



# Deep phylogeny, net primary productivity, and global body size gradient in birds

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Body size is evolutionarily constrained, but the influence of phylogenetic relationships on global body size (i.e. body mass) gradients is unexplored. We quantify and map the family-level phylogenetic and non-phylogenetic structure of the global gradient of birds, evaluating the extent to which it is influenced by phylogenetic inertia in contrast to heat conservation, resource availability, starvation resistance, niche conservatism, or interspecific competition. Phylogenetic eigenvector regression (PVR) partitioned the global bird body size gradient into phylogenetically autocorrelated (PA) and phylogenetically independent (PI) components. Simple, piecewise, and partial regressions were used to investigate associations between the PA and PI components of body size and environmental correlates, and to quantify independent and overlapping contributions of environment, phylogenetic autocorrelation, and species richness to the body size gradient. Two-thirds of the geographic variation in bird body size can be explained by phylogenetic relationships at the family level. The global variation in body size, independent of phylogenetic relationships, is most strongly associated with net primary productivity, which is consistent with 'starvation resistance'. However, the New and Old worlds have very different patterns. We found no independent association of species richness with body size. Despite major unresolved regional differences, deep phylogenetic relationships, heat conservation, and starvation resistance probably operate in concert in shaping the global bird body size gradient in different parts of the world. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, ●●, ●●–●●.

**ADDITIONAL KEYWORDS:** Bergmann's rule – heat conservation – phylogenetic eigenvector regression – phylogenetic inertia – phylogenetic niche conservatism – starvation resistance.

## INTRODUCTION

The pattern of body size increasing towards the poles in endotherms (Bergmann, 1847) is amongst the most studied by macroecologists (Blackburn, Gaston & Loder, 1999; Rodríguez, López-Sañudo & Hawkins, 2006; Rodríguez, Olalla-Tárraga & Hawkins, 2008). A variety of approaches have been used (i.e. intraspecific, cross-species, and assemblage based), and their differences and advantages have been evaluated (see Blackburn & Hawkins, 2004; Gaston, Chown & Evans, 2008; Olalla-Tárraga *et al.*, 2010; Adams & Church, 2011). Although choice of method can influence the interpretation of results (Ruggiero

& Hawkins, 2006), explanations derived from one approach are commonly used to explain the outcomes of a different approach (see Gaston *et al.*, 2008). For instance, a physiological mechanism may explain intraspecific variation in body size across space, but it does not necessarily account for geographical trends in the body sizes of multi-species assemblages.

The assemblage perspective is most appropriate to identify the geographical structure of patterns and processes (Ruggiero & Hawkins, 2006; Olalla-Tárraga *et al.*, 2010), and has been used to document body size gradients of both ectotherms and endotherms, including insects (Cushman, Lawton & Manly, 1993; Hawkins, 1995; Hawkins & Lawton, 1995; Chown & Klok, 2003; Kaspari, 2005), fish (Knouft, 2002), amphibians (Olalla-Tárraga & Rodríguez, 2007;

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Olalla-Tárraga *et al.*, 2009, 2010), reptiles (Olalla-Tárraga, Rodríguez & Hawkins, 2006), birds (Blackburn & Gaston, 1996; Ramirez, Diniz-Filho & Hawkins, 2008; Olson *et al.*, 2009), and mammals (Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006, 2008; Diniz-Filho *et al.*, 2009). But although taxonomically extensive geographical patterns of body size have been generated, the underlying mechanisms remain subject to debate.

Recent assemblage-based studies of birds have validated the generality of Bergmann's rule in the Northern Hemisphere for the New World (Ramirez *et al.*, 2008), and globally (Olson *et al.*, 2009). In both studies, temperature was the single strongest correlate of body size, whereas variables related to resource availability were less strongly associated with gradients. Comparing the correlations of these environmental variables with body size gradients is of interest because they can be linked to proposed explanations for Bergmann-like patterns for endotherms: the *heat conservation hypothesis*, in which large-bodied species are favoured in cold climates because of their reduced surface area-to-volume ratios (Bergmann, 1847; Hamilton, 1961; James, 1970), and/or thicker insulation layers, that give them a higher tolerance to cold (Blackburn *et al.*, 1999); the *resource availability hypothesis*, in which body size increases with productivity because resource availability sets a limit to the body size that an animal can reach (Rosenzweig, 1968; Geist, 1987); and the *starvation resistance (or fasting endurance) hypothesis*, in which larger animals are favoured in seasonal and unpredictable environments because they metabolize fat stores at lower weight-specific rates, and thus withstand starvation better than smaller animals (Lindsey, 1966; Calder, 1984; Lindstedt & Boyce, 1985; Cushman *et al.*, 1993). These hypotheses are not mutually exclusive (e.g. Olson *et al.*, 2009), and furthermore were originally generated from the results of intraspecific and cross-species studies, and need not apply equally to assemblage-based body size gradients.

