

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

Erik Joaquín Torres-Romero^{1,2*} and Miguel Á. Olalla-Tárraga^{2*}

¹PhD Program in Ecology, Department of Life Sciences, University of Alcalá, 28871 Alcalá de Henares, Madrid, Spain; and ²Biodiversity and Conservation Unit, Department of Biology and Geology, Rey Juan Carlos University, Móstoles 28933, Madrid, Spain

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 × 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,

*Correspondence author. E-mails: ejtr23@hotmail.com, miguel.olalla@urjc.es

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 96.5×96.5 km cells with an equal-area Berhmann projection (*c.* 1° 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 100×100 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 10×10 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 100×100 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° 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° 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 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

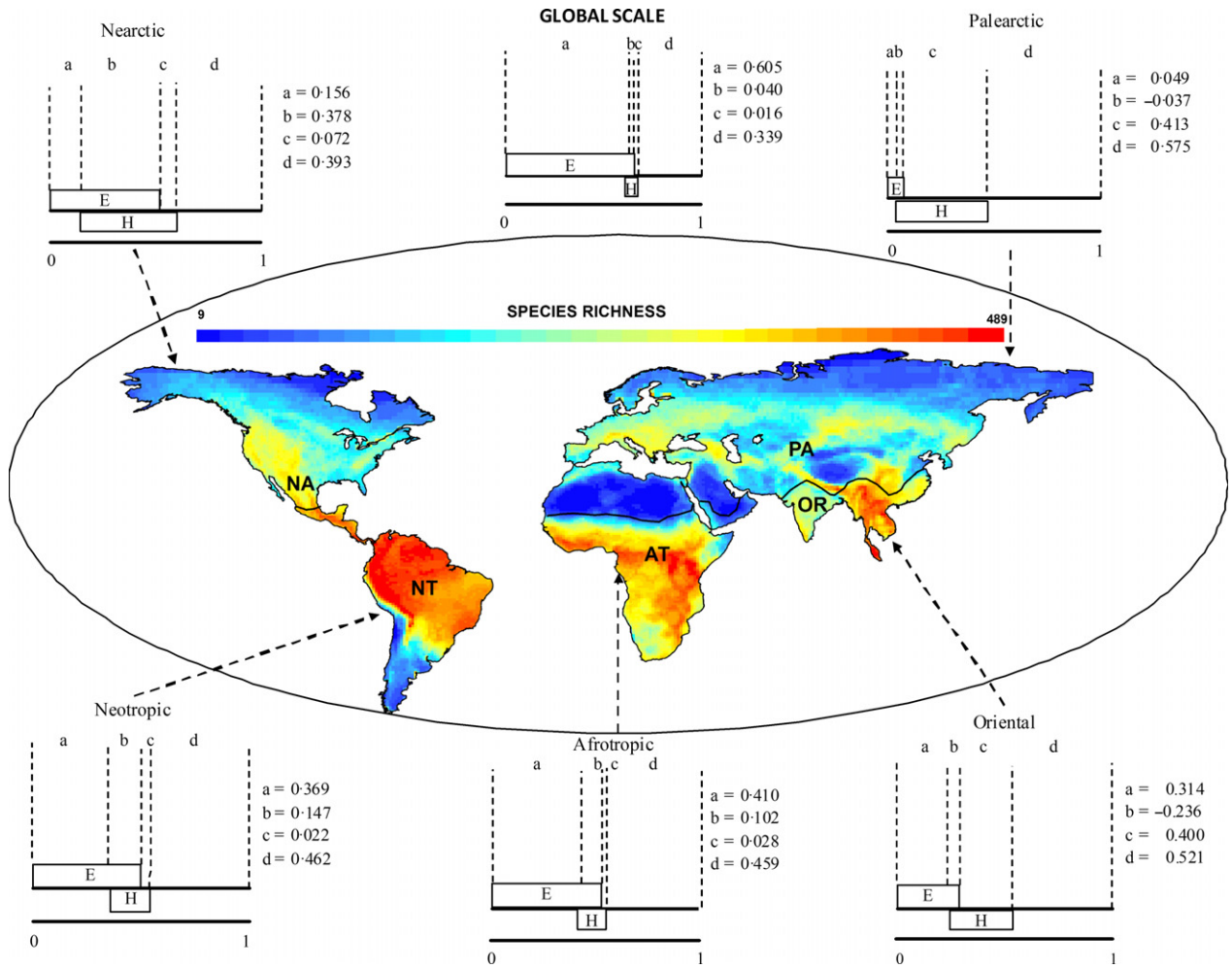


Fig. 1. Richness patterns of terrestrial mammal species at the global scale. Abbreviations for biogeographical realms are: Afrotropic (AT), Nearctic (NA), Neotropic (NT), Palearctic (PA) and Oriental (OR). Results of partial regression analyses at the global and biogeographical realm levels, using species 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										Δ 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	
Palaearctic	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 Palaearctic, 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 Palaearctic 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 Palaearctic, 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 Palaearctic 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, Palaearctic 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).

References

- Andrews, P. & O'Brien, E.M. (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*, **251**, 205–231.
- Araújo, M.B. (2003) The coincidence of people and biodiversity in Europe. *Global Ecology and Biogeography*, **12**, 5–12.
- Araújo, M.B. & Rahbek, C. (2007) Conserving biodiversity in a world of conflicts. *Journal of Biogeography*, **34**, 199–200.
- Badgley, C. & Fox, D.L. (2000) Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography*, **27**, 1437–1467.
- Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P. *et al.* (2001) Conservation conflicts across Africa. *Science*, **291**, 2616–2619.
- Barbosa, A.M., Pautasso, M. & Figueiredo, D. (2013) Species–people correlations and the need to account for survey effort in biodiversity analyses. *Diversity and Distributions*, **19**, 1188–1197.
- Belmaker, J. & Jetz, W. (2011) Cross-scale variation in species richness–environment associations. *Global Ecology and Biogeography*, **20**, 464–474.

