Journal of Biogeography (J. Biogeogr.) (2008) 35, 1202–1214

ORIGINAL ARTICLE

Regional and environmental effects on the species richness of mammal assemblages

Joaquín Hortal[1,2,3*], Jesús Rodríguez[4], Manuel Nieto-Díaz[1,5] and Jorge M. Lobo[1]

[1]*Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain,* [2]*Center for Macroecology, Institute of Biology, University of Copenhagen, Copenhagen, Denmark,* [3]*NERC Centre for Population Biology, Imperial College London, Ascot, UK,* [4]*Centro Nacional de Investigación de la Evolución Humana (CENIEH), Burgos, Spain and* [5]*Instituto de Neurobiología Ramón y Cajal (CSIC), Madrid, Spain*

*Correspondence: Joaquín Hortal, NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK.
E-mail: j.hortal@imperial.ac.uk

ABSTRACT

Aim Variation in species richness has been related to (1) environmental conditions (water, energy and habitat characteristics) and (2) regional differences (contingent historical events and regional particularities that result in differences between regional faunas acting at broad extents). Whereas climatic factors have been widely studied, the effects of regional differences are less often quantified. This work aims to characterize global trends in the species richness of mammal assemblages with respect to both current and historical influences.

Location All terrestrial biogeographical realms except Antarctica.

Methods Species richness in checklists from 224 sites distributed worldwide were investigated by partitioning the variation between a general set of habitat/climate factors, biogeographical regions, and their overlaps. Additional analyses studied the specific overlaps of region, water and energy. Data were also divided according to area to determine if the strength of these effects varies according to the size of sites.

Results Environmental effects explained 38% of richness variation across all sites, whereas environmentally independent regional effects explained 11% and the overlap between region and environment explained 13%. Results were similar when only larger sites (between 1000 km^2 and 10,000 km^2) were considered. However, the importance of the overlap between region and all environmental variables was greater in smaller sites (between 100 km^2 and 1000 km^2). In contrast, the specific importance of water and energy variables and their overlap with region was greater in larger sites. The strength of the independent effect of region remained almost invariant regardless of the size of the sites studied.

Main conclusions The relationship between species richness and climate varies with scale and among regions. Although environmental variables are the strongest correlates of richness, the unique history and physiographic characteristics of a region produce differences between the richness of mammal assemblages and their response to environmental gradients. The importance of environmental variables varies with scale: climatic gradients are more important at coarse grain (larger sites), possibly as a result of their effects on species ranges, whereas habitat type is more important at the smaller sites, where the importance of ecological interactions increases. Therefore, regional differences and the scale at which richness is measured should be taken into account when evaluating species richness–energy hypotheses.

Keywords

Climate, environmental factors, grain, habitat, local communities, macroecology, mammals, regional effects, scale, water–energy dynamics.

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2007.01850.x

INTRODUCTION

Geographic gradients in species richness can be related statistically to many variables (Rahbek & Graves, 2001). Among them, the characteristics of the sites where the species occur, including the environment (climate and habitat) and its physical characteristics (area and topographic and landscape heterogeneity), are frequently mentioned as the primary drivers of species richness (Kerr & Packer, 1997; Francis & Currie, 1998, 2003; Waide *et al.*, 1999; Jetz & Rahbek, 2001; Kerr *et al.*, 2001; Rahbek & Graves, 2001; Currie *et al.*, 2004; Tognelli & Kelt, 2004; Evans & Gaston, 2005; Evans *et al.*, 2005; Field *et al.*, 2005; Scheiner & Willig, 2005). Communities are not, however, affected only by the characteristics of the site where they occur; they are also the result of the assembling of species from those available in the regional pool (Ricklefs, 2004), which includes the characteristics and evolutionary history of the species present in the regional pool (Nieto *et al.*, 2005; Rodríguez *et al.*, 2006; J. Hortal, J. Rodríguez, D. Nogués-Bravo, M. B. Araújo & C. Rahbek, unpublished), the geomorphological and environmental characteristics of the region (Jetz & Rahbek, 2001; Rahbek & Graves, 2001), and region-specific historical variation in climate and habitat (see, for example, Hawkins & Porter, 2003; Hawkins *et al.*, 2005; Svenning & Skov, 2005, 2007; Montoya *et al.*, 2007). Therefore, some differences in the species richness of similar assemblages in different regions are to be expected (Ricklefs, 1987, 2004; Ricklefs & Schluter, 1993; Ricklefs *et al.*, 1999; Hawkins *et al.*, 2003a,b; Willig *et al.*, 2003; Wiens & Donoghue, 2004). Regional effects are often unmeasured, however, in spite of their widely appreciated potential importance in shaping biodiversity patterns at broad extents.

In this paper, we study the effects of environmental and regional factors on the species richness of non-volant mammal assemblages at the global extent. To do this, we use species inventories from a large set of localities of variable size distributed worldwide, and a set of predictors to account for broad-extent environmental gradients. Species-richness estimates come from exhaustive checklists. Our approach differs from that of most large-scale studies, in which richness is estimated as the sum of species range maps overlapping in grid cells (grid cell richness; see Kerr *et al.*, 2001; Whittaker *et al.*, 2001; Qian & Ricklefs, 2004; Grenyer *et al.*, 2006). Here we use high-quality checklists instead of gridded richness because they provide the most reliable information of the species that actually co-occur as assemblages in spatially defined areas. However, these localities vary substantially in area, and the relative importance of correlates of richness are known to be sensitive to the grain size used to measure species richness (Whittaker & Field, 2000; Whittaker *et al.*, 2001; Hawkins *et al.*, 2003b; Evans *et al.*, 2005; Hurlbert & White, 2005; Rahbek, 2005; Hurlbert & Jetz, 2007). To assess this, we chose checklists for sites ranging in area from 100 to 10,000 km^2. We also investigate the effects of area and habitat heterogeneity in our analyses. Furthermore, we split the data into two groups according to the area sampled (100–1000 and 1000–10,000 km^2) to examine possible effects of grain size.

We examine four factors that have been widely related to species richness: three environmental factors, namely (1) energy, i.e. temperature and productive energy (following Hawkins *et al.*, 2003b; see also Mittelbach *et al.*, 2001; Evans *et al.*, 2005), (2) water, i.e. precipitation and water balance, and (3) habitat type, i.e. the kind of biome (*sensu lato*) where the mammal assemblages occur; and a proxy for long-standing historical differences between locations, namely (4) biogeographic region (see, for example, Huston, 1999; Ricklefs, 2004; Hawkins *et al.*, 2005). Since these factors are collinear (e.g. Hawkins *et al.*, 2003b), we used variation partitioning (see Legendre & Legendre, 1998; Lobo *et al.*, 2001) to separate their joint and independent effects.

DATA AND METHODS

Data

A data base of checklists of continental non-volant mammal species (i.e. all orders except Chiroptera, Cetacea, and Pinnipedia) was used to calculate species richness in 311 localities distributed worldwide (see the data base description in Rodríguez, 1999; and examples of its application in Nieto *et al.*, 2005 and Rodríguez *et al.*, 2006). For this analysis we selected the 224 sites ranging from 100 to 10,000 km^2 in area. These sites were further divided into two groups: 119 sites ranging from 100 km^2 to 1000 km^2, and 105 sites ranging from 1000 km^2 to 10,000 km^2 (Fig. 1; Appendix S1 in the Supplementary Material). Analyses were conducted in all sites combined, and for small and large sites separately. Although the geographic coverage of the localities has gaps (see Fig. 1), most of the world's environmental and species-richness gradients are included within these data.

Area (*Ar*), spatial location (central latitude and longitude), and the shape of each site were obtained from the original sources or digitized from information available on the internet. We used four variables to account for topographic and landscape heterogeneity within each site: altitude range (Altrng), mean slope (Slopemed), aspect variability (the standard deviation of the aspects; AspectSD), and land-cover diversity (i.e. the number of different land-cover categories; GLC_DIV). Topographic variables were calculated from a global Digital Elevation Model at 1-km^2 resolution (Clark Labs, 2000), and the number of land-cover categories was obtained using the Global Land Cover 2000 data base at 1-km^2 resolution (European Commission, 2003).

Environmental factors (*Env*) were obtained from available worldwide coverage sources, re-sampled at 0.5° grain in a GIS (Idrisi 32; Clark Labs, 2001). Climatic variables were obtained from the United Nations Environmental Programme GRID data set (Deichmann & Eklundh, 1991; GRID data base available at http://www.grid.unep.ch/).

Five annual variables were used to measure energy (*Eg*): actual evapotranspiration (AET) and potential evapotranspi-

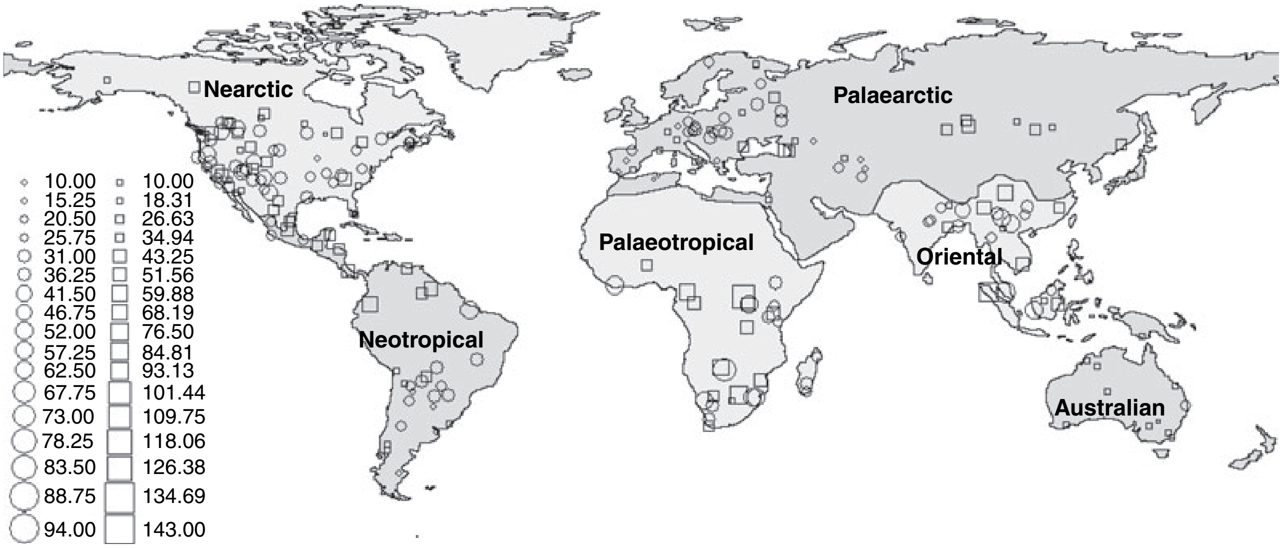


Figure 1 The geographical location of the 224 sites used for the analyses. Circles represent small sites (areas ranging from 100 to 1000 km^2) and squares represent large sites (from 1000 to 10,000 km^2); the size of the symbol indicates the site richness. The biogeographical regions used in the analyses have been adapted from the mammal zoogeographic regions proposed by Cox (2001).

ration (PET) [both calculated in millimetres through a combination of the Priestley-Taylor and Thornwaite methods (Ahn & Tateishi, 1994)], and mean, maximum and minimum monthly temperatures (TMEAN, TMAX and TMIN) (from Leemans & Cramer, 1991). AET is equivalent to energy when precipitation exceeds PET, and equivalent to precipitation when PET exceeds precipitation. It can therefore be considered either as an indirect measure of water balance or as a surrogate for net primary production. Hence, for animals AET can be regarded as a measure of available energy, in the sense of the general availability of plant food. Therefore, although AET does not represent the thermal energy regime, we have included it within the energy components instead of within the water measures because it can represent one component of the energy regime for mammals (see discussion in O'Brien, 1998, 2006; Andrews & O'Brien, 2000; Whittaker & Field, 2000).