Additional potential influences on body size gradients from an assemblage perspective include species richness, acting via more intense interspecific competition in species-rich environments (Blackburn & Gaston, 1996; Cardillo, 2002; Olson *et al.*, 2009), and species turnover in space, acting via differential diversification of clades with different body sizes (Olson *et al.*, 2009) or differential colonization of deglaciated areas after the Pleistocene (Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006). This has been explored to some extent for birds by examining changes in body size patterns across multiple taxonomic levels (Olson *et al.*, 2009). However, although Olson *et al.* (2009) have shown that taxonomic turn-

over has influenced the global bird body size gradient, whether phylogenetic patterns of body size have responded to the same environmental drivers as patterns arising from the responses of birds independent of their evolutionary history, remains unknown. If the configuration of phylogenetic patterns has responded to macroclimate through evolutionary time, we might expect a signature of the current climate on phylogenetic patterns.

Here we use phylogenetic eigenvector regression (PVR) to quantify and map the phylogenetic and non-phylogenetic structure of the global bird body size gradient, based on the pattern of phylogenetic autocorrelation among bird families. Using a correlative approach, we also evaluate as far as possible three widely studied hypotheses for body size patterns: heat conservation, as measured by temperature; resource availability, as measured by net primary productivity (NPP); and resistance to starvation, evaluated using seasonal variation in actual evapotranspiration as a proxy of within-year variability in resource availability (Ramirez *et al.*, 2008). Furthermore, we revisit Olson *et al.*'s (2009) proposal that species richness directly influences bird body size gradients. Finally, our approach allows us to compare relationships between environmental gradients and phylogenetic autocorrelation, including patterns unrelated to measured environmental gradients (interpreted by some as phylogenetic inertia, Desdevises *et al.*, 2003), environmental signal independent of phylogeny, and environmentally structured phylogenetic signal (phylogenetic niche conservatism *sensu* Desdevises *et al.*, 2003).

## MATERIAL AND METHODS

### THE DATA

Maps of bird breeding ranges on continental landmasses (data taken from Hawkins *et al.*, 2007) were projected onto a global Behrmann equal-area grid, comprising 9319-km<sup>2</sup> cells, which after the removal of small coastal cells and cells supporting fewer than 20 bird species (i.e. 2224 cells of less than 50% of the area or containing few species) resulted in 12 639 cells available for analysis. Cells with species richness under 20 species were removed from analyses to avoid idiosyncratic patterns derived from averaging body size in cells with few species. Islands were also excluded (except for Great Britain and Tierra del Fuego), because different constraints on body size may operate on islands (e.g. the Island Rule; Lomolino *et al.*, 2006). Afghanistan was excluded because we could not locate any range maps for that country. Only breeding ranges were analysed, as non-breeding ranges are not well known on the global scale.

Body masses were  $\log_{10}$ -transformed for 7518 species of terrestrial birds (the species checklist and body masses are provided in Table S1). Body mass data were obtained from various sources (see Table S2). For 461 species (6%), direct mass data were not available, and we used linear regressions of mass against length for species in the same genus or family to estimate body mass (see Ramirez *et al.*, 2008). For 28 species (< 0.4%) neither mass nor length data were available, so we assigned family mean masses. Body masses of sexually dimorphic species were averaged over both genders (simple averages were used). To confirm that the inclusion of indirect body sizes for some species did not affect our results, we correlated the spatial pattern of the phylogenetically independent components (see below) with and without these species, and found virtually identical patterns globally ( $r = 0.980$ ).

The temperature variable used to evaluate the heat conservation hypothesis was derived from BIO1 (mean annual temperature, TEMP) in the WORLDCLIM database (Hijmans *et al.*, 2005). Resource availability was evaluated with average gridded values of annual NPP, extracted from Imhoff *et al.* (2004; data available at: <http://sedac.ciesin.columbia.edu/es/hanpp.html>, accessed January, 2011). Additionally, the Ahn & Tateishi (1994) global data set was used to generate gridded values of actual evapotranspiration (AET), the annual values of which were strongly correlated with NPP ( $r = 0.910$ ). Starvation resistance was evaluated using seasonal range in actual evapotranspiration (rAET), computed as the absolute difference between AET in January and July. Species richness within cells was calculated from the range maps. Geographical information was processed in ArcGIS 9.3 (ESRI, 2008).

