0.046	-0.023	0.024	0.087	1.000	0.153	-53.652
Pinnipeds	-0.311*	-1.189	0.363	0.275	0.125*	1.062	0.000	0.292	-95.818
Pinnipeds.PGLS	-0.015	-0.690*	0.112	-0.015*	-0.151	0.434	1.000	0.253	-31.758
Cetaceans	0.199	-0.187*	-0.063	-0.286	0.484	0.064	0.000	0.262	-31.891
Cetaceans.PGLS	-0.028	-0.178*	0.097	-0.143	-0.028	0.094	1.000	0.190	-23.525

In accordance with our initial expectation, the largest species of marine mammals (i.e. cetaceans) show a positive association between environmental salinity and body size. The osmoregulatory capacity of marine mammals remains to be further studied experimentally, but a critical factor to maintain water and electrolyte homeostasis in the oceans has been the evolution of reniculate kidneys. Because this physiological adaptation is linked to the evolution of body sizes and diving abilities (Vardy & Bryden, 1981), we speculate on the possibility that the largest cetaceans would have better abilities to cope with hyperosmotic environments than the relatively small-bodied pinnipeds. Contrarily to Tittensor *et al.* (2010), who examined global environment-richness relationships across different marine

taxa, we could not detect stronger positive relationships with primary productivity than sea surface temperature. This, together with our multiple regression models with species richness as a weighting factor, is a strong indication that our findings on the determinants of large-scale body size gradients for marine mammals are not a statistical artifact of the uneven distribution of species richness or the assemblage method (Meiri & Thomas, 2007).

Cross-species analyses consistently show negative associations between sea surface temperature and species' body sizes once their evolutionary relationships are accounted for (Table 2), supporting the traditional heat conservation hypothesis. The strong phylogenetic signal in mammal body size (with Pagel's  $\lambda$  values equal to

unity) is consistent with previous findings for carnivores (Diniz-Filho *et al.*, 2009), mammals (Morales-Castilla *et al.*, 2012a; Clauss *et al.*, 2013), birds (Morales-Castilla *et al.*, 2012b) or salamanders (Olalla-Tárraga *et al.*, 2010), and calls for phylogenetically-explicit cross-species analyses of body size. Nonetheless, most previous studies on Bergmann's rule have focused on the role of temperature and other environmental variables as explanations for size gradients, but have often neglected the potential effects of human impacts. Over the last two centuries, the intensity of human activities (i.e. hunting, human population growth and habitat loss among others) has increased dramatically and has resulted in a main source of biodiversity loss (Ceballos & Ehrlich, 2002). The effects of these interactions with humans can provoke the contraction of geographical ranges and the extinction of populations or even species of marine mammals. For instance, Turvey *et al.* (2007) and Harkonen *et al.* (2012) have pointed towards human impacts as the principal cause of mortality in many populations of cetaceans worldwide. Our phylogenetic analyses might not be able to adequately capture the role of such contemporary impacts on body size gradients if these are phylogenetically structured as well. So is reflected by the significant

association of body size with human impacts (and also habitat preferences) for cetaceans and for all species in non-phylogenetic models (Table 2). Both predictors have a relatively high ( $\lambda > 0.79$ ) and significant ( $p < 0.001$ ) phylogenetic signal, and hence the significance of their associations with a phylogenetically structured response variable disappears in a PGLS context. That is, OLS cross-species regressions identify an effect of human impacts on body size clines but since such impacts are only recent and affect certain species (i.e. large-sized ones) more than others, environmental variables prevail over human impacts as an explanation of size gradients once the evolutionary history of the clades is considered.

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## **BIOSKETCHES**

E. Joaquín Torres-Romero is a PhD student under the supervision of Assoc. Prof. Miguel Á. Olalla Tàrraga. Both share a scientific interest in macroecology, macroevolution and conservation biogeography of terrestrial vertebrates. Ignacio Morales-Castilla is a postdoctoral fellow at McGill University in Canada.

## Supporting Information

### **Bergmann's rule in the oceans? Temperature determines global interspecific patterns of body size in marine mammals**

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**Appendix S1.** Pearson correlation coefficients of environmental and human variables against body size at the global and taxonomic level. Abbreviations: HIM (human impact), SST (sea surface temperature), SAL (salinity), NPP (net productivity primary), LD (land distance), SSTxDEPTH (interaction between sea surface temperature and depth range). Significance levels are corrected for spatial autocorrelation using the modified t-test developed by Dutilleul (1993). Asterisks (\*) identify significant level ( $p < 0.05$ ) after the modified t-test of Dutilleul. We also include correlation coefficients for species richness (SR) as predictor.

	Predictors						
Region	HIM	SST	SAL	NPP	LD	SST X DEPTH	SR
<u>800 km x 800 km</u>							
Global	0.263*	0.025	0.442*	0.178*	0.231*	-0.009	0.518*
Pinnipeds	-0.388*	-0.821*	-0.292*	-0.069	-0.091	-0.641*	0.775*
Cetaceans	0.235*	0.035	0.292*	0.218*	0.009	0.021	0.272*
Sirenians	0.201*	0.465*	0.111	0.214*	-0.281*	0.552*	0.995*
<u>400 km x 400 km</u>							
Global	0.104	-0.041	0.464*	0.054	0.307*	-0.042	0.501*
Pinnipeds	-0.378*	-0.841*	-0.310*	-0.012	-0.103	-0.663*	0.787*
Cetaceans	0.088	-0.009	0.303*	0.152*	0.068	-0.013	0.239*
Sirenians	0.119	0.369*	0.066	0.218*	-0.267*	0.343*	0.997*
<u>200 km x 200 km</u>							
Global	0.141	-0.009	0.451*	0.051	0.298*	-0.035	0.537*
Pinnipeds	-0.372*	-0.848*	-0.331*	-0.011	-0.102	-0.595*	0.782*
Cetaceans	0.134*	0.047	0.312*	0.174*	0.078	0.019	0.310*
Sirenians	0.075	0.290*	0.028	0.251*	-0.237*	0.282*	0.999*

**Appendix S2.** Multiple-regression models for body size against environmental and human variables. We provided results of the standardized regression coefficients of the predictors included for OLS. In the models included Weighting factor (SR). Additionally, we show their corresponding coefficients of determination ( $R^2$ ) according to ordinary least-squares (OLS), and spatial eigenvector mapping (SEVM). Abbreviations as in Appendix S1.