Water (*Wt*) was measured using six variables accounting for precipitation and water balance: monthly precipitation (Leemans & Cramer, 1991) was transformed into five variables, namely mean annual precipitation (PMEAN), and winter, spring, summer and autumn precipitation (PWTR, PSPR, PSUM and PFALL, respectively); and water balance (WBL), a measure of the deficit or surplus of available water derived from AET, precipitation and soil water-holding capacity, was obtained from the GRID data set (Ahn & Tateishi, 1994).

Habitat type (*Hb*) (i.e. the general biome type within which the localities are placed; see Bailey, 1989/1993) was measured using Bailey Divisions (BECDIV, a multinomial qualitative variable), extracted from the World Ecoregions map (Bailey Ecoregions of the Continents, available at http://www.ngdc.noaa.gov/; see Bailey, 1989/1993).

Finally, to account for regional effects (*Rg*), we used the biogeographical realm in which each site is located (BgReg) (Fig. 1; realm limits as in Cox, 2001). As biogeographical realms/regions were designed to account for major divisions in mammal faunas, all species present in each realm are assumed to constitute the region's species pool, which, to some extent, is common to all localities of the region.

Statistical analyses

Mammal species richness (*S*) was analysed with respect to the environmental and regional variables. All predictors were modelled separately using generalized linear models (GLMs), in which the variability explained by the model is estimated from the change in deviance from a null model and statistical significance measured by an *F*-ratio test (McCullagh & Nelder, 1989). A Poisson distribution was assumed for richness (see Dobson, 1999), and was related to the explanatory variables by a logarithmic link function. The cubic, quadratic or linear function of each continuous variable was selected in order to account for curvilinear relationships. Since the autocorrelation in the data might affect this selection, we used a restrictive approach to the inclusion of these high-order terms, using a mixed forward-backward stepwise analysis, in which the term was selected if it produced a significant change in deviance from the former model (calculated as above) and if the parameters of the resulting model were significant (stable) according to the Wald statistic (StatSoft Inc., 2003).

Variation partitioning

Partial regression analyses (Borcard *et al.*, 1992; Legendre, 1993; Legendre & Legendre, 1998; Lobo *et al.*, 2001) were used to identify the relative statistical effect on local species richness of the regional factors and the environmental factors identified by the GLMs. Here, each predictor is regressed against other predictors, and the residuals of these regressions are used to produce 'residual models' (see Appendix S3). Environmental and geographic variables are often mutually non-independent and usually show the same autocorrelated pattern (Miller, 2004), making it difficult to discriminate their isolated influence. The estimation of these residual models helps to elaborate hypotheses on the independent influences of each factor. Positive values in the shared variability of factors indicate collinear variation, whereas negative values indicate probable synergistic effects (i.e. a function of the two factors together is able to explain more than the sum of the separate functions of these two factors; see Legendre & Legendre, 1998). Although using partial regression (i.e. using the residuals of regressing predictors against some of the other explanatory variables as new predictors) could lead to biased parameter estimates, it allows estimation of the magnitude of the independent effects of factors (see Freckleton, 2002).

Two partial regression analyses were performed. First, the magnitude of the effects of all environmental factors and the effect of region were examined. Here, variation in species richness is partitioned into four fractions: two account for the independent effects of environment and region, one accounts for the collinear variation of both sets of factors, and a fourth is for the unexplained variation (see, for example, Hawkins *et al.*, 2003a; Nieto *et al.*, 2005). In the second analysis, region, water and energy were analysed in concert to partition their effects. Here, variation in species richness is broken down into eight components: three account for the pure effects of each predictor variable, four quantify their shared variation, both by pairs and by all three combined, and the eighth accounts for unexplained variation (see Lobo *et al.*, 2001 and Appendix S3).

Additional analyses

Model predictions and residuals of environmental and regional factors are shown on a global scale using interpolated maps (generated with the simple-mean mobile techniques in IDRISI 32). The maps are used only as spatial representations of the geographical richness patterns in local mammal communities.

Spatial autocorrelation

To evaluate the ability of our statistical models to account for the spatial structure of species richness, we followed Diniz-Filho *et al.* (2003). First, we generated correlograms of the residuals of the environmental and regional models, as well as of the residuals obtained after adding region to the environmental model. The correlograms identified region-dependent spatially structured effects by identifying the spatial structure remaining unexplained in each model (i.e. the autocorrelation remaining in the residuals). These analyses were undertaken using SAM (Rangel *et al.*, 2006).

RESULTS

Region had a significant effect on richness across all localities. The Palaeotropical and Oriental regions had the richest localities (60.5 and 47 median richness, respectively), Nearctic, Neotropical and Palaearctic sites were similar in richness (41, 38 and 34.5 median species, respectively), and Australian localities were much less rich (28 median species) (Fig. 2).

Area accounted for small, although significant, amounts of the variance, especially in larger sites (Fig. 3; Appendix S2). However, its effect was independent from the rest of the factors (not shown), so we did not include it in the partial regressions. The heterogeneity models also had very low explanatory power (usually non-significant; see Fig. 3 and Appendix S2), so they too were excluded from further analyses.

In contrast, water, energy, habitat type and region explained significant amounts of variation in species richness (Fig. 3 and Appendix S2). In general, the variation explained by single factors was greater in large sites, although the general pattern was consistent across scales; the three environmental factors and region were of similar importance when studied separately (between 20% and 30% of total variability except for larger sites, where the variation by these factors was always higher than 30%). The three environmental factors together explained more variation in richness, from 41% in the subset of small sites, to 59% in the subset of large sites, although the addition of regional effects to the environmental functions increased the explained deviance in all three data sets (Fig. 3). In spite of the generally better fit for the large-sites subset, the strongest model was that for the small sites (76% of explained variability), probably as a result of the increased importance of habitat type and its overlap with region at this grain size (see below). The inclusion of area or heterogeneity in these models did not significantly increase explained variability (not shown).

The structure of the partial regressions varied depending on the size of the areas (Fig. 4; Appendix S3). Across all sites, the region-independent environmental factors represented the greatest fraction of explained variation, whereas region and the overlap between region and environment explained

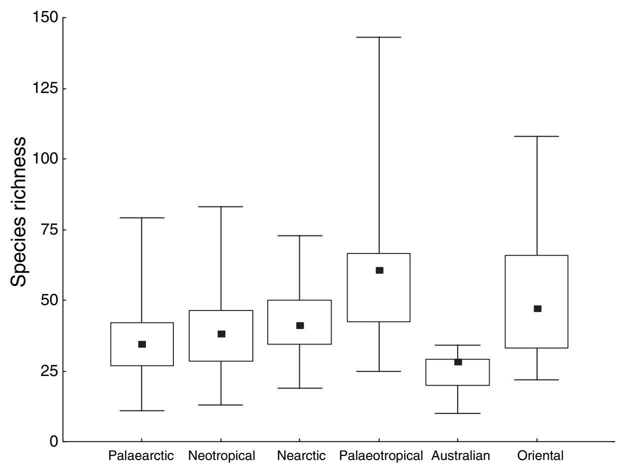


Figure 2 Differences in species richness between biogeographical regions. The central points are the median, boxes are the first and third quartiles, and whiskers are minimum and maximum values.

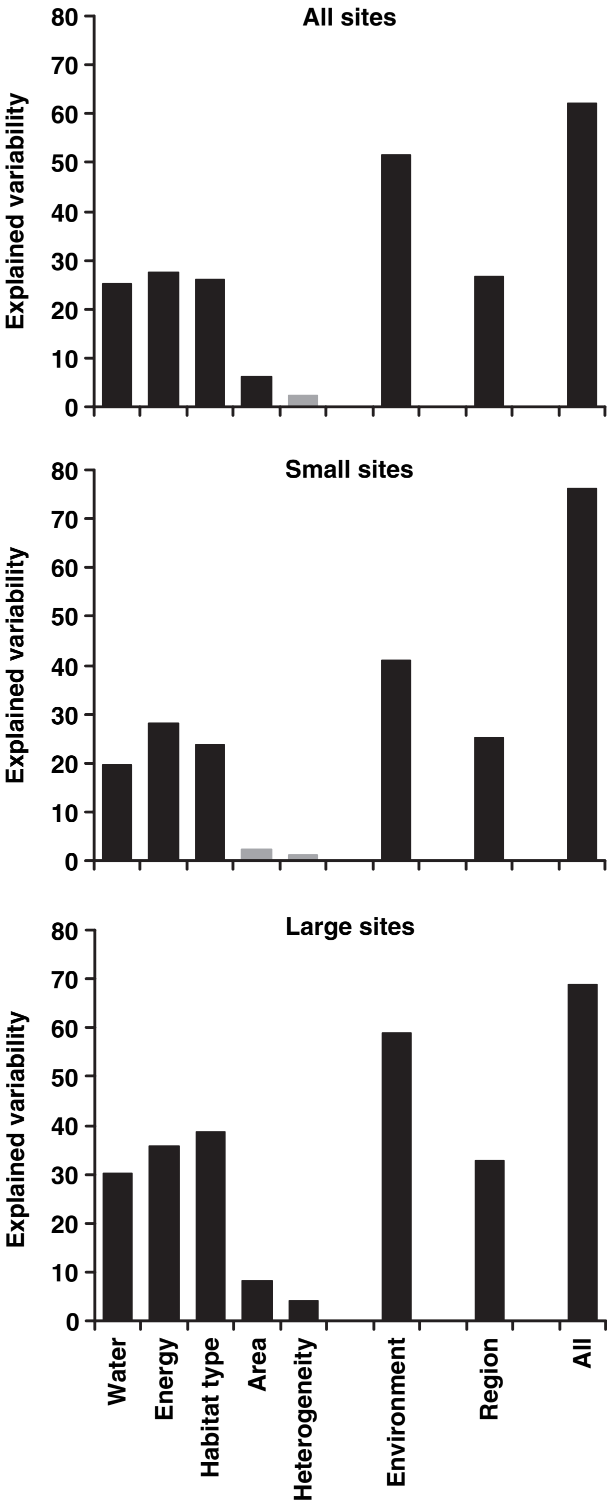


Figure 3 Variation in mammal species richness explained by GLMs; the columns to the left correspond to the models of the three environmental factors (water, energy and habitat type), and of the area and landscape/topographic heterogeneity; Environment represents a model of water, energy and habitat type, and All is a model including these factors and Region. Small sites have areas between 100 and 1000 km^2, and large sites have areas between 1000 km^2 and 10,000 km^2. Grey bars indicate non-significant factors. GLM results are listed in Appendix S2.

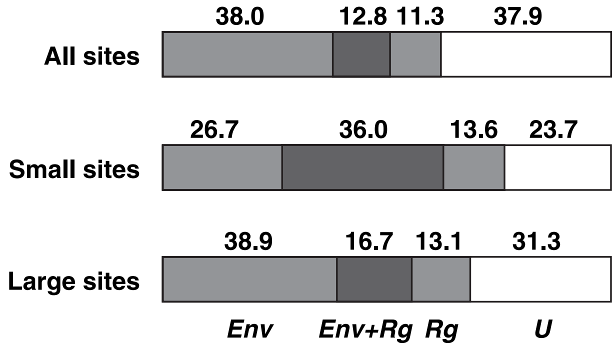


Figure 4 Variation partitioning of mammal species richness into the independent effects of Environmental (*Env*) and Regional (*Rg*) factors, as well as into their overlap (*Env+Rg*) (see Appendix S3). *U* is the unexplained variation. Small sites have areas between 100 and 1000 km^2, and large sites have areas between 1000 and 10,000 km^2. GLM results are listed in Appendix S3.

substantially less variation (Fig. 4). The model of the large sites was very similar. However, in small sites the overlap between region and environment was much stronger, with a smaller independent effect of environment. Interestingly, the independent effect of region was very similar in all analyses (Fig. 4).