#### PHYLOGENETIC ANALYSIS

A species-level supertree for all birds is not yet available, so we used a family-level phylogeny combining the non-passerine part of Sibley & Ahlquist's (1990) phylogeny and the Barker *et al.* (2004) phylogeny for passerines (for evaluations of the robustness of this phylogenetic combination, see Hawkins, Diniz-Filho & Soeller, 2005; Hawkins *et al.*, 2006). A total of 122 bird families were analysed, and  $\log_{10}$ -transformed body masses of the species in each family were averaged for the phylogenetic analysis. Three families comprising four species were excluded because their extreme body masses distorted patterns and destabilized statistical models: Struthionidae, Rheidae, and Casuaridae.

Phylogenetic eigenvector regression (PVR; Diniz-Filho, Sant'Ana & Bini, 1998) was used to partition the phylogenetically autocorrelated (PA) and phyloge-

netically independent (PI) components of body size. This method transforms a pairwise phylogenetic distance matrix, in our case based on the numbers of nodes separating families (e.g. Montoya *et al.*, 2008; Ramirez *et al.*, 2008), into phylogenetic eigenvectors through a principal coordinate analysis (PCoA). The use of node counting instead of branch lengths to define phylogenetic distances does not alter our results, at least for a family-level phylogeny (see Figure S1). The goal of PVR is to regress a biotic trait (i.e. bird body size) against representative eigenvectors (*sensu* Diniz-Filho *et al.*, 2011a) to generate values predicted by the pattern of phylogenetic autocorrelation among taxa, and residuals representing sources of variation after removing the autocorrelation (Diniz-Filho *et al.*, 1998, 2007, 2009; Martins, Diniz-Filho & Housworth, 2002; Ramirez *et al.*, 2008).

Phylogenetic eigenvector regression (PVR) has been criticized because of the lack of a hypothesized process, and because all eigenvectors would be necessary to take the entire phylogeny into account, which would result in a perfect fit ( $r^2 = 1$ ), and thus would leave no residual variation in which to investigate associations with other variables (Rohlf, 2001). However, unless the trait evolved according to a Brownian motion (BM) model (i.e. in which the variation of the trait accumulates randomly across the phylogenetic tree), only eigenvectors that account for the existing phylogenetic autocorrelation in the trait are necessary to model trait variation among taxa (Diniz-Filho *et al.*, 2011a; Diniz-Filho *et al.*, 2011b). To determine if bird family body size evolution is Brownian, we used Blomberg's  $K$ , a phylogenetic signal metric with an expected value of 1.0 under BM (Blomberg, Garland & Ives, 2003; see also Revell, Harmon & Collar, 2008 for additional details). We found a phylogenetic signal significantly higher than 1 (Blomberg's  $K = 1.824$ ,  $P < 0.005$ ), which supports the use of PVR in this case. Accordingly, we followed Diniz-Filho *et al.* (2011a) and selected representative phylogenetic eigenvectors using the optimization algorithm developed by Griffith & Peres-Neto (2006) in the spatial context. This procedure generates successive regression models of the trait against the phylogenetic eigenvectors, and at each step selects the eigenvector that reduces the largest level of residual phylogenetic autocorrelation. The search stops when residual autocorrelation is reduced below an arbitrary autocorrelation threshold (Moran's  $I < 0.05$ , in our case). As an additional test, we built a phylogenetic correlogram to check how effective this procedure was in removing phylogenetic autocorrelation in bird family body size across phylogenetic distances.

To quantify how the number of eigenvectors selected affected our estimation of the phylogenetic

signal, we randomly reshuffled mean family body masses across the phylogeny 1000 times, regressed each of these random samples against the set of selected phylogenetic eigenvectors, and then computed the mean and standard error of the resulting  $r^2$  distribution, which we compared against the observed  $r^2$ .