		Predictor in model						R <sup>2</sup>			
Taxonomic level	Region	HIM	SST	SAL	NPP	LD	SST X DEPTH	SR	Wi	OLS	SEVM
<u>200 km x 200 km</u>											
Global	Both hemispheres	0.008	-0.591	0.271	-0.044	0.141	0.011	0.739	0.348	0.565	
	Northern hemisphere	0.156	-0.542	0.172	0.019	0.109	0.022	0.899	0.303	0.618	
	Southern hemisphere	0.195	-0.791	0.066	-0.014	0.211	-0.018	-0.079	0.285	0.612	
Pinnipeds	Both hemispheres	0.037	-0.718	-0.001	0.121	0.059	0.038	0.251	0.728	0.761	
	Northern hemisphere	0.084	-0.692	-0.062	0.017	0.043	0.031	0.311	0.762	0.799	
	Southern hemisphere	0.062	-0.76	0.037	0.211	0.035	0.022	0.214	0.831	0.757	
Cetaceans	Both hemispheres	-0.009	-0.444	0.259	0.129	-0.022	0.009	0.477	0.371	0.228	
	Northern hemisphere	0.071	-0.376	0.134	0.184	-0.026	0.007	0.594	0.517	0.285	
	Southern hemisphere	0.043	-0.694	0.068	0.007	-0.029	-0.011	-0.364	0.303	0.865	
Sirenians	Both hemispheres	0.001	-0.001	0.006	0.001	-0.001	0.001	0.999	0.178	0.991	
<u>400 km x 400 km</u>											
Global	Both hemispheres	-0.021	-0.586	0.313	-0.039	0.156	0.043	0.658	0.353	0.541	0.653
	Northern hemisphere	0.138	-0.519	0.227	0.025	0.108	0.058	0.781	0.383	0.571	0.855
	Southern hemisphere	0.199	-0.765	0.041	-0.004	0.218	-0.016	-0.148	0.343	0.619	0.901
Pinnipeds	Both hemispheres	0.024	-0.719	-0.001	0.141	0.062	0.051	0.256	0.551	0.755	0.794
	Northern hemisphere	0.083	-0.709	-0.053	0.035	0.045	0.054	0.308	0.664	0.784	0.796
	Southern hemisphere	0.039	-0.691	0.006	0.237	0.043	0.008	0.245	0.435	0.758	0.649
Cetaceans	Both hemispheres	-0.021	-0.419	0.288	0.121	-0.022	0.011	0.371	0.231	0.195	0.226
	Northern hemisphere	0.049	-0.343	0.182	0.169	-0.039	0.006	0.467	0.202	0.219	0.668
	Southern hemisphere	0.031	-0.689	0.062	-0.005	-0.029	0.001	-0.371	0.398	0.863	0.961
Sirenians	Both hemispheres	0.006	-0.007	0.007	-0.008	-0.003	0.005	0.998	0.715	0.996	0.996
<u>800 km x 800 km</u>											
Global	Both hemispheres	0.144	-0.412	0.281	-0.085	0.062	-0.112	0.617	0.611	0.471	0.686
	Northern hemisphere	0.341	-0.311	0.178	-0.027	-0.005	-0.104	0.617	0.307	0.545	0.676
	Southern hemisphere	0.233	-0.808	0.087	-0.045	0.179	-0.011	-0.264	0.367	0.697	0.817
Pinnipeds	Both hemispheres	0.021	-0.709	-0.031	0.141	0.074	0.073	0.281	0.263	0.736	0.785
	Northern hemisphere	0.091	-0.738	-0.072	0.025	0.073	0.093	0.313	0.232	0.741	0.775
	Southern hemisphere	0.046	-0.712	0.091	0.261	0.041	0.014	0.313	0.222	0.764	0.805
Cetaceans	Both hemispheres	0.171	-0.315	0.247	0.054	-0.117	-0.126	0.344	0.418	0.203	0.423
	Northern hemisphere	0.244	-0.195	0.152	0.084	-0.146	-0.127	0.334	0.195	0.248	0.416
	Southern hemisphere	0.035	-0.739	0.087	-0.037	-0.022	0.045	-0.381	0.148	0.878	0.926
Sirenians	Both hemispheres	0.006	-0.005	0.005	-0.007	-0.004	0.011	0.991	0.075	0.991	0.991

## Capítulo 5

Análisis de ruta filogenética revela la importancia de los rasgos biológicos relacionados con nichos sobre el tamaño del rango geográfico en mamíferos

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Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Olalla-Tárraga M.Á., Torres-Romero E.J., Ferreira-Amado T., & Martínez P.A. (2015) Phylogenetic path analysis reveals the importance of niche-related biological traits on geographic range size in mammals. *Global Change Biology*. DOI: 10.1111/gcb.12971

## **Phylogenetic path analysis reveals the importance of niche-related biological traits on geographic range size in mammals**

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The geographic range of a species is arguably the basic unit in biogeography and macroecology (Brown *et al.*, 1996). In particular, there has been a long-standing interest in understanding the mechanisms that shape the immense interspecific variation in geographic range size, a question often framed around Rapoport's rule (Whitton *et al.* 2012). As an emergent species-level trait, range sizes reflect the interplay of ecological and evolutionary processes and are of utmost importance for predicting speciation-extinction dynamics (Jablonski 2008). Species tend to have a higher risk of extinction if they occupy a small geographical range (Purvis *et al.* 2000), which also places the investigation of patterns and processes in the variation of species' range sizes as a central question in applied conservation science.

In a recent paper, Di Marco & Santini (2015, and hereafter DM&S) analysed which are the determinants of range size variation in extant terrestrial mammals globally. They concluded that extrinsic factors (climate and human impacts), not intrinsic biological traits, are the most influential variables. This study brings to the table the importance of considering anthropogenic effects in macroecological research. Surprisingly, even for the best-studied taxa in macroecology such as mammals and birds, workers have traditionally overlooked the influence of human

pressures on the observed patterns. We ourselves have called the attention on the need to incorporate human impact metrics, such as human footprint or accessibility, to better understand the spatial distribution of extant mammal species in some biogeographical realms (Torres-Romero & Olalla-Tárraga, 2015). However, we do not agree that human effects prevail over biological traits in determining the range sizes of mammalian species and would like to call the attention on a few conceptual and methodological aspects of DM&S's analyses and interpretation that are not at all correct to our view.