- Beyer, H.L. (2012) *Geospatial Modelling Environment* (Version 0.7.2.0) (software). <http://www.spatial-ecology.com/gme>.
- Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Akre, T.S.B., Albaladejo, R.G., Albuquerque, F.S., *et al.* (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193–204.
- Brooks, T., Mittermeier, R., da Fonseca, G., Gerlach, J., Hoffman, M., Lamoreux, J. *et al.* (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.
- Brown, J.H. (1995) *Macroecology*. University of Chicago, Chicago, 269 p.
- Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B*, **274**, 1167–1173.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, New York, USA.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biology*, **2**, 0909–0913.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W. *et al.* (2005) Multiple causes of high extinction risk in large mammal species. *Science*, **309**, 1239–1241.
- Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J. & Purvis, A. (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B*, **275**, 1441–1448.
- Ceballos, G. & Ehrlich, P.R. (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 19374–19379.
- Ceballos, G., Ehrlich, P.R., Soberon, J., Salazar, I. & Fay, J.P. (2005) Global mammal conservation: what must we manage? *Science*, **309**, 603–607.
- Chown, S.L., Van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & van Jaarsveld, A.S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications*, **13**, 1233–1241.
- Collen, B., McRae, L., Deinet, S., De Plama, A., Carranza, T., Cooper, N. *et al.* (2011) Predicting how populations decline to extinction. *Philosophical Transactions of the Royal Society B*, **366**, 2577–2586.
- Cox, C.B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography*, **28**, 511–523.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist*, **137**, 27–49.
- Cusens, J., Wright, S.D., McBride, P. & Gillman, L.N. (2012) What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. *Ecology*, **93**, 2241–2252.
- Davies, T.J., Buckley, L.B., Grenyer, R. & Gittleman, J.L. (2011) The influence of past and present climate on the biogeography of modern mammal diversity. *Philosophical Transactions of the Royal Society B*, **366**, 2526–2535.
- Ding, T.S., Yuan, H.W., Geng, S., Koh, C.N. & Lee, P.F. (2006) Macro-scale bird species richness patterns of the East Asian mainland and islands: energy, area and isolation. *Journal of Biogeography*, **33**, 683–693.
- Diniz-Filho, J.A.F. & Bini, L.M. (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, **14**, 177–185.
- Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Bini, L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479–488.
- Diniz-Filho, J.A.F., Bini, L.M., Pinto, M.P., Rangel, T.F.L.V.B., Carvalho, P. & Bastos, R.P. (2006) Anuran species richness, complementarity and conservation conflicts in Brazilian Cerrado. *Acta Oecologica*, **29**, 9–15.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bol-liger, J., Carl, G. *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.
- Dutilleul, P. (1993) Modifying the t-test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.
- Ellis, E.C., Kaplan, J.O., Fuller, D.Q., Vavrus, S., Klein Goldewijk, K. & Verburg, P.H. (2013) Used planet: a global history. *Proceedings of the National Academy of Sciences*, **110**, 7978–7985.
- Evans, K.L. & Gaston, K.J. (2005) People, energy and avian species richness. *Global Ecology and Biogeography*, **14**, 187–196.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1–25.