Following Diniz-Filho *et al.* (2011a), we also used phylogenetic generalized least squares (PGLS) to generate a PGLS transform of mean family log<sub>10</sub>-body size ( $Z$ -vector) consisting of the body size values that would be expected if species were phylogenetically independent (see Diniz-Filho *et al.* 2011a for technical details). This  $Z$ -vector is the PGLS equivalent to the PI component of the PVR, and allowed us to evaluate the extent to which the patterns were consistent across methods. Both PVR and PGLS analyses were performed in R 2.10 (R Development Core Team, 2009) and in MATLAB 7.0 (MathWorks Inc, 2004).

Finally, we assigned the PA and PI components given by PVR for each family to its constituent species, and then calculated their mean values in the grid cells to compare their spatial patterns and examine associations with environmental gradients and species richness (e.g. Diniz-Filho *et al.*, 2009). It should be noted that because we used a family-level phylogeny to examine species-level body sizes, the PI component will contain any phylogenetic signal occurring below the family level. The magnitude of lower-level phylogenetic autocorrelation is expected to be small, given that about 90% of the variation in bird life-history traits is explained at the family level (Bennett & Owens, 2002). Even so, we explored the potential extent of low-level phylogenetic signal in body size among endotherms (mammals; Table S3). Although we cannot directly test this for birds, the available evidence for both birds and mammals suggests that for endotherms, using less than fully resolved trees to measure phylogenetic autocorrelation in body masses does not greatly underestimate its magnitude.

#### GEOGRAPHICAL ANALYSIS

Just as the hypotheses we investigate are not mutually exclusive, the predictors we use to evaluate them are collinear to varying degrees ( $r_{\text{TEMP vs NPP}} = 0.493$ ,  $r_{\text{TEMP vs rAET}} = 0.087$ , and  $r_{\text{NPP vs rAET}} = 0.219$ ). Variation partitioning based on partial regression has been designed to be applied in these situations (see Legendre & Legendre, 1998), for which we used two- and three-way partial ordinary least squares (OLS) to explore relationships between the observed mean log<sub>10</sub> body sizes in the cells and the three environmental variables (TEMP, NPP, and rAET) at the global extent, and in the New and Old worlds sepa-

rately. The same techniques were also used to investigate associations for the mean PA and mean PI values. In all cases, our goal was to isolate the unique and shared components in variation of mean body size associated with the predictors to evaluate the extent to which each variable (and the hypothesis to which it was linked), either individually or in concert with other variables, could underlie the observed patterns. Although a correlative approach cannot unambiguously resolve which hypotheses actually explain mean body size patterns, it identifies to what extent each could potentially do so.

Given both the broad geographical extents of our analyses and the use of a grid-based approach, the occurrence of spatial autocorrelation in the data is guaranteed. Although it is known that spatial autocorrelation does not bias OLS regression coefficients (see Hawkins, 2012, and references therein), and that autocorrelation is not an issue for OLS regression unless while using inferential statistics (i.e.  $P$  values), which we avoid here, we also acknowledged that spatial autocorrelation is a matter of concern to some workers. Consequently, we evaluated the robustness of the coefficients of determination (i.e. of the elements used for variation partitioning analysis) of our global, and New and Old world models by comparing them with those obtained from subsampled sets in which positive spatial autocorrelation was forced to be low. For this we randomly selected cells for each region, imposing the constraint that the cells had to be separated by at least 1000 km. This distance represented a balance between the level of positive autocorrelation in the residuals of our environmental models beyond this distance (Moran's  $I$  values  $\leq 0.2$  in all cases) and reasonably large sample sizes (100 cells for the global extent, and 50 cells for the New and Old worlds). Thus, we generated 100 random subsamples per region, repeated the partial regression analysis for each subsample, computed the mean coefficient of determination value per subsample set, and then used Student's  $t$ -tests to compare these means with the coefficients of determination obtained for the complete data sets (see Figure S4 for details).

We also used piecewise regression if a visual inspection of scatter plots of mean size (or of mean PA or mean PI) against environmental predictors revealed an inflection point in the relationships. However, we took into account that scarce data at the extremes of the scatter plots may cause the appearance of spurious inflection points, so we only retained a piecewise regression if its coefficient of determination was at least 5% higher than that of its linear counterpart.