First, DM&S neglect the relevance of phylogenetic relatedness on the geographic range sizes of species. Intrinsic autoecological features of mammals often reflect shared ancestry, so that closely related species will tend to share similar biological traits and possibly similar range sizes (Brown, 1996, Jablonski 2008). A number of comparative methods have been designed to address potential phylogenetic correlation issues in model residuals (as long as there is an underlying robust phylogenetic hypothesis, as is the case for mammals). Second, DM&S also ignore the importance of the relationship niche breadth-range size as a biological explanation (Slatyer *et al.* 2013). The concept of ecological niche was indeed formalized to describe the set of biotic

and abiotic conditions where a species can persist and maintain stable population sizes. Its projection onto geographical space (i.e. the duality niche-biotope) is inextricably linked to the spatial distribution of a species and is highly relevant to analyse biogeographical patterns (Colwell & Rangel 2009). DM&S only incorporate a simplistic diet category variable that classifies mammals in terms of trophic position (i.e. carnivores, herbivores or omnivores), but do not consider diet breadth. Perhaps more importantly, DM&S characterized and included in the analyses the realized climatic niches of each mammal species (see also Olalla-Tárraga *et al.* 2011 for a similar estimation method), but erroneously referred to them as extrinsic variables. These measures of environmental tolerance breadth typically have a strong positive relationship with range size (Slatyer *et al.* 2013). Third, DM&S use random forest regression models that allow estimating direct effects between each predictor and the response variable, but cannot calculate indirect effects via other dependent variables.

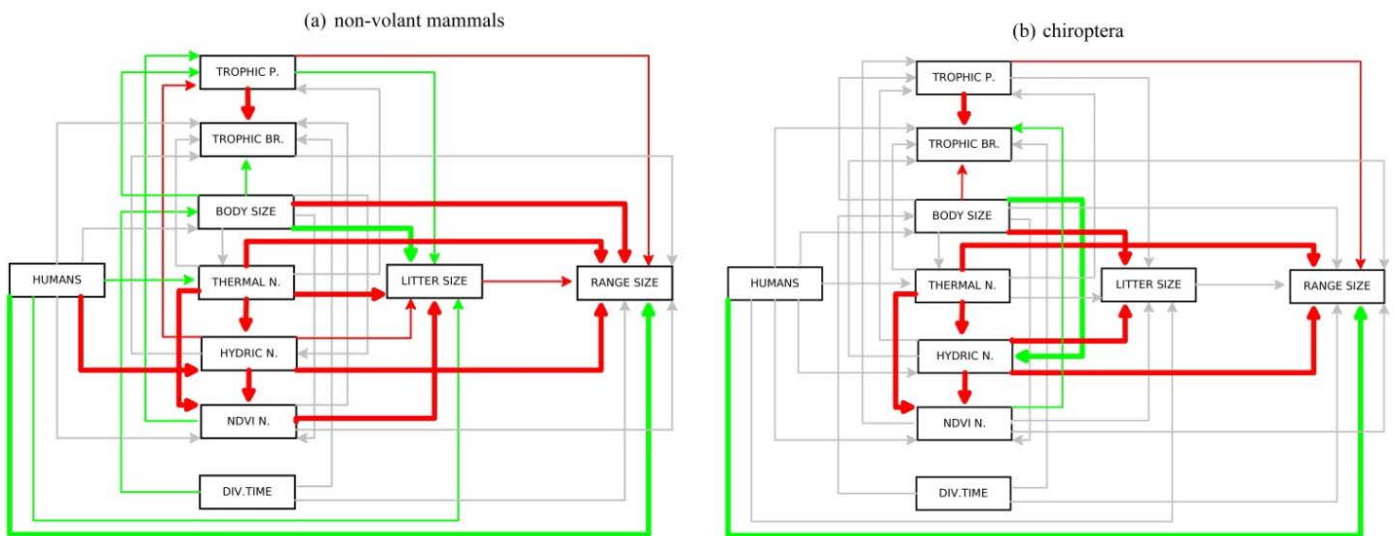
We have used a recently developed phylogenetic confirmatory path analysis (von Hardenberg & Gonzalez-Voyer, 2013) and included previously untested variables to provide a reassessment on which are the main determinants of range size in mammals globally (for

methodological details see supplementary information). We find that the range sizes of both non-volant mammals and chiropterans strongly depend on their thermal and hydric niches, an intrinsic biological property, followed by a secondary extrinsic effect of human impacts (Figure 1, Table 1). Although these results essentially concur with DM&S, note that our interpretation differs (see above). More strikingly, for non-volant mammals we detect that the total effects of body size on range size are quantitatively similar, albeit of different sign, to those of human impacts (Table 1) a relationship not unveiled by DM&S's analyses. The importance of other niche-related biological traits for range size also emerges when we conduct separate analyses at the level of taxonomic order. In rodents, litter size shows total effects again similar to those of human impacts and also becomes of secondary importance in determining range size. Primates and Cetartiodactyla also display a leading role of climatic niches in determining range size, but for these two taxonomic orders our analyses identify the secondary importance of trophic niche breadth (with total effects even higher than those of human impacts in the latter case).

In sum, using phylogenetically-informed path analyses our results agree with those of DM&S in identifying the

importance of human impacts for the distribution of extant mammal species worldwide. However, we cannot conclude, as DM&S do, that such effects are prevalent over those of niche-related biological traits. The climatic niches of extant mammalian species primarily determine their

observed range sizes and intrinsic biological characteristics of species such as their body sizes or dietary niche breadths are of secondary importance, together with human impacts.



**Figure 1.** Phylogenetic Path Analysis (PPAs) with arrows representing direct and indirect effects of explanatory variables on mammal range sizes. Green arrows represent negative effects and red arrows represent positive effects significant at  $p$  values < 0.05. Thick lines correspond to relationships with standardized partial regression coefficients greater than 0.10. Light gray arrows represent non-significant relationships ( $p$  values > 0.05). These figures represent the best-fit model (Model 7, see Figure S1 and Appendix S1, S2 in Supporting Information for further details) according to a CIC-based approach (i.e. a modified version of Akaike Information Criterion) that considers all possible links between explanatory variables. A) non-volant mammals and B) Chiroptera . Abbreviations as in Table 1.