- Fisher, D.O., Blomberg, S.P. & Owens, I.P.F. (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society B*, **270**, 1801–1808.
- Fisher, J.B., Whittaker, R. & Malhi, Y. (2011) ET Come Home: potential evapotranspiration in geographical ecology. *Global Ecology and Biogeography*, **20**, 1–18.
- Fjeldsá, J. & Burgess, N.D. (2008) The coincidence of biodiversity patterns and human settlement in Africa. *African Journal of Ecology*, **46**, 33–42.
- Fjeldsá, J. & Rahbek, C. (1998) Continent-wide conservation priorities and diversification processes. *Conservation in a Changing World* (eds G.M. Mace, A. Balmford & J.R. Ginsberg), pp. 139–160. Cambridge University Press, Cambridge.
- Flojgaard, C., Normand, S., Skov, F. & Svenning, J.C. (2011) Deconstructing the mammal species richness pattern in Europe e towards an understanding of the relative importance of climate, biogeographic history, habitat heterogeneity and humans. *Global Ecology and Biogeography*, **20**, 218–230.
- Gaston, K.J. & Evans, K.L. (2004) Birds and people in Europe. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1649–1655.
- Gouveia, S.F., Hortal, J., Cassemiro, F.A.S., Rangel, T.F. & Diniz-Filho, J.A.F. (2013) Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography*, **36**, 104–113.
- Griffith, D.A. & Peres-Neto, P.R. (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analysis. *Ecology*, **87**, 2603–2613.
- Hawkins, B.A. (2001) Ecology's oldest pattern? *Trends in Ecology & Evolution*, **16**, 470.
- Hawkins, B.A. (2012) Eight (and a half) deadly sins of spatial analysis. *Journal of Biogeography*, **39**, 1–9.
- Hawkins, B.A. & Porter, E.E. (2003) Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography*, **12**, 475–481.
- Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003b) Productivity and history as predictors of the latitudinal diversity gradient for terrestrial birds. *Ecology*, **84**, 1608–1623.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M. *et al.* (2003a) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hortal, J. (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. *Journal of Biogeography*, **35**, 1355–1356.
- Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 13384–13389.
- Huston, M.A. (1994) *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Huston, M.A. (2005) The three phases of land-use change: implications for biodiversity. *Ecological Applications*, **15**, 1864–1878.
- Jetz, W. & Fine, A. (2012) Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, **10**, e1001292.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.
- Koh, C.N., Lee, P.F. & Lin, R.S. (2006) Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Diversity and Distributions*, **12**, 546–554.
- Lan, D. & Dunbar, R. (2000) Bird and mammal conservation in Gaoligongshan Region and Jingdong County, Yunnan, China: patterns of species richness and nature reserves. *Oryx*, **34**, 275–286.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd English edn. Elsevier, Amsterdam.
- Luck, G.W. (2007) The relationships between net primary productivity, human population density and species conservation. *Journal of Biogeography*, **34**, 201–212.
- Luck, G.W., Ricketts, T.H., Daily, G.C. & Imhoff, M. (2004) Alleviating spatial conflict between people and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 182–186.
- McKinney, M.L. (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, **11**, 161–176.