The residual model based only on environmental variables underpredicted the richness of the Palaeotropical realm, as well as that of some areas of tropical South America and Malaysia, although the level of underprediction was less in the large-sites data set (Fig. 5). This model overpredicted richness in Australia, and to a lesser extent that in some parts of the Mediterranean basin and southern South America. The residual model based on region (independent from the environment) showed within-region differences in richness (Fig. 5). Richness was underpredicted in sub-Saharan Africa, in tropical America, in the Rocky Mountains, and in south-eastern Asia (including central China). Underpredictions also appeared in northern Africa and in Australia, especially when all sites were considered together (Fig. 5).

The environmental models removed almost all significant spatial autocorrelation in the all-sites and small-sites data sets, although some residual autocorrelation remained in the small-sites data at both short and long distances (Fig. 6). The inclusion of region in the models eliminated all remaining residual spatial structure in all three data sets. Interestingly, the spatial structure of the residuals from the regional models was quite similar to the structure of the models of environment and region (although with higher Moran's *I* coefficients in some distance lags), and significantly smaller than the structure remaining in the residuals of the environmental models in all three data sets (not shown).

The importance of water, energy and region in the partial regressions also varied with the size of the areas considered (Fig. 7). The variability in species richness explained by water and energy variables was greater in large sites, or when all the areas were considered. In these cases, energy explained the largest independent fraction of the variation (*c.* 20%). Region explained a similar amount of richness variance to previous

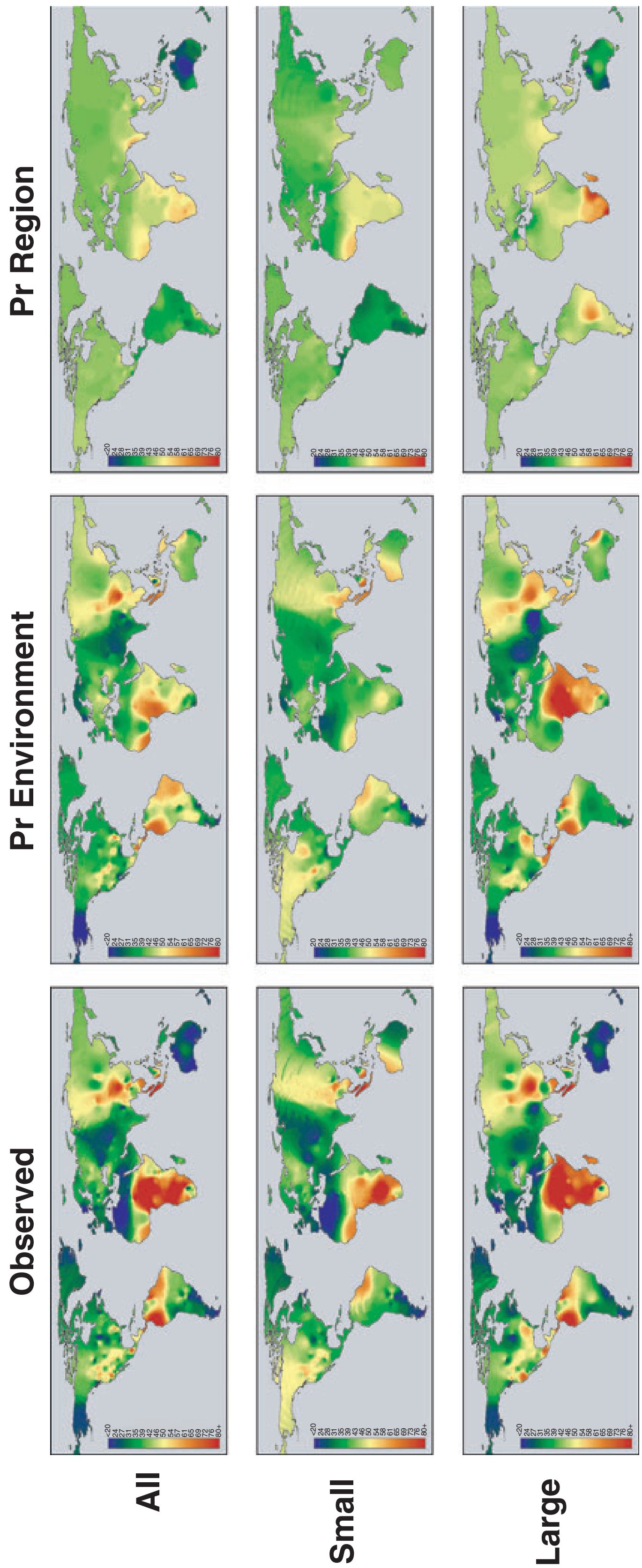


Figure 5 Spatial representation of the results of Environmental and Regional models for three sets of sites: all areas (upper row), small areas (central row) and large areas (lower row). The left column (Observed) shows maps of the observed richness of non-volant mammal richness interpolated from the original data (see Appendix S1). Maps in the central column (Pr Environment) show the richness predicted by the independent effect of Environmental factors (raw *Env*; see Fig. 4 and Appendix S3). The right column (Pr Region) shows maps of the environment-independent relationship between richness and region (raw *Rg*; see Fig. 4 and Appendix S3). All maps were spatially interpolated from the results of the original data points for representation purposes, using a mobile mean procedure (Clark Labs, 2001). Richness values (the number of species per locality) are grouped in equal intervals that vary from blue (fewer species) to red (more species); all maps have the same richness scaling to allow direct comparison.

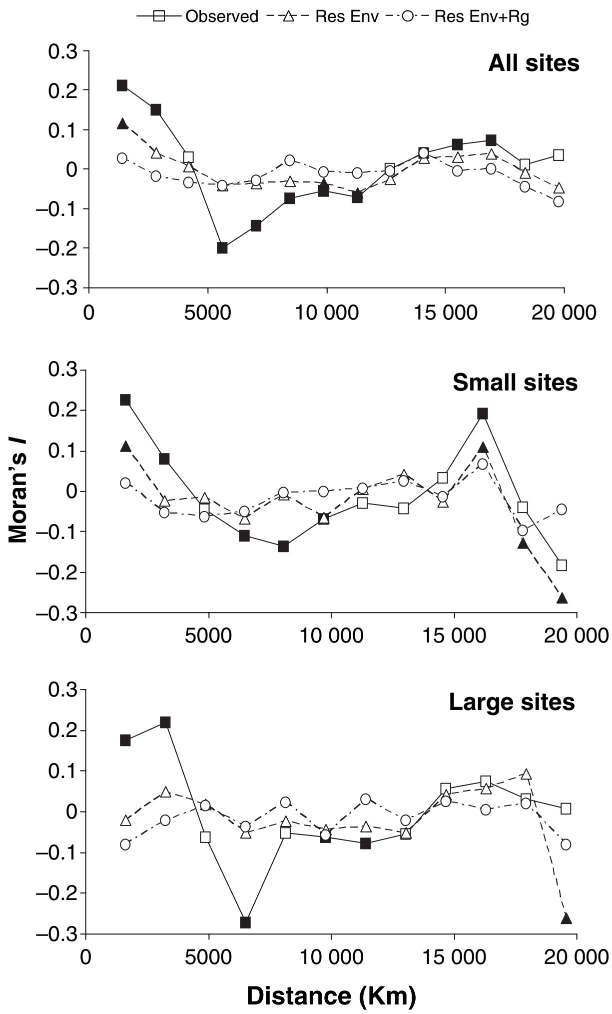


Figure 6 Correlograms for the raw richness data (Observed), for the residuals of the model built from environmental variables (Res Env), and for the residuals of the model of environmental and regional variables combined (Res Env+Rg). Significant Moran's *I* scores are marked as filled symbols. The correlograms for the residuals of the regional models are not shown because of their high overlap with the correlograms of the Environmental+Regional models (see text).

models, this amount of variance being also similar in the three data sets. However, the overlaps between region and water–energy variables varied with the scale of analysis in an opposite direction to the overlaps in the region versus environment analyses; their overlaps were greater in large sites, where both kinds of variables account for 25% of total variability (Fig. 7).

The variability explained by the overlap between region and environment in the small-sites data set varied widely between the two partition analyses; whereas this overlap explained more than a third of the variation in the general analysis (Fig. 4), the sum of the overlaps of region with water and energy was much smaller (Fig. 7). Because of this, the overlap between regional and all environmental effects could be attributed almost exclusively to habitat type (the only factor not included in the

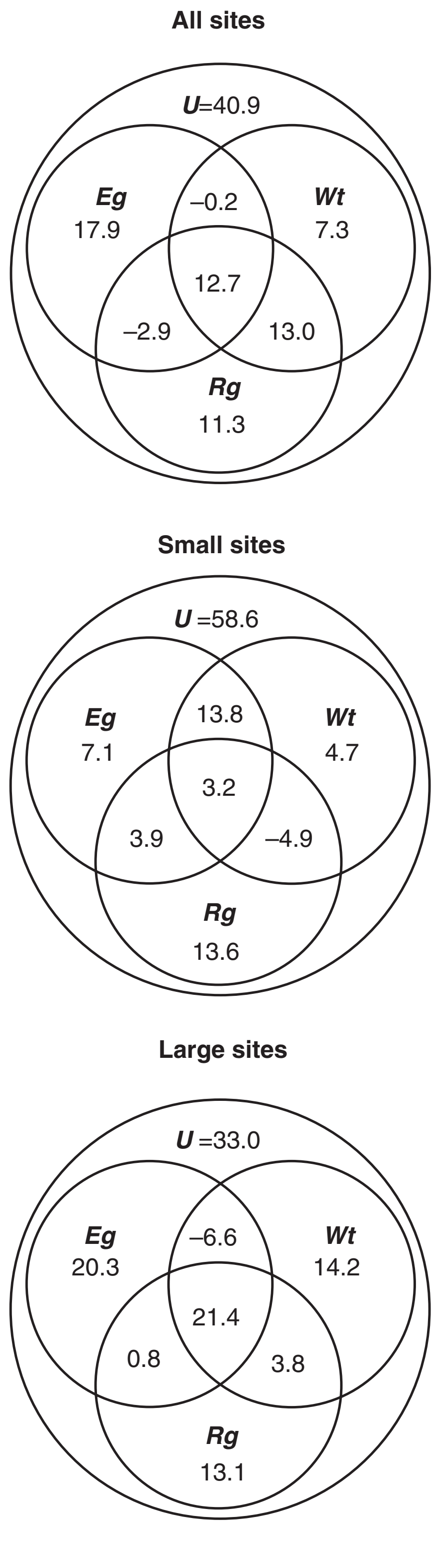


Figure 7 Variation partitioning of mammal species richness into the independent effects of Energy (*Eg*), Water (*Wt*) and Regional (*Rg*) factors, and their overlaps (see Appendix S3). *U* is the unexplained variation. Negative values indicate synergy, i.e. the combined effect of both groups of variables explains species richness better than the sum of individual effects. Small sites have areas between 100 and 1000 km^2, and large sites have areas between 1000 km^2 and 10,000 km^2. GLM results are listed in Appendix S3.