**Table 1.** Standardized total effects, direct effects and indirect effects between explanatory variables and the global range sizes of mammal species estimated through Phylogenetic Path Analysis. Abbreviations are: HUMANS, human footprint; TROPHIC P, trophic position; TROPHIC BR, trophic breadth; THERMAL N, thermal niche; HYDRIC N, hydric niche; NDVI N, productivity niche, DIV. TIME, evolutionary divergence time.

Group	Effect	Explanatory variables								
		Humans	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Div.Time	Litter size
Non-volant mammals	Direct	-0.201	0.047	-	0.151	0.256	0.233	-	-	0.055
	Indirect	0.014	-0.002	-	-0.019	0.042	0.008	0.007	-	-
	Total	-0.187	0.045	-	0.132	0.298	0.241	0.007	-	0.055
Chiroptera	Direct	-0.236	0.089	-	-	0.315	0.246	-	-	-
	Indirect	-	-	-	-0.031	0.084		-	-	-
	Total	-0.236	0.089	-	-0.031	0.399	0.246	-	-	-

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## Supporting Information

### **Phylogenetic path analysis reveals the importance of niche-related biological traits on geographic range size in mammals**

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#### **MATERIAL AND METHODS**

##### **GEOGRAPHIC RANGE SIZE AND LIFE- HISTORY TRAITS**

Mammal range maps were compiled from the IUCN Red List (<http://www.iucnredlist.org>, accessed in November 2014). The maps were processed using ARCGIS 10.0 to extract presences-absences of each species in a global grid comprising 96.5 x 96.5 km cells with an equal-area Berhmann projection (approximately 1° at the equator). We excluded from the analysis marine mammals as well as introduced and extinct species. The database comprises a total of 5002 mammal species at the global level, whose distribution ranges sizes were calculated in square kilometers for each species.

We compiled information on adult body size and litter size, two biological traits that are commonly used as predictors of extinction risk in terrestrial mammals (Cardillo et al. 2004; Murray et al. 2011) and have a potential relationship with range size. The data were obtained from "Pantheria" (Jones et al. 2009), which contains more than 5416 species records. To fill missing values, we used the imputation method proposed by Penone et al. (2014, see also Di Marco et al. 2012; Pacifici et al. 2013 for further

details). We followed Wilson & Reeder's (2005) taxonomy. Body size, litter size and range size were log-10 transformed.

We also included "Trophic position" and "Trophic Breadth" as biological traits. Data were obtained from Kissling et al. (2014) and Wilmann et al. (2014). We defined the trophic position of a species as a measure of its particular diet preferences, which can have an influence on spatial requirements (Santini et al. 2014). We classified species as carnivores (coded as 4), omnivorous (3), insectivorous (2) and herbivorous (1). This latter category includes species whose principal diet items are plant, seed, fruit, nectar, root, leaf, woody and herbaceous species. Trophic breadth was quantified taking into account the range of food sources utilized. We classified all species from generalists to specialists along a trophic specialization gradient using Levin's index, given by:

$$\hat{B} = \frac{1}{\sum p_i^2}$$

Where  $p_i$  is the proportion of all food items in the diet of the individual  $i$ .

We characterized the realized climatic niche of species following Olalla-Tárraga et al. (2011). The thermal niche was estimated from the difference between maximum temperatures of the warmest month (Bio5) and minimum temperatures of the coldest month (Bio6) experienced by each species and obtained from World-Clim (Hijmans et al. 2005). Hydric Niche was estimated from the difference between precipitations in the wettest month (bio13) and the driest month (bio14) from World-Clim (Hijmans et al. 2005). All World-clim variables were obtained at a spatial resolution of 2.5 arc-min.

As a complement to diet variables, we also estimated the productivity niche as the difference between maximum and minimum NDVI data experienced by each species. NDVI were calculated from monthly values for the period 1982–2000 with a resolution of 5 arc-min (=0.083°).

To quantify the effect of human impacts on mammal's range size, we used the human footprint metric, a variable combining global records of population density, land use, transport access (roads, rivers, etc.), and electrical power infrastructure with resolution of 1 km (Sanderson et al. 2002). This variable has already been shown to have an influence on mammal distributional ranges (Torres-Romero & Olalla-Tárraga, 2015).

We used the mammal supertree of Fritz et al. (2009), an almost-complete species-level phylogeny of mammals, to calculate divergence time and account for the possible effect of the evolutionary time of origin of species on range sizes. The evolutionarily oldest species have had more time to explore all potential geographic areas according to their life-history traits than younger species (Willis 1922).

## STATISTICAL ANALYSES

### PHYLOGENETIC PATH ANALYSIS

The use of phylogenetic comparative methods has become widely used and allowed ecologists to incorporate information about species relatedness to analyze evolutionary processes (Felsenstein 1985). Despite the facility of use of comparative analyses to explore the relationship between several variables and traits of interest, such analyses do not allow the interpretation of causality among variables all together (Gonzalez-Voyer & von Hardenberg 2014). Thereby, when the relationship between explanatory variables is not clear the use of alternative methods is needed. Confirmatory path analysis is one method that was specifically developed to consider simultaneous interactions among traits (Shipley 2009). In path analysis, pre-specified causal hypothesis are represented in form of directed acyclic graphs (DAGs) which are supported by published literature. In DAGs of hypothesized causal models is possible to identify pairs of variables that are probabilistically independent by holding constant some other variables. This is the principle of *d-separation* (d-sep) proposed by Shipley (2000) and it is similar to a statistical control. With d-sep, the conditional probabilistic independencies can be tested with traditional statistical tests and also be tested if they are fulfilled by our observations. The last is done using the Fisher's C test and when the causal model is correct the C statistic is not significant. However, as has been discussed in the literature, observed data points in multiple species are not statistically independent due a common ancestry shared by species of our interest (Felsenstein 1985, Harvey & Pagel 1991). Thus, von Hardenberg & Gonzalez-Voyer (2013) proposed to combine confirmatory path analysis with phylogenetic generalized least squares (PGLS). This is achieved by translating the set of conditional probabilistic independencies, derived from d-sep, into linear models that will be tested with PGLS methods.