- Nelson, A. (2008) Travel time to major cities: a global map of Accessibility. Global Environment Monitoring Unit – Joint Research Centre of the European Commission, Ispra, Italy. Available at: <http://gem.jrc.ec.europa.eu/> (accessed March 2012).
- New, M., Hulme, M. & Jones, P.D. (1999) Representing twentieth century space–time climate variability. Part 1: development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12**, 829–856.
- Nogués-Bravo, D., Araujo, M.B., Romdal, T. & Rahbek, C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216–219.
- O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*, **20**, 181–198.
- Olalla-Tárraga, M.Á., Rodríguez, M.Á. & Hawkins, B.A. (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography*, **33**, 781–793.
- Olalla-Tárraga, M.Á., Diniz-Filho, J.A.F., Bastos, R.P. & Rodríguez, M.Á. (2009) Geographic body size gradients in tropical regions: water deficit and anuran body size in the Brazilian Cerrado. *Ecography*, **32**, 581–590.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C. *et al.* (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, **51**, 933–938.
- Pautasso, M. (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecology Letters*, **10**, 16–24.
- Pearson, R.G. & Dawson, T.E. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pillsbury, F.C. & Miller, J.R. (2008) Habitat and landscape characteristics underlying anuran community structure along an urban–rural gradient. *Ecological Applications*, **18**, 1107–1118.
- Price, S.A. & Gittleman, J.L. (2007) Bushmeat hunting, habitat loss and global extinction in the Artiodactyla. *Proceedings of the Royal Society B*, **274**, 1845–1851.
- Qian, H. (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, **25**, 629–637.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, **33**, 46–50.
- Real, R., Barbosa, A.M., Porras, D., Kin, M.C., Marquez, A.L., Guerrero, J.C. *et al.* (2003) Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. *Journal of Biogeography*, **30**, 939–947.
- Rickart, E.A. (2001) Elevational diversity gradients, biogeography and the structure of mountain mammals communities in the intermountain region of North America. *Global Ecology & Biogeography*, **10**, 77–100.
- Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P. *et al.* (2011) Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B*, **366**, 2633–2641.
- Sanderson, E., Jaiteh, M., Levy, M., Redford, K., Wannebo, A. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.
- Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W.D., Lenoir, J., Sandel, B. *et al.* (2013) Mammal predator and prey species richness are strongly linked at macroscales. *Ecology*, **94**, 1112–1122.
- Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Kataraya, V. *et al.* (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, **322**, 225–230.
- Schloss, A.L., Kicklighter, D.W., Kaduk, J., Wittenberg, U. & The Participants of the Potsdam NPP Model Intercomparison. (1999) Comparing global models of terrestrial net primary productivity (NPP): comparison of NPP to climate and the Normalized Difference Vegetation Index (NDVI). *Global Change Biology*, **5**, 25–34.
- Terribile, L.C., Diniz-Filho, J.A.F., Rodriguez, M. & Rangel, T.F.L.V. (2009) Richness patterns, species distributions and the principle of extreme deconstruction. *Global Ecology and Biogeography*, **18**, 123–136.
- Torres-Romero, E.J. & Olalla-Tárraga, M.A. (2015) Data from: Untangling human and environmental effects on geographical gradients of mammal species richness: a global and regional evaluation. *Dryad Digital Repository*. doi:10.5061/dryad.qc700.
- Vázquez, L.B. & Gaston, K.J. (2006) People and mammals in México: conservation conflicts at a national scale. *Biodiversity and Conservation*, **15**, 2397–2414.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I. *et al.* (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.
- Whittaker, R.J., Nogués-Bravo, D., Araújo, M.B. (2007) Geographical gradients of species richness: a test of the water–energy conjecture of Hawkins *et al.* (2003) using European data for five taxa. *Global Ecology and Biogeography*, **16**, 76–89.

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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.