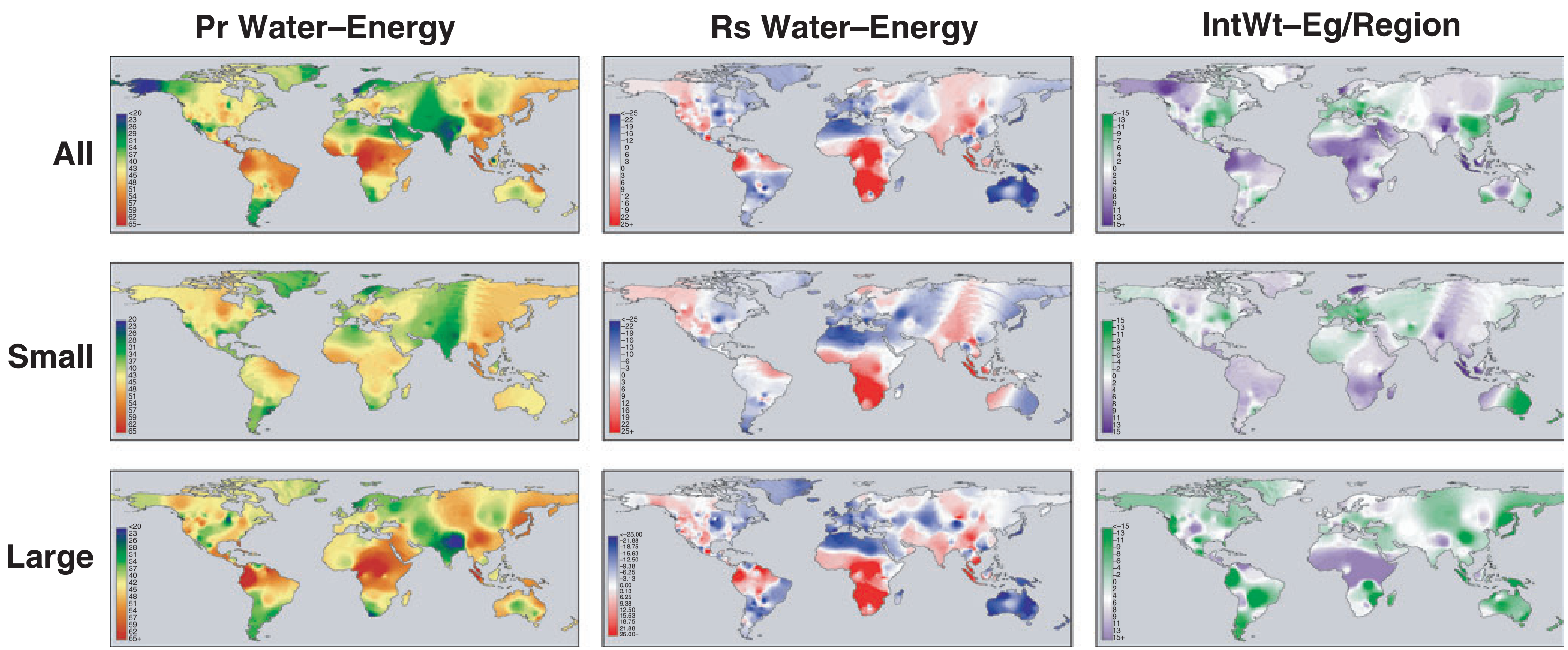


Figure 8 Spatial representation of the results of water and energy models, and of their overlap with region. The maps in the left column (Pr Water–Energy) show the relationships between species richness and the region-independent fractions of energy and water variables (see Fig. 6 and Appendix S3); colour scaling is similar to that used in Fig. 5. The central column (Rs Water–Energy) shows the residuals of models of the region-independent fractions of water and energy variables (raw *Eg* plus raw *Wt*; see Fig. 6 and Appendix S3); colours identify areas where the number of species is overpredicted (blue) or underpredicted (red) (i.e. blue areas are where there are fewer species than expected by water–energy effects, and red areas are where there are more species than expected). Maps in the right-hand column (Int Wt-Eg/Region) show the richness predicted solely by the overlap between energy and water, and region (*Eg+Rg*, *Wt+Rg*, and *Eg+Wt+Rg*; see Fig. 7 and Appendix S3); positive (purple) and negative (green) are, respectively, where the increase or decrease in the predicted number of species is attributable to the overlap between water–energy and region (i.e. purple areas are located where regional differences in water–energy predict more species than expected by the global trend, whereas green areas identify areas where these regional differences result in fewer species than expected). These values were calculated by subtracting the predictions of the *Eg* and *Wt* predictors independent from *Rg*, and the predictions of *Rg* independent from *Eg* and *Wt*, from the predictions of a model of the three factors altogether. All maps were interpolated using the same technique as for those presented in Fig. 5.

water–energy analyses), as the amount of variation non-overlapping with region was similar when either all environmental variables (Fig. 4) or only water and energy correlates (Fig. 7) were included in the analyses (*c.* 26%). Shared effects of habitat type and region on species richness at small sites appeared to be synergistic, as their shared variance was greater than the single effect of habitat type (36 vs. 24%; see Fig. 4 and Table S2.2 in Appendix S2).

Water–energy models for the three data sets predicted high species richness in tropical areas, especially towards the south, and low richness in the Holarctic, southern South America, the Transvaal region at South Africa, and some parts of central and southern Australia (Fig. 8). These predicted gradients were weaker in the small sites than in the large sites or in all sites combined. When the residual models of water and energy (which depict the relationships with these variables that are independent from the region) were considered, they under-predicted richness in most tropical areas, overpredicting especially in the north, east and west of Australia, although less so in the small-sites data set (Fig. 8). When the overlap between water–energy and region (which identifies differences between regions in the water–energy relationship with richness) was mapped, it showed a positive effect (increasing richness) in the Palaeotropics, and a negative effect in Australia and the western coast of Northern Africa (Fig. 8, right column). Whereas these shared effects increase the richness of small localities in South America, they also decrease the modelled number of species in larger localities.

DISCUSSION

We found that more than 60% of the variation in non-volant mammal species richness of a large set of globally scattered localities was accounted for by environment (including water, energy and habitat) and region. Thus, mammal richness patterns, even when derived from actual presence data gathered from checklists of natural areas, show strong deterministic structure, although the nature of this structure varies across scales.

Environmental effects and scale dependence

The environmental factors affecting biodiversity patterns are presumed to be essentially climatic gradients (Currie, 1991); species richness is usually related to the availability of both water and energy (water–energy dynamics; see O'Brien, 1998, 2006; Andrews & O'Brien, 2000; Whittaker & Field, 2000; Hawkins *et al.*, 2003b; Whittaker *et al.*, 2007). Since the geographic patterns of these factors are often collinear, separating the specific effects of energy and water on richness is difficult (see, for example, H-Acevedo & Currie, 2003). Here, we use an analytical approach that partitions the variability explained by these correlates into the independent parts and their overlaps. Although it is impossible to separate the effects of water and energy, since life requires that both are suitable, it is possible to identify partially independent effects within the general framework of water–energy dynamics. We argue that (1) the independent effect of energy is the result of both productivity and ambient temperature (i.e. the effect of physiological restrictions to life; see Brown *et al.*, 2004) in places where water is not limiting, (2) the independent effect of water is the result of water availability in places where temperature is not limiting (i.e. the constraints imposed by the physical properties of the water to organisms, see O'Brien, 2006), and (3) the overlap of energy and water operates in places where neither of these factors is the main constraint.

The relationship between mammal richness and the various environmental factors varied according to the size of the localities analysed, both in strength and relative importance. This is consistent with the widely recognized realization that the strength of species richness correlates is contingent on the type and scale of the data (Whittaker *et al.*, 2001; van Rensburg *et al.*, 2002; Willis & Whittaker, 2002; Hurlbert & White, 2005; Hurlbert & Jetz, 2007), and that climate does not account for many local/landscape patterns of diversity (Whittaker & Field, 2000). By splitting the data into two grains we obtain a crude representation of the perspectives of diversity discussed by O'Brien (2006): large sites represent *geographic richness* (i.e. the result of the current aggregation of the distributional ranges of species in the geographic space); and small sites represent *ecological richness/diversity* (i.e. the outcome of biotic dynamics in ecological time). Our results suggest that climatic gradients (energy and water) are stronger predictors of geographic richness (i.e. in large areas), whereas other interactions partly related to the overlap of habitat type and region become more important for the ecological richness of mammal assemblages in small areas. We hypothesize that: (1) regional effects correspond to the general limitations of the evolutionary solutions (species) available, and therefore remain more or less constant regardless of the scale, although they also interact with the environmental variables most relevant at each scale (see below); (2) the frequently reported correlation between climate and species richness occurs mainly at the large scale, probably owing to the effect of climatic gradients on species ranges (see Rahbek *et al.*, 2007); and (3) habitat selection, between-species interactions and other ecological factors become increasingly important at finer scales, so the importance of water and energy as drivers of biodiversity patterns becomes less evident.

Regional differences in global determinants of species richness

Although biological relativity to water–energy dynamics (*sensu* O'Brien, 2006) clearly influences species-richness patterns at broad scales (at least for woody plants), the climate patterns driving these dynamics are not the only effects shaping diversity gradients. Strong relationships between energy, water and species richness have been extensively reported (e.g. Currie, 1991; Kerr & Packer, 1997; Francis & Currie, 1998;

O'Brien, 1998; Hawkins *et al.*, 2003b; Field *et al.*, 2005; Whittaker *et al.*, 2007). Based on this evidence, environmental factors have been claimed as the main determinants of biodiversity pattern (Francis & Currie, 1998, 2003). However, regional effects were not appropriately tested in many analyses (Qian & Ricklefs, 2004), as either: (1) their scope was reduced to a single biogeographical region (e.g. Nearctic: Currie, 1991; Neotropical: Tognelli & Kelt, 2004); or (2) species-richness estimates were standardized by the size of the regional pool (e.g. Olff *et al.*, 2002).

In our analyses, region was always a significant correlate of richness, accounting for 25–33% of the spatial structure of richness, both overlapping with environmental correlates and independently. The exact nature of the relationship between biodiversity and the environment can vary from region to region (Ricklefs *et al.*, 1999; Hawkins *et al.*, 2003b, 2007a; Qian & Ricklefs, 2004; our results). We also found that covariation between regional and environmental effects varies with scale (see above): at the larger grains region overlaps mainly with water–energy factors, whereas at the smaller grains it overlaps with habitat. However, regional effects appear not only as regional differences in the relationship between richness and environment. The independent effect of region explained a significant proportion of richness in all data sets. More importantly, the proportion of the variance was almost scale-invariant.

Regions are a crude proxy for historical processes (Hawkins *et al.*, 2003a). However, environmentally independent regional differences are not a black box for all unknown historical processes (Harrison & Cornell, 2007). Rather, regional differences arise from evolutionary differences, the effects of climate change through time, and current differences in climate, topography, and the distribution of biomes (Jetz & Rahbek, 2001; Ricklefs, 2004, 2007; Hawkins *et al.*, 2005, 2007a). Owing to the correlation between current and past climate, most of the historical signal in the diversity gradient is masked by current climate (see Hawkins *et al.*, 2007a, and references therein), making it difficult to disentangle their effects (Whittaker & Field, 2000). Our results show that, although a portion of the differences among regions cannot be separated from environmental effects, other portions are independent from these factors. We hypothesize that: (1) the overlap between region and environment is caused by the interactions between the characteristics of the species available in the regional pool and current and past climate and habitat conditions, which shape the richness–environment relationships within each region (see, for example, Hawkins *et al.*, 2003a); and (2) the independent effects of region are a consequence of the constraints of the regional species pool (i.e. the functional characteristics of clades), which limit the partitioning of ecological space within each region (see discussion in Ricklefs, 2007). Although an integration of effects operating in both ecological and evolutionary time certainly provides more powerful explanations for current richness gradients (Ricklefs, 2004; Hawkins *et al.*, 2007a), some macroevolutionary processes operating at regional scales have a distinct effect on the richness of mammal communities.

In sum, although environmental variables are the most important correlates of mammal richness at the global scale, the inclusion of region increases the explanatory power of the models. The overlap between regional and environmental variables (Hawkins *et al.*, 2003a; our results) and the correlation between current and past climate (see, for example, Hawkins *et al.*, 2005, 2007a) demonstrate that geographic differences in species richness and community structure are linked not only to present-day environmental conditions but also to historical processes acting at evolutionary and ecological time-scales (see Hawkins *et al.*, 2005; Svenning & Skov, 2005; Rodríguez *et al.*, 2006). Although our results are restricted to terrestrial non-volant mammal assemblages, it is likely that they can be extrapolated to many other groups. The evolutionary history and *bauplan* of each group within each region imposes several constraints, which determine their regional responses (see Hawkins *et al.*, 2003b; Ricklefs, 2004; Nieto *et al.*, 2005). Variable relationships between richness and environment also appear when different groups are studied within the same region (see, for example, Hawkins *et al.*, 2007b), so different global patterns for groups with different environmental requirements and/or dispersal dynamics should also be expected (see Svenning & Skov, 2005; Whittaker *et al.*, 2007). As Ricklefs (2004, 2007) points out, the species present in a given locality are the outcome of the interactions of species distributions within the region as a whole, not only of local environmental effects. Any explanation of global diversity patterns that ignores the influence of the species pool leaves untested one determinant affecting local communities.