In this work, we used phylogenetic path analysis based on the abovementioned set of variables (each linked to a hypothesis that may account for range size gradients). Variables were represented in DAGs to determine the minimum of conditional probabilistic independencies in seven hypothetical causal models (Fig. S1). We then translated these independencies pairs into linear models to test which causal model best fit our data. To select the best fitting model we used a modified version of Akaike Information Criterion (Akaike 1974) which is called corrected C statistic Information Criterion (CICc) (Gonzalez-Voyer & von Hardenberg 2014). The models were ranked and those with a difference between CICc bigger than two were considered to have a substantial support. We estimated the standardized coefficients for the best models,

and calculated direct and indirect effects for each variable following Mitchell (1992). We performed the analyses for non-volant mammals and we repeated the analyses for different taxonomic groups: Carnivora, Chiroptera, Primates, Rodentia and Cetartiodactyla. For the phylogenetic path analysis we used the mammal super-tree of Fritz et al. (2009). The species for which we had data but not the exact position in the phylogeny from Fritz et al. (2009), were randomly incorporated in the most derived consensus clade, using the algorithm proposed by Martins et al. (2013). All statistical analyses were conducted at the global scale using R 2.15 (R Development Core Team 2012).

## RESULTS

Our best-fit model according to the parameters before mentioned is Model 7 for non-volant mammals, Chiroptera, Rodentia and Primates (which had no difference between Model 6 and 7) (Table S1). For Carnivora and Cetartiodactyla the best model was Model 2, which also did not had substantial difference with Model 4 (Carnivora) and Model 6 (Cetartiodactyla), but we choose to present only Model 2. In all analyzed groups, the variable that had the strongest total effect under Range Size was the Thermal Niche (Fig S2, Table S2, Table S3).

**Table S1.** Number of parameters estimated with their corresponding ranking of all models: C statistic information criterion,  $\Delta\text{CICc}$ , CICc values, and p values for each CICc for the seven path models.

Non-volant mammals				
Model	statistic	p-value	CICc	$\Delta\text{CICc}$
7	23.693	0.096	118.856	0
6	31.898	0.023	125.012	6.156
2	42.849	0.002	133.915	15.059
5	41.846	0.001	135.963	17.107
4	93.946	0.000	166.63	47.774
3	306.772	<0.001	379.457	260.601
1	506.598	<0.001	567.075	448.219

## Chiroptera

Model	statistic	p-value	CICc	$\Delta$ CICc
7	6.853	0.976	105.251	0
2	13.949	0.833	107.976	2.725
6	12.256	0.834	108.467	3.216
5	11.559	0.869	110.159	4.908
4	50.422	0.086	124.991	19.74
3	66.421	0.003	140.99	35.739
1	292.096	<0.001	353.88	248.629

## Rodentia

Model	statistic	p-value	CICc	$\Delta$ CICc
7	19.997	0.22	116.154	0
6	25.896	0.102	119.962	3.808
2	31.869	0.045	123.846	7.692
5	31.46	0.026	125.935	9.781
4	68.032	0.002	141.299	25.145
3	194.371	<0.001	267.638	151.484
1	440.144	<0.001	501.026	384.872

## Primates

Model	statistic	p-value	CICc	$\Delta$ CICc
6	22.088	0.228	128.55	0
7	20.726	0.189	129.867	1.317
2	28.227	0.104	132.027	3.477
5	25.461	0.113	134.689	6.139
4	64.582	<0.001	145.203	16.653
3	133.412	<0.001	214.033	85.483
1	378.853	<0.001	444.757	316.207

## Carnivora

Model	statistic	p-value	CICc	$\Delta$ CICc
2	20.391	0.434	131.953	0
4	48.663	0.115	133.917	1.964
6	20.064	0.329	134.703	2.75
5	18.061	0.452	135.03	3.077
7	19.628	0.237	137.375	5.422
3	127.688	<0.001	212.942	80.989
1	359.162	<0.001	428.147	296.194

## Cetartiodactyla

Model	statistic	p-value	CICc	$\Delta$ CICc
2	21.881	0.347	136.234	0
6	20.593	0.3	138.179	1.945
5	8.99	0.96	139.466	3.232
7	20.589	0.195	141.446	5.212
4	63.547	0.006	150.429	14.195
3	132.84	<0.001	219.723	83.489
1	346.695	<0.001	416.749	280.515

**Table S2.** A comparison of path coefficients between response variables against explanatory variables and significance level (\*\*\*P ≤ 0.001; \*\*P ≤ 0.01; \*P ≤ 0.05; not \* significant P > 0.05). Abbreviations are: HUMANS, human footprint; TROPHIC P, trophic position; TROPHIC BR, trophic breadth; THERMAL N, thermal niche; HYDRIC N, hydric niche; NDVI N, productivity niche; DIV.TIME, evolutionary divergence time.

Non-volant mammals									
Response\Explanatory	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Litter size	Humans	Div.Time
Trophic P.			-0.065**	0.014	0.032*	-0.027*			
Trophic Br.	0.105***		-0.038*	-0.006	0.003	0.011		0.011	0.011
Body size								0.004	-0.022*
Thermal N.			0.048					-0.048***	
Hydric N.			0.044	0.113***				0.127***	
NDVI N.			-0.066	0.330***	0.413***			-0.011	
Litter size	-0.045*		-0.316***	0.141***	0.061***	0.155***		-0.035*	
Range size	0.047*	0.020	0.151***	0.256***	0.233***	0.020	0.055***	-0.201***	-0.025

Chiroptera									
Response\Explanatory	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Litter size	Humans	Div.Time
Trophic P.			0.019	0.001	0.003	0.016			
Trophic Br.	0.178***		0.076***	0.002	-0.009	-0.043**		-0.013	-0.020
Body size								0.032	-0.023
Thermal N.			-0.053					0.037	
Hydric N.			-0.124***	0.343***				-0.037	
NDVI N.			-0.045	0.324***	0.341***			-0.049	
Litter size	-0.024		0.158***	-0.056	0.111***	0.019		-0.055	
Range size	0.089*	0.004	-0.055	0.315***	0.246***	0.017	-0.041	-0.236***	-0.009