Finally, based on Desvignes *et al.* (2003) we used three-way partial regression to partition the global and New and Old world bird body size gradients into

the proportion of the variation accounted for by: (1) phylogenetic autocorrelation, independent of both the environmental gradients captured by our three environmental variables and species richness (assumed to estimate phylogenetic inertia); (2) the component comprising variation caused by environment, independent of phylogeny and species richness (within-lineage adaptation); (3) the spatially structured phylogenetic components (an estimate of phylogenetic niche conservatism); and (4) the direct contribution of species richness to the gradient, independent of phylogenetic relationships and environment. Also, the non-phylogenetic component was partitioned using a two-way partial regression to quantify covariation of environment and bird species richness.

## RESULTS

### PHYLOGENETIC PATTERNS IN BIRD BODY SIZE

The 17 selected phylogenetic eigenvectors predicted much of the variation in body size at the family level ( $r^2 = 0.688$ ), and this was significantly greater than a random expectation ( $r^2_{\text{null}} = 0.131$ ,  $P < 0.001$ ). Body sizes among families show positive phylogenetic autocorrelation at short phylogenetic distances, becoming negative or null at opposite ends of the tree (Figure S2). Residuals from the PVR (the PI component) contained minimal phylogenetic autocorrelation at all phylogenetic distances, indicating that variation in this component is independent of phylogeny at the family level (see Figure S2). Also, comparison of the PI component with the  $Z$ -vector obtained through PGLS indicated that they reflect similar trends, either when comparing their values across families, and geographically after averaging their respective values in the cells (see Figure S3). This indicates that the patterns are robust to method. Overall, these results indicate that approximately two-thirds of the variation in body masses among bird families is linked to a combination of phylogenetic inertia and phylogenetic niche conservatism.

### PHYLOGENETIC AND NON-PHYLOGENETIC CONTRIBUTIONS TO THE GLOBAL BODY SIZE GRADIENT

The global body size pattern is very similar to that reported by Olson *et al.* (2009), although we do not share identical data sources, and we use means of  $\log_{10}$  body masses rather than medians (Figure 1A). As expected, given the strong phylogenetic signal in body size at the family level, a very similar pattern was found for mean PA values (Figure 1B), which in turn were strongly correlated with the mean observed body sizes ( $r = 0.867$ ). Alternatively, mean PI values showed a clear latitudinal gradient in the New World, with

greater positive deviations from body sizes predicted by phylogeny towards the north and south (Figure 1C).

The average divergence from phylogenetic expectation was negative (i.e. body sizes were smaller than expected) for most of the Neotropics and southern Nearctic. In the Old World, patterns were geographically complex, with species being larger than expected in the Saharan, Arabic, Kalahari, Namibian, Karakun, Takla Makan, and Gobi deserts, as well as in the Himalayas, India, and the Australian central lowlands. Negative to null expectations were found in central Europe, tropical Africa, the Yangtze River basin, and the Australian western plateau. Mean PI values were also correlated with mean body sizes globally ( $r = 0.755$ ), but not as strongly as mean PA values, and the correlation between mean PA and mean PI was weakly positively correlated ( $r = 0.328$ ), suggesting largely independent responses to current environmental gradients.

Major regional differences in the relationships of the components to the observed gradient were also apparent. In the Old World the observed gradient was strongly correlated with mean PA ( $r = 0.933$ ), and less so with mean PI ( $r = 0.661$ ): i.e. the observed body size pattern is largely the result of spatial variation in the phylogenetic composition of the avifaunas. In the New World the observed gradient was a more even mix of phylogenetic and non-phylogenetic components ( $r = 0.831$  for mean PA and  $r = 0.817$  for mean PI).

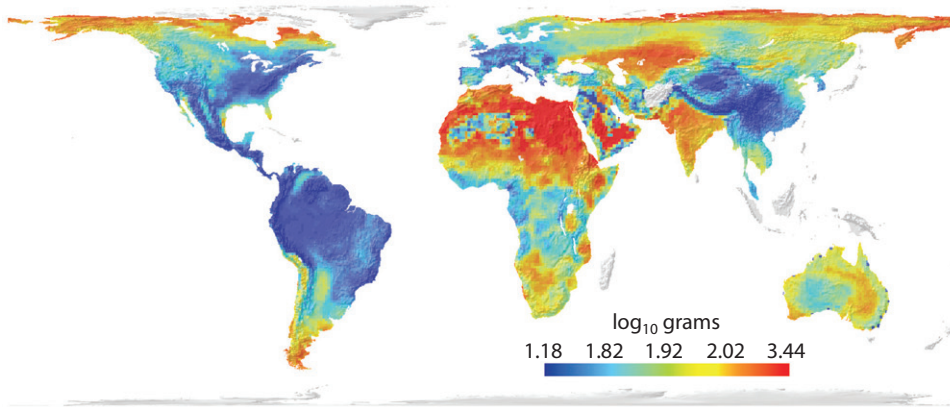
### ENVIRONMENTAL PREDICTORS OF BODY SIZE PATTERNS AND THEIR PI AND PA COMPONENTS