ACKNOWLEDGEMENTS

We are indebted to Brad Hawkins, Bob Ricklefs, John Wiens, Steven Chown, Shai Meiri and two anonymous referees for their critical review and useful comments on earlier drafts of the manuscript, and also to David Nogués, Miguel Araújo, Carsten Rahbek and Rob Whittaker for fruitful discussion on the topic. This work was supported by the Spanish MEC project CGL2004-0439/BOS, the DGI projects CGL2006-13532-C03/BTE and BTE 2002-00410, and also by the Fundación BBVA project 'Yámana - Diseño de una red de reservas para la protección de la biodiversidad en América del Sur Austral utilizando modelos predictivos de distribución con taxones hiperdiversos'. J.H. was supported by a CM/CSIC/MNCN grant, a Portuguese FCT (Fundação para a Ciência e Tecnologia) grant (BPD/20809/2004), and by the UK Natural Environment Research Council.

REFERENCES

Ahn, C.-H. & Tateishi, R. (1994) Development of a global 30-minute grid potential evapotranspiration data set. *Journal of the Japan Society of Photogrammetry and Remote Sensing*, **33,** 12–21.

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.

Bailey, R.G. (1989/1993) *Bailey Ecoregions of the Continents (reprojected) from the World Conservation Monitoring Center. Global Ecosystems Database Version 2.0*. NOAA National Geophysical Data Center, Boulder, CO.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73,** 1045–1055.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85,** 1771–1789.

Clark Labs (2000) *Global Change Data Archive Vol. 3. 1 km Global Elevation Model*. CD-Rom, Clark University, Worcester, MA.

Clark Labs (2001) *Idrisi 32 Release 2. GIS software package*. Clark Labs, Worcester, MA.

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. *The American Naturalist*, **137,** 27–49.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7,** 1121–1134.

Deichmann, U. & Eklundh, L. (1991) *Global digital data sets for land degradation studies: a GIS approach*. UNEP/GEMS and GRID, Nairobi, Kenya.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12,** 53–64.

Dobson, A. (1999) *An introduction to generalized linear models*. Chapman & Hall/CRC, London.

European Commission (2003) *Global Land Cover 2000 (GLC2000) Database*. European Commission Joint Research Centre, Ispra, Italy. Available at http://www-gvm.jrc.it/glc2000/defaultGLC2000.htm.

Evans, K.L. & Gaston, K.J. (2005) Can the evolutionary-rates hypothesis explain species-energy relationships? *Functional Ecology*, **19,** 899–915.

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.

Field, R., O'Brien, E. & Whittaker, R.J. (2005) Global models for predicting woody plant richness from climate: development and evaluation. *Ecology*, **86,** 2263–2277.

Francis, A.P. & Currie, D.J. (1998) Global patterns of tree species richness in moist forests: another look. *Oikos*, **81,** 598–602.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, **161,** 523–536.

Freckleton, R.P. (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology*, **71,** 542–545.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature*, **444,** 93–96.

H-Acevedo, D. & Currie, D.J. (2003) Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. *Global Ecology and Biogeography*, **12,** 461–473.

Harrison, S. & Cornell, H.V. (2007) Introduction: merging evolutionary and ecological approaches to understanding geographic gradients in species richness. *The American Naturalist*, **170,** S1–S4.

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. (2003a) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84,** 1608–1623.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E., Porter, E.E. & Turner, J.R.G. (2003b) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84,** 3105–3117.

Hawkins, B.A., Diniz-Filho, J.A.F. & Soeller, S.A. (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. *Journal of Biogeography*, **32,** 1035–1042.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007a) Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, **170,** S16–S27.

Hawkins, B.A., Albuquerque, F.S., Araújo, M.B., Beck, J., Bini, L.M., Cabrero-Sañudo, F.J., Castro Parga, I., Diniz-Filho, J.A.F., Ferrer-Castán, D., Field, R., Gómez, J.F., Hortal, J., Kerr, J.T., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Moreno, J.C., Olalla-Tárraga, M.Á., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.Á., Sanders, N.J. & Williams, P. (2007b) A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology*, **88,** 1877–1888.

Hurlbert, A.H. & White, E.P. (2005) Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters*, **8,** 319–327.

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 USA*, **104,** 13384–13389.

Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, **86,** 393–401.

Jetz, W. & Rahbek, C. (2001) Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences USA*, **98,** 5661–5666.

Kerr, J.T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high energy regions. *Nature*, **385,** 252–254.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences USA*, **98,** 11365–11370.

Leemans, R. & Cramer, W.P. (1991) *The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid*. IIASA, Laxenburg, Austria.

Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74,** 1659–1673.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd English edition. Elsevier, Amsterdam.

Lobo, J.M., Castro, I. & Moreno, J.C. (2001) Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. *Biological Journal of the Linnean Society*, **73,** 233–253.

McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd English Edition. Chapman & Hall, London.

Miller, H.J. (2004) Tobler's first law and spatial analysis. *Annals of the Association of American Geographers*, **94,** 284–289.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82,** 2381–2396.

Montoya, D., Rodríguez, M.Á., Zavala, M.Á. & Hawkins, B.A. (2007) Contemporary richness of Holarctic trees and the historical pattern of glacial retreat. *Ecography*, **30,** 173–182.

Nieto, M., Hortal, J., Martínez-Maza, C., Morales, J., Ortiz-Jaureguizar, E., Pelaez-Campomanes, P., Pickford, M., Prado, J.L., Rodríguez, J., Senut, B., Soria, D. & Varela, S. (2005) Historical determinants of mammal diversity in Africa: evolution of mammalian body weight distribution in Africa and South America during Neogene and Quaternary times. *African biodiversity: molecules, organisms, ecosystems* (ed. by B.A. Huber, B.J. Sinclair and K.-H. Lampe), pp. 287–296. Springer, New York, NY.

O'Brien, E. (1998) Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography*, **25,** 379–398.

O'Brien, E.M. (2006) Biological relativity to water–energy dynamics. *Journal of Biogeography*, **33,** 1868–1888.

Olff, H., Ritchie, M.E. & Prins, H.H.T. (2002) Global environmental controls of diversity in large herbivores. *Nature*, **415,** 901–904.

Qian, H. & Ricklefs, R.E. (2004) Taxon richness and climate in angiosperms: is there a globally consistent relationship that precludes region effects? *The American Naturalist*, **163,** 773–779.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species richness patterns. *Ecology Letters*, **8,** 224–239.

Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, **98,** 4534–4539.

Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society B: Biological Sciences*, **274,** 165–174.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15,** 321–327.

van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *The American Naturalist*, **159,** 566–577.

Ricklefs, R.E. (1987) Community diversity – relative roles of local and regional processes. *Science*, **235,** 167–171.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7,** 1–15.

Ricklefs, R.E. (2007) History and diversity: explorations at the intersection of ecology and evolution. *The American Naturalist*, **170,** S56–S70.

Ricklefs, R.E. & Schluter, D. (1993) Species diversity: regional and historical influences. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 350–363. The University of Chicago Press, Chicago, IL.

Ricklefs, R.E., Latham, R.E. & Qian, H. (1999) Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos*, **86,** 369–373.

Rodríguez, J. (1999) Use of cenograms in mammalian palaeoecology. A critical review. *Lethaia*, **32,** 331–347.

Rodríguez, J., Hortal, J. & Nieto, M. (2006) An evaluation of the influence of environment and biogeography on community structure: the case of the Holarctic mammals. *Journal of Biogeography*, **33,** 291–303.

Scheiner, S.M. & Willig, M.R. (2005) Developing unified theories in ecology as exemplified with diversity gradients. *The American Naturalist*, **166,** 458–469.

StatSoft Inc. (2003) *STATISTICA (data analysis software system), version 6.1.* StatSoft, Inc., Tulsa, OK. http://www.statsoft.com.

Svenning, J.-C. & Skov, F. (2005) The relative roles of environment and history as control of tree species composition and richness in Europe. *Journal of Biogeography*, **32,** 1019–1033.

Svenning, J.-C. & Skov, F. (2007) Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, **16,** 234–245.

Tognelli, M.F. & Kelt, D.A. (2004) Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography*, **27**, 427–436.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.

Whittaker, R.J. & Field, R. (2000) Tree species richness modelling: an approach of global applicability? *Oikos*, **89**, 399–402.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species richness. *Journal of Biogeography*, **28**, 453–470.

Whittaker, R.J., Nogués-Bravo, D. & Araújo, M.B. (2007) Geographic 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.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics*, **34**, 273–309.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity – scale matters. *Science*, **295**, 1245–1248.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Sites used for the analyses.
Appendix S2 Generalized linear model analyses.
Appendix S3 Variation partition analyses.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01850.x

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCHES

Joaquín Hortal is interested in the factors influencing current and past biodiversity patterns, especially those affecting the assemblage and structure of communities through time, as well as evolutionary processes in a biogeographical context. He is also interested in biodiversity estimators, conservation biogeography, predictive modelling, island biogeography, and the ecology, evolution and biogeography of dung beetles.

Jesus Rodríguez is a palaeoecologist with research interests in macroecology and the factors influencing the assemblage of ecological communities. His research is focused on the evolution of Pleistocene European mammalian communities in relation to environmental and historical factors.

Manuel Nieto-Díaz is a palaeontologist interested in the evolution of mammal communities, as well as the study of ruminant diversity and evolution, with a special focus on the Iberian Miocene, including the reconstruction of the past biology of Bovidae. He is now working on the regulation of gene expression in the neurons of common deer horns.

Jorge M. Lobo is interested in the patterns and processes of species distributions from a macroecological perspective, and in the management of biodiversity and conservation biogeography. He is a specialist in the biogeography and ecology of dung beetles (Scarabaeoidea).

Editor: Bradford Hawkins

SUPPLEMENTARY MATERIAL

Regional and environmental effects on the species richness of mammal assemblages

Joaquín Hortal[1,2,3*], Jesús Rodríguez[4*], Manuel Nieto-Díaz[1,5], Jorge M. Lobo[1]

[1]Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal, 2 – 28006, Madrid, Spain

[2]Center for Macroecology, Institute of Biology, University of Copenhagen. Universitetsparken, 15 - DK-2100 Copenhagen O, Denmark

[3]NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK.

[4]Centro Nacional de Investigación de la Evolución Humana (CENIEH). Avda. de la Paz, 28. 28004. Burgos (Spain)

[5]Instituto de Neurobiología Ramón y Cajal (CSIC), Avda. del Doctor Arce, 37 – 28002, Madrid, Spain

* Correspondence: J. Hortal, NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK.

E-mail: j.hortal@imperial.ac.uk

Editor: Bradford Hawkins

Supplementary material

Appendix S1.- Sites used for the analyses

Appendix S2.- GLM Analyses

Appendix S3.- Variation Partition Analyses

Appendix S1: Sites used for the analyses.
Codes are those in the database developed by Rodríguez (1999). Each locality represents a territory of homogeneous biome that is managed as a whole, so it can be treated as a single land unit at a global extent. Twenty-two sites from the 333 currently available in the database have been discarded due to possible errors in their inventories and/or area covered, or because they were composed of multiple biomes or land units. An additional set of 87 localities has been excluded because they were too large (area > 10,000 km^2) or too small (area < 100 km^2).