Rodentia									
Response\Explanatory	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Litter size	Humans	Div.Time
Trophic P.			-0.047*	0.019	0.036	-0.031			
Trophic Br.	0.089***		0.009	-0.014	0.006	0.000		0.005	0.021
Body size								0.015	-0.021
Thermal N.			-0.029					-0.068***	
Hydric N.			-0.005	0.137***				0.122 ***	
NDVI N.			-0.072**	0.333***	0.476***			-0.050*	
Litter size	-0.069**		-0.140***	0.188***	0.070**	0.210***		-0.041	
Range size	0.019	0.039	0.046*	0.287***	0.269***	0.021	0.129***	-0.179***	-0.034

Primates									
Response\Explanatory	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Litter size	Humans	Div.Time
Trophic P.			-0.170*	0.017	-0.009	0.014			
Trophic Br.	0.196***		-0.153 *	0.018	0.041	0.051		-0.074*	-0.074
Body size								0.040	-0.065
Thermal N.			0.123					0.306* **	
Hydric N.			0.078	0.324***				0.023	
NDVI N.			0.088	0.111*	0.293***			0.276***	
Litter size	-0.041		-0.600***	0.127**	-0.019	-0.004		0.033	
Range size	0.035	0.126*	0.150	0.270***	0.155**	0.194 ***	0.072	-0.378***	0.076

Carnivora									
Response\Explanatory	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Litter size	Humans	Div.Time
Trophic P.				0.174**	0.015	-0.099			
Trophic Br.	-0.202**		-0.014	0.067	-0.057	0.115*		0.153**	-0.065
Body size								-0.067	0.105
Thermal N.			0.211*					-0.143*	
Hydric N.			0.309***	0.124				0.353***	
NDVI N.			-0.152*	0.368***	0.329***			-0.274	
Litter size	0.006		-0.362***	-0.096	0.234***	-0.003			
Range size	0.295	-0.765	-0.284	0.367***	0.314***	0.469	-0.836	-0.329***	-0.345

Cetartiodactyla									
Response\Explanatory	Trophic P.	Trophic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Litter size	Humans	Div.Time
Trophic P.				-0.004	0.049	0.005			
Trophic Br.	0.899***		-0.055	-0.033	-0.023	-0.020		0.046	0.006
Body size								-0.111	-0.034
Thermal N.			0.128					-0.168**	
Hydric N.			0.066	0.028				0.244 ***	
NDVI N.			0.130*	0.018	0.377***			-0.091	
Litter size	0.048		-0.345***	-0.088	0.007	0.222**			
Range size	0.358*	-0.267	0.133*	0.474***	0.286***	0.140*	0.114	-0.186**	0.045

**Table S3.** Standardized total effects, direct effects and indirect effects between explanatory variables and the global range sizes of mammal species for all major mammalian orders estimated through Phylogenetic Path Analysis. Abbreviations are: HUMANS, human footprint; TROPHIC P, trophic position; TROPHIC BR, trophic breadth; THERMAL N, thermal niche; HYDRIC N, hydric niche; NDVI N, productivity niche, DIV. TIME, evolutionary divergence time.

Group	Effect	Explanatory variables								
		Humans	Trophic P.	Throphic Br.	Body size	Thermal N.	Hydric N.	NDVI N.	Div.Time	Litter size
Rodentia	Direct	-0.179	-	-	0.046	0.287	0.269	-	-	0.129
	Indirect	0.010	-0.009	-	-0.020	0.073	0.022	0.027	-	-
	Total	-0.169	-0.009	-	0.026	0.360	0.291	0.027	-	0.129
Primates	Direct	-0.378	-	0.126	-	0.270	0.155	0.194	-	-
	Indirect	0.166	-	-	-0.021	0.090	0.057	-	-	-
	Total	-0.212	-	0.126	-0.021	0.360	0.212	0.194	-	-
Carnivora	Direct	-0.329	-	-	-	0.367	0.314	-	-	-
	Indirect	0.058	-	-	0.077	-	-	-	-	-
	Total	-0.271	-	-	0.077	0.367	0.314	-	-	-
Cetartiodactyla	Direct	-0.186	-	0.358	0.133	0.474	0.286	0.140	-	-
	Indirect	0.003	-	-	0.018	-	0.053	-	-	-
	Total	-0.183	-	0.358	0.151	0.474	0.339	0.140	-	-

## FIGURE LEGENDS

**Figure S1.** Tested hypothetical cause-effect models depicting the relationship between explanatory variables and range size in terrestrial mammals.

**Figure S2.** Phylogenetic Path Analysis (PPAs) with arrows representing direct and indirect effects of explanatory variables on mammal range sizes. Green arrows represent negative effects and red arrows represent positive effects significant at  $p$  values  $< 0.05$ . Thick lines correspond to relationships with standardized partial regression coefficients greater than 0.10. Gray arrows represent non-significant relationships ( $p$  values  $> 0.05$ ). Three PPAs are represented: Model 7 and Model 2. The best models for each taxonomic order are: Rodentia (Model 7), Primates (Model 7), Carnivora (Model 2) and Cetartiodactyla (Model 2). Abbreviations are: HUMANS, human footprint; TROPHIC P, trophic position; TROPHIC BR, trophic breadth; THERMAL N, thermal niche; HYDRIC N, hydric niche; NDVI N, productivity niche, DIV. TIME, evolutionary divergence time.