In the New World, average values of body size and its PI component were strongly negatively associated with both temperature (Figure 2A, I) and NPP (Figure 2C, K). In contrast, in the Old World simple regressions of mean body size and mean PI against temperature and productivity were weaker (Figure 2B–J, D–L): body size and its PA component appear to decrease with increasing temperature only in cold and temperate areas (below about  $-8^\circ\text{C}$ ), with a reversal at high temperatures, reflecting larger body sizes in the deserts (Figure 2B, F).

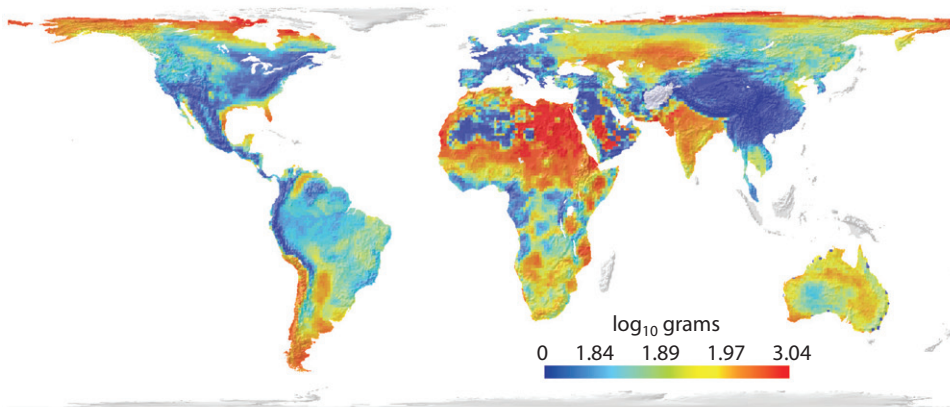
The relationship between the phylogenetically autocorrelated portion of body size and temperature had two distinctive domains in the New World (Figure 2E), with mean PA values increasing towards colder areas in the first domain, but being independent of temperature (New World) in warmer areas. A piecewise regression had a substantially better fit (Figure 2E) than its linear counterpart ( $r^2_{\text{New}} = 0.158$ ).

Globally, three-way partial regressions revealed productivity as the predictor more strongly associated with body size and the PA and PI components (Figure 3A–C). This was largely linked to the Old