Area (Ar) is given in km^2, and geographic position (Lat and Long) in decimal degrees (negative values correspond to the southern hemisphere and the sites west of Greenwich Meridian). Regions (BgReg) follow the mammal zoogeographic regions proposed by Cox (2001) (see text and Fig. 1). *S* is the number of mammal species (excluding Chiroptera) present in each site. NP means National Park, and BR Biosphere Reserve.

Code	**Locality**	**Ar**	**Lat**	**Long**	**BgReg**	***S***
5	Petrified forest	379	35.1	-109.5	Nearctic	43
8	White sands	582	32.4	-106.2	Nearctic	33
10	Zinave	5000	-21.15	33.3	Palaeotropical	61
11	Rancho Acurizal	137	-17.45	-57.37	Neotropical	42
12	Crater Lake	742	42.55	-122.1	Nearctic	54
15	Mount Rainier	954	46.5	-121.5	Nearctic	46
16	Badlands NP	982	43.5	-102	Nearctic	47
17	Chamela, Jalisco (Mexico)	350	19.31	-104.3	Neotropical	36
18	Canyonlands	1366	38.2	-109.5	Nearctic	42
22	Big Cypress	2898	25.55	-81.1	Nearctic	28
25	Shenandoah	795	38.3	-78.5	Nearctic	38
26	North Cascades	2043	48.45	-121.2	Nearctic	58
27	Organ Pipe Cactus	1339	32	-112.5	Nearctic	35
33	Dinosaur NM	853	40.3	-109	Nearctic	53
34	Zion	593	37.2	-112.5	Nearctic	57
35	Doñana	773	37.3	-6.35	Palearctic	24
36	Los Tuxlas	540	18.25	-95	Neotropical	38
39	Kalahari Transvaal 39	5019	-27	25.2	Palaeotropical	25
40	Hardangervida	3422	60.5	6.25	Palearctic	19
42	Transvaal 42	8784	-25.15	27.15	Palaeotropical	98
45	El Cielo	1145	23.5	-99.15	Nearctic	40
46	Cedarberg 46	644	-32.21	19.1	Palaeotropical	43
49	Repetek	346	38.16	63.13	Palearctic	21
50	Guadalupe Mountains	349	31.55	-104.5	Nearctic	56
52	Mount Kenya	718	0.1	37.19	Palaeotropical	40
53	Cazorla	1900	38.1	-2.41	Palearctic	23
54	Capitol Reefs	979	38.2	-111.3	Nearctic	44
55	Isle Royal	2314	48	-88.83	Nearctic	19
56	Voyagers NP	882	48.3	-94	Nearctic	48
58	El Malpais	462	35	-107.2	Nearctic	40
59	Lassen Volcanic NP	430	40.3	-121.3	Nearctic	49
63	Cercedilla/Navacerrada	131	40.45	-4.3	Palearctic	28
64	Buffalo N River	382	36	-93.1	Nearctic	40
66	Rocky Mountain NP	1067	40.2	-105.4	Nearctic	51
69	Krkonose 69	603	49.4	15.38	Palearctic	48
70	Berezinsky	1139	54.3	28.3	Palearctic	37
71	Bialowieza	105	52.44	23.52	Palearctic	32
72	Karkonosze 72	603	50.22	15.4	Palearctic	32
73	Montes Tatra	1236	49.15	19.56	Palearctic	26

Code	Locality	Ar	Lat	Long	BgReg	*S*
74	Baikal-Barguizinsky	2005	51.5	105.5	Palearctic	33
75	Oka Valley	772	54.43	39.2	Palearctic	48
76	Voronezshkiyi	388	52	39.41	Palearctic	42
78	Lago Torne	965	68.25	19	Palearctic	37
79	Carpathian Ukrania	578	48.36	23.55	Palearctic	43
80	Big Bend	2832	29.3	-102.3	Nearctic	50
81	Sta Mónica	607	34.09	-118.77	Nearctic	38
82	Redwood NP	446	41.45	-124.5	Nearctic	45
83	Point Reyes National Seashore	288	38.5	-122.5	Nearctic	31
84	Big South Fork	506	36.3	-84.4	Nearctic	41
85	Everglades NP	8717	25.22	-80.55	Nearctic	33
86	Denali	7820	63.2	-150.3	Nearctic	24
87	Yosemite NP	3081	37.5	-119.3	Nearctic	72
88	Glacier	4101	48.37	-113.5	Nearctic	54
90	Yoshua Tree NM	3205	34.9	-116.2	Nearctic	31
91	East Usambara	900	-4.45	38.2	Palaeotropical	39
92	Great Smoky Mountains NP	2109	35.3	-83.3	Nearctic	60
93	Sequoia & Kings Canyon	3495	36.45	-118.3	Nearctic	62
94	Augabries Falls	147	-28.35	20.21	Palaeotropical	46
95	Olympic NP	3734	47.49	-123.5	Nearctic	39
96	Delta del Danubio	5762	44.47	28.58	Palearctic	42
98	Trebon Basin	700	49	14.5	Palearctic	39
99	Vosges du Nord	1200	48.57	7.35	Palearctic	31
101	Eastern Beskid	271	49.1	22.2	Palearctic	45
102	Spreewald	476	51.53	13.47	Palearctic	34
103	Aggtelek	197	48.3	20.36	Palearctic	35
104	Long point	270	43.35	-80.2	Nearctic	34
105	Guatopo	1224	10	-66	Neotropical	40
111	Belém	150	-1.27	-48.29	Neotropical	64
120	Sikhote-Alinskiy	3402	45.15	135.12	Palearctic	46
121	Tsentral'no-lesnoy	213	56.3	32.52	Palearctic	46
123	Astrakhanskiy	668	46.1	48.38	Palearctic	24
124	Laplandskiy	2784	67.37	32.15	Palearctic	31
125	Waterton	526	49.6	-113.5	Nearctic	56
128	Kahuzi Biéga	6000	2.31	28.45	Palaeotropical	143
129	Mahale	1613	-6.12	29.4	Palaeotropical	63
130	Yasuni	6797	0.47	-76.2	Neotropical	83
131	Sian Ka'an	4080	19.53	-87.66	Neotropical	50
132	Mlawula	144	-26	32	Palaeotropical	65
133	Dja	5260	3.6	13	Palaeotropical	95
134	Gunung Palung	900	-1.19	110.24	Oriental	69
135	Kanha	940	22.2	89.39	Oriental	51
136	Badghyz Zapovednik	880	36	62	Palearctic	35
140	Wolong	2000	31.5	102.38	Palearctic	79
142	Fujian Wuyi Shan	1000	27.4	117.45	Oriental	47
143	Prince Regent	6338	-15.5	125.25	Australian	20
144	Ubsunurskaya Kotlovina	2843	50.15	92.35	Palearctic	66
147	Fang Jing Shan)	383	27.53	108.47	Palearctic	48
149	Cilento and Vallo di Diano	1810	40.2	15.2	Palearctic	27
150	Kavkazskiy	2957	43.47	40.15	Palearctic	58
151	Sokhondinskiy Zapovednik	2110	49.44	110.58	Palearctic	54
154	Kogelberg	1036	-34.14	19	Palaeotropical	55
156	Malolotjia Nature Reserve)	180	-26	31.3	Palaeotropical	68
157	Kibale Forest Corridor	560	0.3	30.2	Palaeotropical	65
158	Mae Sa-Kog Ma	421	18.8	98.52	Oriental	40
159	Gunung Leuser	7927	3.54	97.6	Oriental	108
160	Manas NP	658	26.53	90.56	Oriental	55

Code	Locality	Ar	Lat	Long	BgReg	*S*
161	Andringitra	312	-22.15	46.54	Palaeotropical	41
162	Uluru	1330	-24.25	131	Australian	32
163	Croajingolong	1010	-37.37	149.29	Australian	28
164	Shoalwater and Corio Bays	2391	-22.57	150.45	Australian	29
165	The Grampians	1670	-34.16	142.7	Australian	24
167	Purnululu NP	2000	-17.29	128.15	Australian	21
169	Aguas Emendadas	105	-15.34	-46.36	Neotropical	42
170	Mamili	320	-18.23	23.38	Palaeotropical	94
171	Katunsky	6953	49.45	86	Palearctic	43
172	Sierra Gorda	3836	21.2	-99.5	Nearctic	73
179	Iguazú NP	492	-25.3	-54.2	Neotropical	46
181	Mujib (Jordan)	205	31.27	35.48	Palearctic	27
182	Anjanaharibe-S	321	-14.45	49.2	Palaeotropical	32
183	Andohahela	760	-24.4	46.44	Palaeotropical	37
185	Terra Nova NP	400	48.31	-53.57	Nearctic	20
186	Nahanni	4765	61.35	-125.5	Nearctic	40
187	Namdapha NP	1985	27.31	96.37	Oriental	58
188	Prespa NP	277	40.45	21.5	Palearctic	28
189	West Caprivi Game Reserve	6371	-17.55	22.37	Palaeotropical	89
191	Chernye Zemli BR	5329	46.13	43.1	Palearctic	22
192	Daurskiy BR	2277	49.85	115.46	Palearctic	36
193	Darvinsky Zapovednik	1127	58.32	37.48	Palearctic	39
194	Teberdinskiy BR	5360	43.21	41.42	Palearctic	41
195	Sayano-Shushenskiy BR	3900	51.9	91.67	Palearctic	49
196	Syunt-Khasardagh Zapovednik	264.61	38.5	55.5	Palearctic	40
197	Amudarya Zapovednik	485	41	61.8	Palearctic	24
198	Royal Chitwan NP	932	27.29	84.33	Oriental	39
199	Iwokrama Forest	3700	4.5	-59	Neotropical	75
200	Ulu Temburong	489	4.27	115.11	Oriental	35
201	Nechisar NP	700	6	37.54	Palaeotropical	46
202	Tierra Del Fuego NP	630	-54.38	-68.31	Neotropical	13
203	Laguna de Pozuelos	4000	-22.2	-66.48	Neotropical	30
204	Lanin NP	3790	-39.31	-71.29	Neotropical	32
205	El Rey	441	-24.4	-64.34	Neotropical	28
206	Bosque Pertificado	612	-47.39	-68.13	Neotropical	25
208	Mergueb	125	35.35	3.58	Palearctic	11
209	Luberon	1796	43.57	5.25	Palearctic	32
210	Djurdjura	356	36.29	4.8	Palearctic	15
213	Cat Tien	2573	11.34	107.22	Oriental	66
214	Xishuangbanna	2417	21.47	101.6	Oriental	33
216	Wadi Rum	1875	29.58	35.63	Palearctic	22
217	Bayerische Wald	133	48.55	13.23	Palearctic	37
218	Lauca	3583	-18.48	-68.98	Neotropical	28
219	Fitzgerald River	3290	-33.83	119.55	Australian	20
220	Kosciuszko	6255	-36.1	148.28	Australian	28
221	Wasur-Rawa	4138	-8.6	140.8	Australian	34
222	Mapimi	1030	26.67	-103.6	Nearctic	41
224	La Amistad	6556	9.5	-82.4	Neotropical	72
225	Parc National Suisse	1740	46.4	10.1	Palearctic	29
226	Urdaibai	219	43.32	-2.68	Palearctic	30
227	Yellowstone NP	8983	44.58	-110.1	Nearctic	52
228	Craters of the Moon (USA)	3400	43.33	-113.1	Nearctic	38
229	Great Basin	312	38.95	-114.2	Nearctic	50
230	Lake Meredith	182	35.61	-101.6	Nearctic	50
231	Big ticket	391	30.31	-94.19	Nearctic	41
232	Wheeler NWR	140	34.38	-86.56	Nearctic	30
233	Carolinian South Atlantic	1255	33.25	-79.67	Nearctic	32