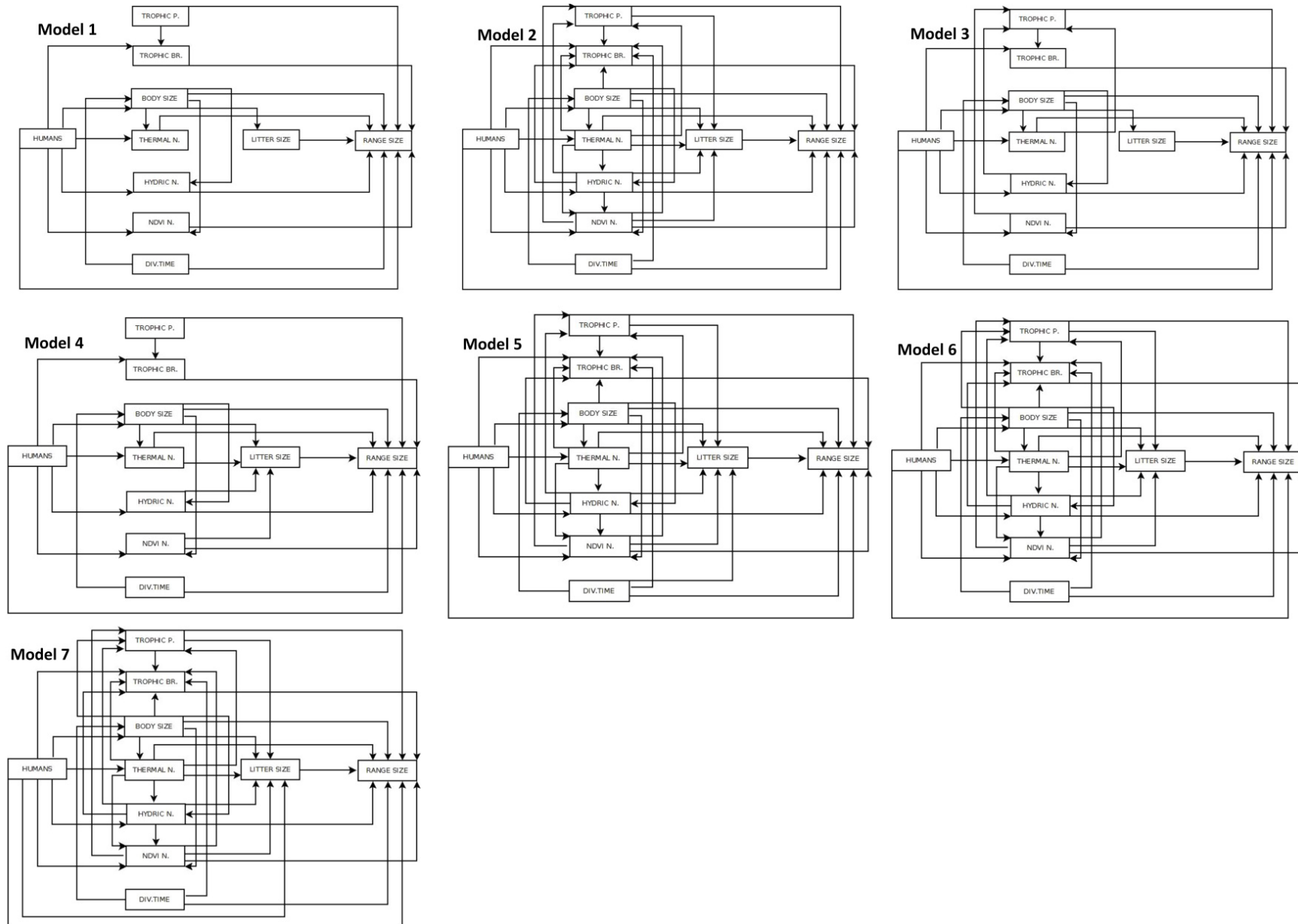


Figure S1

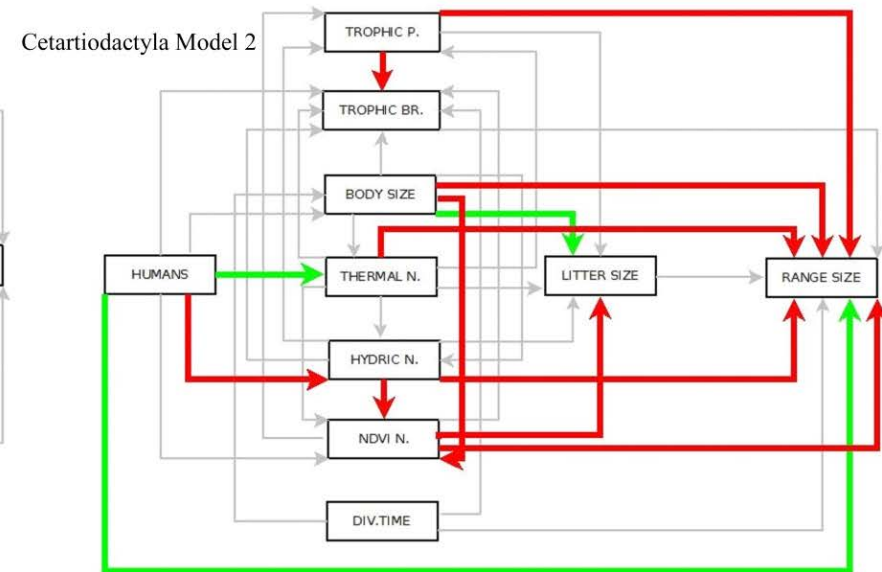
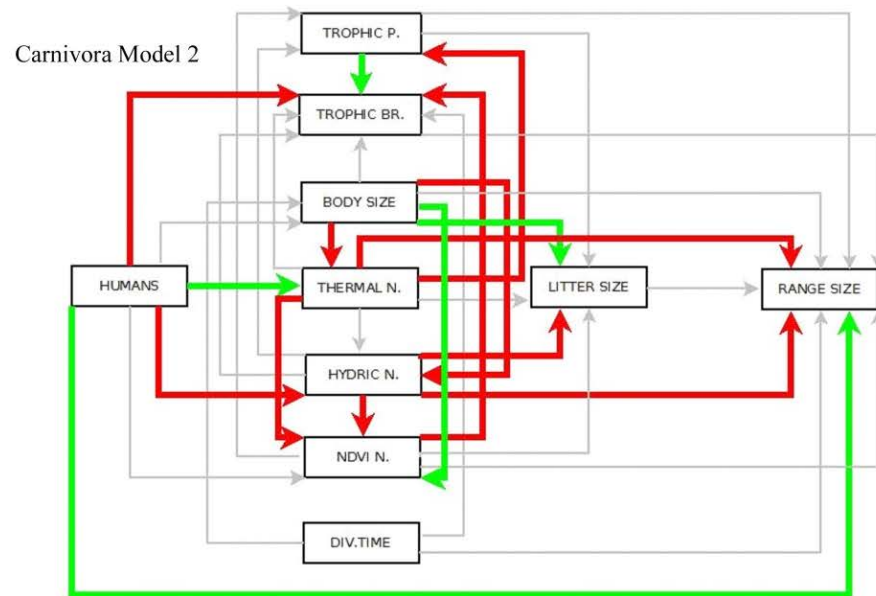
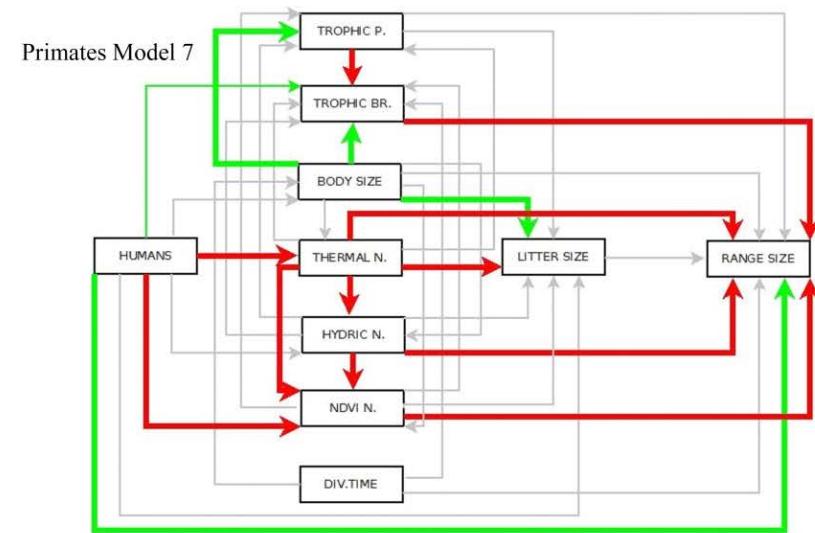
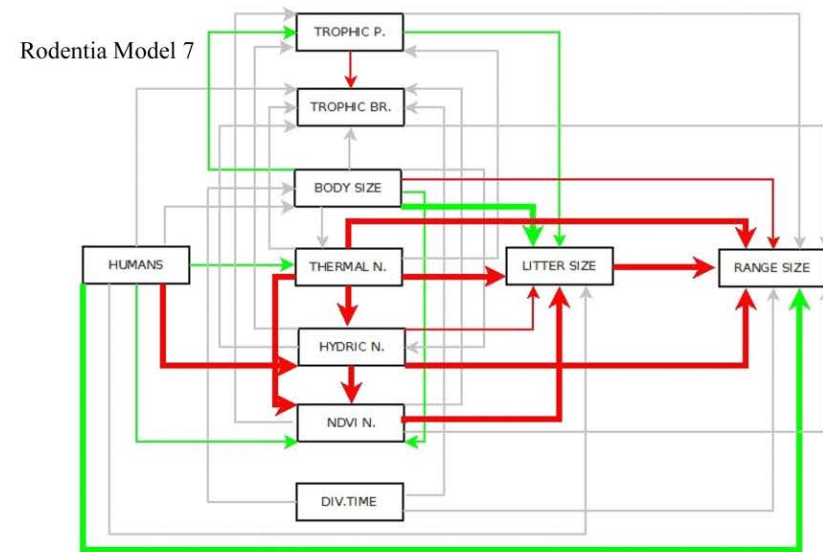