Code	Locality	Ar	Lat	Long	BgReg	*S*
235	Cuyahoga	132	41.17	-91.31	Nearctic	27
236	Redberry Lake	1122	52.42	-107.1	Nearctic	26
238	Grasslands NP	450	49.1	-107.4	Nearctic	42
239	Algonquin Provincial Park	7725	45.83	-78.7	Nearctic	42
240	Cape Breton NP	950	46.71	-60.63	Nearctic	35
241	Forillon NP	240	48.88	-64.35	Nearctic	27
242	Fundy NP	206	45.6	-65.1	Nearctic	37
244	Kejimkujik NP	381	44.36	-65.3	Nearctic	38
246	Kouchibouguac NP	235	45.85	-64.95	Nearctic	37
247	La Mauricie NP	536	46.8	-72.95	Nearctic	42
248	Mount Arrowsmith NP	1186	49.23	-124.48	Nearctic	22
249	Mount Revelstoke	256	51.1	-118.2	Nearctic	45
250	Vessertal Thüringen Forest	170	50.36	10.48	Palearctic	24
252	Pukaskwa NP	1873	48.26	-85.83	Nearctic	42
254	Woodland Caribou NP	4620	51	-94.73	Nearctic	30
255	Baja California	9347	31.52	-114.4	Nearctic	33
257	Kootenay	1378	50.95	-115.98	Nearctic	47
258	Nahuel Huapi	3300	-41	-71.5	Neotropical	38
259	Prince Albert	3875	53.96	-106.21	Nearctic	50
260	Rio Pilcomayo	500	-25.7	-58.14	Neotropical	47
261	Shiga highland	130	36.43	138.3	Palearctic	31
265	Tansa Wildlife Sanctuary	216	19.14	73.2	Oriental	39
266	Krau	530	3.42	102.11	Oriental	83
269	Montes Azules	3310	16.5	-91.1	Neotropical	49
271	Sanjay	365	23.77	81.37	Oriental	30
272	Bandhavgarh	344	23.39	80.77	Oriental	32
273	Simlipal	2750	21.7	86.35	Oriental	40
274	Ñacuñán	123	-34.2	-67.54	Neotropical	30
275	Bañados del Este	2000	-33.5	-54	Neotropical	24
276	Mburucuyá	151	-28.5	-58.4	Neotropical	21
278	Los Alerces	1875	-42.15	-71.72	Neotropical	16
280	Taï NP	350	5.46	-7.35	Palaeotropical	64
284	Amboseli NP	4832	-2.39	37.15	Palaeotropical	67
285	Maolan	213	25.25	107.93	Oriental	30
286	Kaplankyr	2828	41.16	57.1	Palearctic	27
288	Kivach Zapovednik	109	62.18	33.53	Palearctic	40
289	Lake Manyara	230	-3.3	35.6	Palaeotropical	50
290	Queen Elisabeth	2200	0.4	29.92	Palaeotropical	60
291	Anza-Borrego Desert State Park	2226	33.23	-116.26	Nearctic	48
292	Bandelier Natl Mon	133	35.79	-106.3	Nearctic	57
293	Bryce Canyon NP	145	37.58	-112.21	Nearctic	44
294	Carrizo Plains Ca	800	35.7	-119.43	Nearctic	36
300	Lacassine National Wildlife Refuge,	141	29.86	-92.93	Nearctic	24
301	Land Between the Lakes	188	36.85	-88.6	Nearctic	37
302	Lake Roosevelt National Recreation Area	406	48.55	-118.13	Nearctic	59
303	Southern Appalachian	2470	35.5	-83.5	Nearctic	59
304	Wind Cave NP,	114	43.58	-103.42	Nearctic	35
305	Yoho NP	1290	51.38	-116.52	Nearctic	46
306	Baritú NP	724	-22.57	-64.8	Neotropical	36
308	Reserva de la Biosfera de Mar Chiquita	250	-35.65	-57.37	Neotropical	22
309	Sierra de San Javier	202	-26.78	-65.37	Neotropical	37
310	Bentuang Karimun NP	8000	1.23	113.33	Oriental	33
312	Pendjari	8800	11	1.5	Palaeotropical	42
313	Yathong	1072	-32.61	145.53	Australian	10
315	Teniente Enciso NP	400	-21.3	-61.66	Neotropical	41
316	Defensores del Chaco NP	7800	-20.22	-60.24	Neotropical	48
317	Cerro Cora NP	120	-22.61	-56.3	Neotropical	29

Code	Locality	Ar	Lat	Long	BgReg	*S*
318	R B Charlevoix	5600	47.67	-70.53	Nearctic	26
319	Kiskunsag BR	221	46.9	19.36	Palearctic	41
321	Changshanerhai	797	25.78	100.14	Oriental	51
322	Ailaoshan	504	24.26	101.23	Oriental	66
323	Daweishan	440	22.81	103.82	Oriental	66
324	Parc National d'Odzala	1100	0.803	14.88	Palaeotropical	62
325	Naute Dam	225	-26.97	17.96	Palaeotropical	66
326	Mount Everest (Sagarmatha) NP	1148	27.93	86.72	Oriental	22
327	Kalahari Gemsbok NP	9591	-25.676	20.365	Palaeotropical	56
329	Lamington NP	206	-28.25	153.1	Australian	29
330	Maracá Ecological Reserve	1013	3.34	-61.68	Neotropical	42
331	Kutai NP	1986	0.377	117.28	Oriental	60
332	Rio Plátano	5000	15.417	-85	Neotropical	46
333	Reserva de la Michilia	420	23.46	-104.3	Nearctic	35

References cited

Cox, C.B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography*, **28**, 511-523.

Rodríguez, J. (1999) Use of cenograms in mammalian palaeoecology. A critical review. *Lethaia*, **32**, 331-347.

Appendix S2: GLM Results

Table S2.1.- GLM results for the global analyses with all sites. Deviance and change in the deviance from a null model for mammal species number (*S*), considering explanatory variables one by one with their respective code. The linear, quadratic or cubic functions of each variable have been selected if they accounted for a significant change in the deviance ($p<0.05$). *Eg*, *Env* and *Rg* are the functions selected to account for all the effect on *S* of water-energy dynamics, environment and region respectively. *Dev* is deviance, Δ*Dev* is the change in deviance, *F* is the score of the *F* statistic, and *Vexp* is the percentage of explained variability. Ar stands for area, Altrng for altitudinal range, Slopemed for the mean slope in the locality, AspectSD for the standard deviation of the aspects of all the 1 km^2 cells included within the polygon of the natural area, GLC_DIV for the diversity of land cover categories; AET and PET account for Actual and Potential Evapotranspiration, respectively; TMEAN, TMAX and TMIN stand for mean, maximum and minimum annual temperature, respectively; PMEAN, PWIN, PSPR, PSUM, PFALL account for annual, winter, spring, summer and autumn precipitation, respectively; WBL does for Water Balance, BECDIV for the Bayley Divisions of the Ecoregions of the World, and BgReg for the Biogeographic Region. See text for more details on the origin of these variables.

Variables	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Null model	1397.6	223			
Area					
Ar	1397.6	222	89.5	14.21	6.02
Heterogeneity					
Altrng	1478.6	222	8.4	1.26	0.57
Slopemed	1480.5	222	6.6	0.98	0.44
AspectSD	1467.1	222	19.9	3.01	1.34
GLC_DIV	1452.8	222	34.3	5.24	2.30
Energy					
$AET+AET^2$	1220.9	221	266.1	48.17	17.90
PET	1326.2	222	160.8	26.92	10.82
$TMEAN+TMEAN^2+TMEAN^3$	1372.1	220	115.0	18.44	7.73
$TMAX+TMAX^2+TMAX^3$	1408.8	220	78.3	12.22	5.26
$TMIN+TMIN^2+TMIN^3$	1275.5	220	211.5	36.48	14.22
Eg: $AET+PET+TMEAN+TMEAN^2+TMEAN^3+TMAX+TMAX^2+TMAX^3+TMIN$	1078.6	214	408.4	81.03	27.47
Water					
PMEAN	1361.1	220	126.0	20.36	8.47
PWIN	1431.8	220	55.2	8.49	3.71
PSPR	1309.1	220	177.9	29.90	11.97
$PSUM+PSUM^2$	1415.4	220	71.6	11.13	4.82
PFALL	1324.7	220	162.4	26.96	10.92
$WBL+WBL^2+WBL^3$	1453.3	220	33.7	5.10	2.27
Wt: $PMEAN+PSPR+PWIN+PWIN^2+PWIN^3+PFALL+PFALL^2+PFALL^3$	1111.7	215	375.3	72.58	25.24

(cont…)

(…cont)

Variables	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Habitat type					
***Hb*: BECDIV**	1101.3	199	385.7	69.69	25.94
Environmental model: *Eg+Wt+Hb*	722.0	182	765.1	192.9	51.4
Region					
***Rg*: BgReg**	1091.5	218	395.5	79.0	26.6
Complete model: *Eg+Wt+Hb+Rg*	563.9	177	923.1	289.7	62.1

Table S2.2.- GLM results for the global analyses with the small sites (from 100 to 1,000 km^2). Presentation as in Table S2.1.

Variables	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Null model	519.4	118			
Area					
Ar	507.7	117	11.7	2.69	2.25
Heterogeneity					
Altrng	511.2	117	8.2	1.89	1.59
Slopemed	512.5	117	7.0	1.59	1.34
AspectSD	512.3	117	7.1	1.63	1.37
GLC_DIV	514.0	117	5.4	1.23	1.04
Energy					
AET	446.5	117	72.9	19.12	14.04
PET	474.2	117	45.2	11.15	8.70
TMEAN+TMEAN^2	478.2	116	41.3	10.01	7.95
TMAX	519.4	117	0.1	0.01	0.01
TMIN+TMIN^2	451.6	116	67.8	17.41	13.05
Eg: AET+PET+TMEAN+TMEAN^2+TMAX+TMIN	374.0	112	145.4	43.55	28.00
Water					
PMEAN	503.4	117	16.0	3.72	3.08
PWIN+PWIN^2+PWIN^3	453.5	115	65.9	16.71	12.69
PSPR	500.9	117	18.5	4.33	3.57
PSUM	503.2	117	16.3	3.78	3.13
PFALL	501.0	117	18.5	4.31	3.56
WBL	516.8	117	2.7	0.61	0.52
Wt: PWIN+PWIN^2+PWIN^3+ PSPR+PSUM+PFALL	416.9	112	102.5	27.54	19.73
Habitat type					
Hb: BECDIV	395.6	96	123.8	30.05	23.84
Environmental model: *Eg+Wt+Hb*	305.8	86	213.6	60.1	41.1
Region					
Rg: BgReg	388.7	113	130.7	37.99	25.16
Complete model: *Eg+Wt+Hb+Rg*	123.2	56	396.3	180.2	76.3

Table S2.3.- GLM results for the global analyses with the large sites (from 1,000 to 10,000 km^2). Presentation as in Table S2.1.

Variables	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Null model	951.1	104			
Area					
Ar	872.6	103	78.5	9.27	8.25
Heterogeneity					
Altrng	950.2	103	0.9	0.09	0.09
Slopemed	950.6	103	0.4	0.05	0.05
AspectSD	935.2	103	15.9	1.75	1.67
GLC_DIV	913.4	103	37.7	4.26	3.97
Energy					
$AET+AET^2+AET^3$	828.6	101	122.5	14.93	12.88
PET	833.9	103	117.2	14.48	12.32
$TMEAN+TMEAN^2$	873.8	102	77.3	9.02	8.12
$TMAX+TMAX^2+TMAX^3$	849.2	101	101.9	12.12	10.71
$TMIN +TMIN^2$	811.0	102	140.1	17.63	14.73
Eg: $AET+AET^2+PET+TMEAN+TMAX+TMAX^2+TMAX^3+TMIN$	609.8	96	341.3	53.72	35.88
Water					
$PMEAN+PMEAN^2+PMEAN^3$	864.6	101	86.5	10.11	9.10
$PWIN+PWIN^2$	943.7	102	7.4	0.79	0.77
$PSPR+PSPR^2+PSPR^3$	804.0	101	147.1	18.48	15.47
$PSUM+PSUM^2+PSUM^3$	889.8	101	61.3	6.96	6.45
$PFALL+PFALL^2+PFALL^3$	842.8	101	108.3	12.98	11.39
WBL	932.8	103	18.3	2.02	1.92
Wt: $PMEAN+PSPR+PSUM+PSUM^2+PSUM^3+PFALL+PFALL^2+PFALL^3$	663.3	96	287.8	41.65	30.26
Habitat type					
Hb: BECDIV	583.1	82	368.0	51.75	38.69
Environmental model: *Eg+Wt+Hb*	390.5	72	560.6	103.4	58.9
Region					
Rg: BgReg	640.2	99	310.9	48.1	32.7
Complete model: *Eg+Wt+Hb+Rg*	297.4	67	653.7	147.3	68.7

Appendix S3: Variation Partition Analyses

Two different partition analyses were performed to separate the independent and shared contributions (i.e., overlaps) of, respectively, two and three different factors (i.e., environmental and regional factors, and water, energy and region). To do this, partial regressions are used to obtain variables accounting for the variation in each factor that is independent from the others; i.e., to regress each predictor (or set of predictors one by one) against the other factors involved in the analysis, and keep the residuals as a new variable (or a set of new variables) independent of these factors.

For the partition of two factors (see Fig. 4 in the text, Hawkins *et al.,* 2003, or Nieto *et al.,* 2005), each predictor is regressed against the variables pertaining to the other factor, and the residuals are kept as a new predictor. In our case, all environmental variables are regressed against a model of all regional variables (in this case, only one variable) one by one, and all variables in *Rg* are regressed against a model of all variables in *Env* (in this case, all entering in the model for environmental factors, see Appendix S2). These new explanatory variables provide the independent effects of environment and region, and the difference between the variation explained by a model using all original variables (both environmental and regional) and these two models is attributable to their shared contribution or overlap (see Tables S3.1, S3.2 and S3.3).

Table S3.1.- Variation partitioning of mammal species richness into the independent effects of Environmental (*Env*) and Regional (*Rg*) factors, as well as their overlap (*Env+Rg*) for all sites. raw *Env* and raw *Rg* are the independent effects of Environmental variables and Region, respectively. *Dev* is deviance, Δ*Dev* is the change in deviance, *F* is the score of the *F* statistic, and *Vexp* is the percentage of explained variability; the rest of the abbreviations as in the text.

Environmental *vs* Regional effects (All sites)			*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
		null	1487.0	223			
(*a*) raw *Env*	38.0	*Env*	722.0	182	765.1	192.9	51.4
(*b*) raw *Rg*	11.3	*Rg*	1091.5	218	395.5	79.0	26.6
Shared effect	12.8	*Env+Rg*	563.9	177	923.1	289.7	62.1
[(*Env+Rg*) – (*a+b*)]		residuals *Env*	922.1	181	564.9	110.9	38.0
Error [100-(*Env+Rg*)]	37.9	residuals *Rg*	1318.7	217	168.3	27.7	11.3

Table S3.2.- Variation partitioning of mammal species richness into the independent effects of Environmental (*Env*) and Regional (*Rg*) factors, as well as their overlap (*Env+Rg*) for small sites (between 100 and 1,000 km^2). Abbreviations are as in Table S3.1.

Environmental *vs* Regional effects (Small sites)			*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
		null	519.4	118			
(*a*) raw *Env*	26.7	*Env*	305.8	86	213.6	60.1	41.1
(*b*) raw *Rg*	13.6	*Rg*	388.7	113	130.7	38.0	25.2
Shared effect	36.0	*Env+Rg*	123.2	56	396.3	180.2	76.3
[(*Env+Rg*) – (*a+b*)]		residuals *Env*	380.6	85	138.8	31.0	26.7
Error [100-(*Env+Rg*)]	23.7	residuals *Rg*	448.9	113	70.6	17.8	13.6

Table S3.3.- Variation partitioning of mammal species richness into the independent effects of Environmental (*Env*) and Regional (*Rg*) factors, as well as their overlap (*Env+Rg*) for large sites (between 1,000 and 10,000 km^2). Abbreviations are as in Table S3.1.

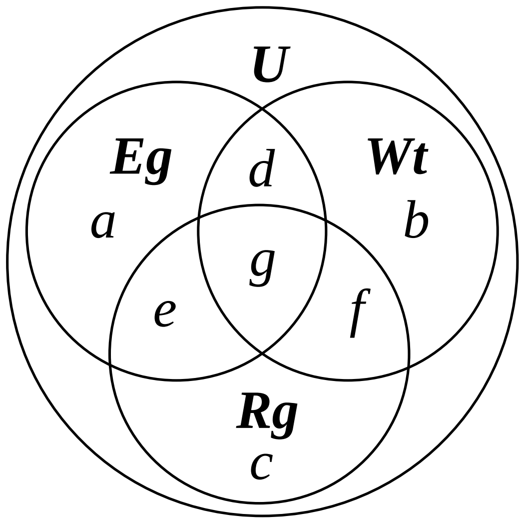
Environmental *vs* Regional effects (Large sites)			*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
		null	951.1	104			
(*a*) raw *Env*	38.9	*Env*	390.5	72	560.6	103.4	58.9
(*b*) raw *Rg*	13.1	*Rg*	640.2	99	310.9	48.1	32.7
Shared effect	16.7	*Env+Rg*	297.4	67	653.7	147.3	68.7
[(*Env+Rg*) – (*a+b*)]		residuals *Env*	581.1	71	370.0	45.2	38.9
Error [100-(*Env+Rg*)]	31.3	residuals *Rg*	826.5	99	124.6	14.9	13.1

For the partition of three factors, total variation is broken down into eight different components (see Venn diagram and Fig. 7 in the text):

(i) three accounting for the pure effects on the dependent variable of each factor considered;

(ii) four quantifying their shared variation, both by pairs and all together; and

(iii) a final component quantifying the variation unexplained by the factors used.



To do this, five consecutive steps are needed:

Step 1) Independent models for each factor (in our case, *Eg*, *Wt* and *Rg*) were developed using all the statistically significant functions of their variables in a backward-stepwise selection procedure. These models are a measure of all the variability explained by each factor (the three circles in the Venn diagram).

Step 2) These models were put together to obtain the percentage of variability explained by each pair of factors (i.e., *Eg*+*Wt*, *Eg*+*Rg* and *Wt*+*Rg*), and of the three factors altogether (i.e., *Eg*+*Wt*+*Rg*).

Step 3) Similarly to the two-factor analysis, each independent variable was regressed against a function of all the significant predictors included in the models of the other two factors. The residuals of such regressions constitute the variability of such a variable that is independent from the predictors included in the other factors (Borcard *et al.*, 1992).

Step 4) These residuals are used as predictors to determine the independent effect of each factor. Here, the variability explained by the models obtained in step 1 is re-calculated using the residual variables obtained in step 3. Such a score is the variability in the dependent variable explained by the factor that is independent from the effect of the other two factors.

Step 5) The variability explained by the remaining fractions (i.e., the shared components, that is, the overlapping sections in the Venn diagram) is calculated by solving two sets of equations (see an example in Lobo *et al.*, 2001):

Set 5.1	*Set 5.2*
$d + e + g = Eg - a$	$d = (Eg + Wt) - (e + f + g) - (a + b)$
$d + f + g = Wt - b$	$e = (Eg + Rg) - (d + f + g) - (a + c)$
$e + f + g = Rg - c$	$f = (Wt + Rg) - (d + e + g) - (b + c)$
	$g = (d + e + g) - d - e = (d + f + g) - d - f = (e + f + g) - e - f$

For example, the results for the case of all localities are shown at Table S3.4.

Table S3.4.- Variation partitioning of mammal species richness into the independent effects of Energy (*Eg*), Water (*Wt*) and Regional (*Rg*) factors, and their overlaps for all sites. Abbreviations are as in Table S3.1.

Energy *vs* Water *vs* Regional effects (All sites)	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Eg+Wt	887.4	206	599.6	139.2	40.3
Eg+Rg	830.6	209	656.5	165.2	44.1
Wt+Rg	874.1	210	613.0	147.3	41.2
Complete model (*Eg+Wt+Rg*)	693.0	201	794.0	230.3	53.4
Partial regressions					
res *Eg* vs. *Env+Rg*	1221.4	214	265.6	46.5	17.9
res *Env* vs. *Eg+Rg*	1377.9	215	109.1	17.0	7.3
res *Rg* vs. *Eg+Env*	1318.7	217	168.3	27.7	11.3

And the two sets of equations are solved from these results (see also Fig. 5):

Step 1	*Eg*	*Wt*	*Rg*	
	27.47	25.24	26.60	

Step 2	*Eg+Wt*	*Eg+Rg*	*Wt+Rg*	*Eg+Wt+Rg*
	40.32	44.15	41.22	53.4

Steps 3/4	*a*	*b*	*c*	
	17.86	7.34	11.32	

Step 5.1	*d+e+g*	*d+f+g*	*e+f+g*	
	9.60	17.90	15.28	

Step 5.2	*d*	*e*	*f*	*g*
	-0.15	-2.94	12.96	12.70

The same is made for the other two sets of sites (Tables S3.5 and S3.6):

Table S3.5.- Variation partitioning of mammal species richness into the independent effects of Energy (*Eg*), Water (*Wt*) and Regional (*Rg*) factors, and their overlaps for small sites. Abbreviations are as in Table S3.1.

Energy *vs* Water *vs* Regional effects (Small sites)	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Eg+Wt	326.4	106	193.1	62.7	37.2
Eg+Rg	313.8	107	205.7	70.1	39.6
Wt+Rg	341.3	107	178.1	55.8	34.3
Complete model (*Eg+Wt+Rg*)	279.7	101	239.7	86.6	46.2
Partial regressions					
res *Eg* vs. *Env+Rg*	482.7	113	36.7	8.6	7.1
res *Env* vs. *Eg+Rg*	495.0	112	24.4	5.5	4.7
res *Rg* vs. *Eg+Env*	448.9	113	70.6	17.8	13.6

Table S3.6.- Variation partitioning of mammal species richness into the independent effects of Energy (*Eg*), Water (*Wt*) and Regional (*Rg*) factors, and their overlaps for large sites. Abbreviations are as in Table S3.1.

Energy *vs* Water *vs* Regional effects (Large sites)	*Dev*	d.f.	Δ*Dev*	*F*	*Vexp*
Eg+Wt	499.9	88	451.2	79.4	47.4
Eg+Rg	473.3	91	477.8	91.9	50.2
Wt+Rg	507.2	91	443.9	79.6	46.7
Complete model (*Eg+Wt+Rg*)	384.8	83	566.3	122.1	59.5
Partial regressions					
res *Eg* vs. *Env+Rg*	758.0	96	193.1	24.5	20.3
res *Env* vs. *Eg+Rg*	816.0	96	135.1	15.9	14.2
res *Rg* vs. *Eg+Env*	826.2	99	124.9	15.0	13.1

References cited

Borcard, D., Legendre, P., & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045-1055.

Hawkins, B.A., Porter, E.E., & Diniz-Filho, J.A.F. (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84**, 1608-1623.

Lobo, J.M., Castro, I., & Moreno, J.C. (2001) Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. *Biological Journal of the Linnean Society*, **73**, 233-253.

Nieto, M., Hortal, J., Martínez-Maza, C., Morales, J., Ortiz-Jaureguizar, E., Pelaez-Campomanes, P., Pickford, M., Prado, J.L., Rodríguez, J., Senut, B., Soria, D., & Varela, S. (2005). Historical determinants of mammal diversity in Africa: Evolution of mammalian body weight distribution in Africa and South America during Neogene and Quaternary times. In *African Biodiversity: Molecules, Organisms, Ecosystems* (ed by B.A. Huber, B.J. SinclairandK.-H. Lampe), pp. 287-296. Springer, New York.