Figure S2

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## Capítulo 6

### Conclusiones Generales

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## Capítulo 2

1) La disponibilidad ambiental conjunta de agua-energía, medida a través de la evapotranspiración real, es el principal motor de la riqueza de especies de mamíferos a nivel mundial. Los efectos humanos sobre la riqueza de especies no se detectan fácilmente a escala global, estos efectos surgen de manera significativa a nivel regional.

2) En las regiones Neártica, Paleártica y Oriental, la contribución independiente de los impactos humanos es casi tan importante como las condiciones ambientales para explicar los patrones de riqueza. Usando una variable de accesibilidad humana mostramos, por primera vez, que las zonas más accesibles a los seres humanos son a menudo aquellas en la que nos encontramos con menor riqueza de especies de mamíferos terrestres.

## Capítulo 3

3) En el Néartico y Paleártico Occidental, las zonas climáticamente inestables a lo largo de los últimos 20000 años presentan especies con distribuciones geográficas más amplias y contienen una menor riqueza de especies de mamíferos terrestres.

4) La inestabilidad climática tiene un efecto sobre la distribución geográfica y sobre el tamaño corporal en los mamíferos de América del Norte. Sin embargo, no fue posible detectar un efecto de la inestabilidad climática sobre otros rasgos de historia de vida (longevidad y tamaño de camada) en ambos dominios biogeográficos: Néartico y Paleártico Occidental.

## Capítulo 4

5) En mamíferos marinos, la hipótesis de conservación de calor propuesta por Bergmann es la que goza de un mayor apoyo empírico para explicar los patrones interespecíficos de tamaño corporal a gran escala. Las especies de mayor porte se tienden a concentrar hacia los polos (sobre todo en el Hemisferio Sur) y las más pequeñas en el ecuador. Este patrón está fuertemente vinculado a la variación espacial de temperatura del mar en superficie.

6) Nuestros resultados para los mamíferos marinos apoyan igualmente, la hipótesis de productividad primaria, salinidad e impacto humano. Esto sugiere que las habilidades de este grupo exhiben una variación de tamaños corporales, y no dependen sólo de la conservación de calor sino también de otros factores antrópicos y ambientales.

## Capítulo 5

7) El método del análisis de rutas filogenéticas permitió identificar la importancia del nicho climático como el principal determinante de los rangos de distribución de las especies de mamíferos existentes en todo el mundo. Características biológicas intrínsecas de las especies como el tamaño corporal, la amplitud de nicho trófico, junto con los impactos humanos se detectados como factores secundarios.

8) A nivel de orden taxonómico, sin embargo, estos factores secundarios fueron relevantes para algunos grupos. En mamíferos no voladores (excluyendo Chiroptera) el tamaño corporal muestra un efecto significativo sobre el tamaño del rango geográfico y cuantitativamente similar, aunque de distinto signo, a los efectos de los impactos humanos. En Roedores, el tamaño de camada muestra efectos similares a los impactos humanos. Finalmente, en Primates y Artiodáctilos la amplitud de nicho trófico mostró efectos más altos que los de impacto humano sobre el tamaño de rango.