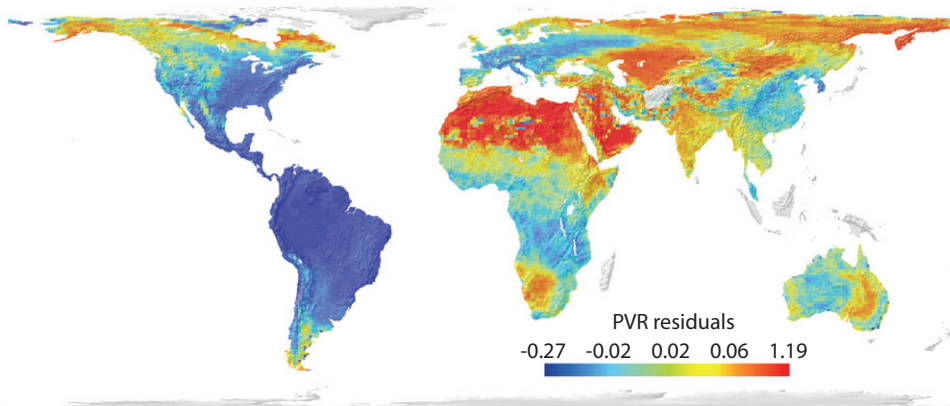
(A) Observed mean log body size



(B) Mean PA-component



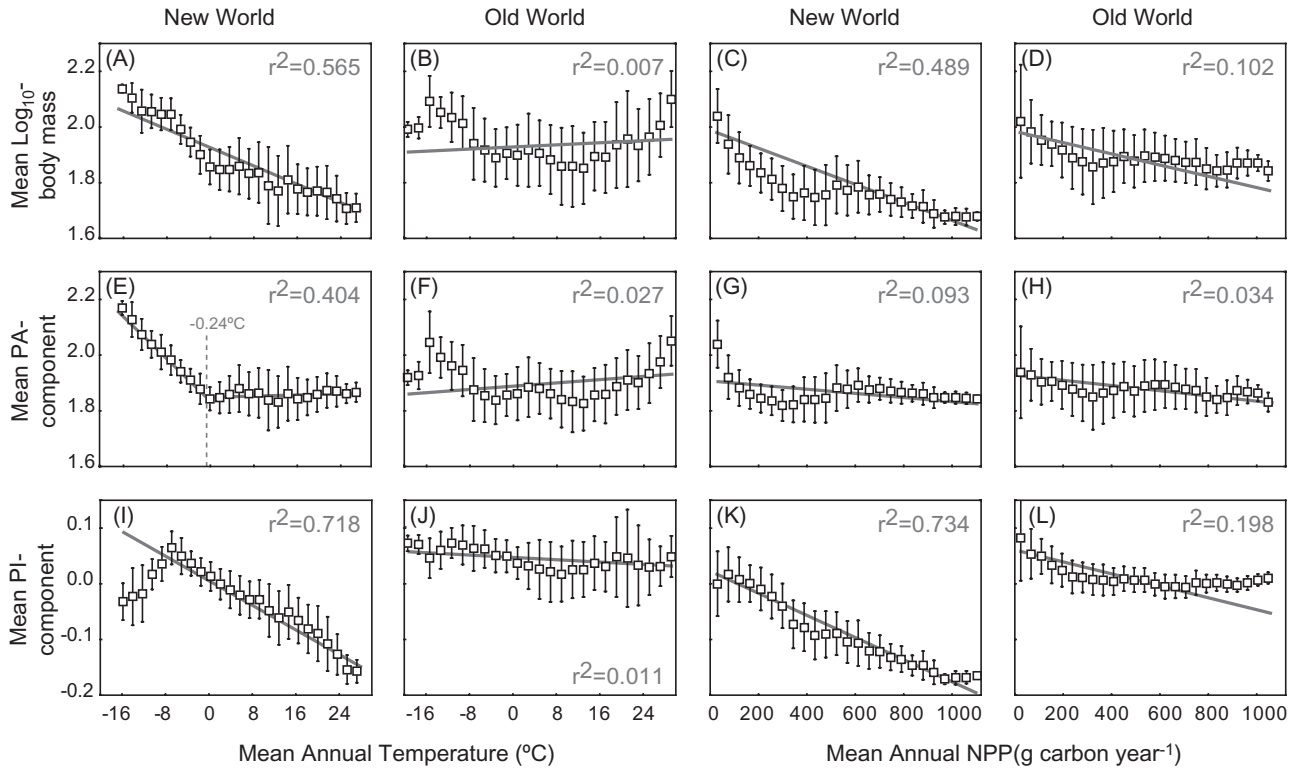
(C) Mean PI-component



**Figure 1.** Geographical patterns of mean body size (A), and of mean values of the phylogenetically autocorrelated (PA; B) and non-phylogenetic (PI; C) components of body size obtained through a phylogenetic eigenvector regression (PVR) analysis of 7518 bird species. Units are  $\log_{10}$  body masses in grams. Note that the values for the PI component can be negative as they are the residuals from a PVR regression, and are averaged over all species in a cell.

World data (Figure 3G, I), whereas for the New World, temperature accounted for more variation in body size and mean PA, but productivity still explained more geographical variation of mean PI than temperature

(Figure 3D–F). Accounting for nonlinear relationships of mean PA with temperature increased the explanatory power of the model in the New World (from  $r^2 = 0.065$  to  $r^2 = 0.300$ ; Figure 3E). It is notable that



**Figure 2.** Relationships of mean observed  $\log_{10}$  body size (A–D), mean phylogenetically autocorrelated component of body size (mean PA; E–H) and non-phylogenetic component of body size (mean PI; I–L) with annual temperature and net primary productivity (NPP) for the New World and the Old World. For representation purposes the data were divided into 25 equal-range categories of the variable in the abscissa, and the average ( $\pm$ SD) value of each category was used. Coefficients of determination ( $r^2$ ) and regression lines of ordinary least squares (OLS) regressions are shown. Piecewise regression fitted to the relationship between the mean-PA and temperature (E) identified a temperature breaking point for the New World ( $-0.24$  °C).

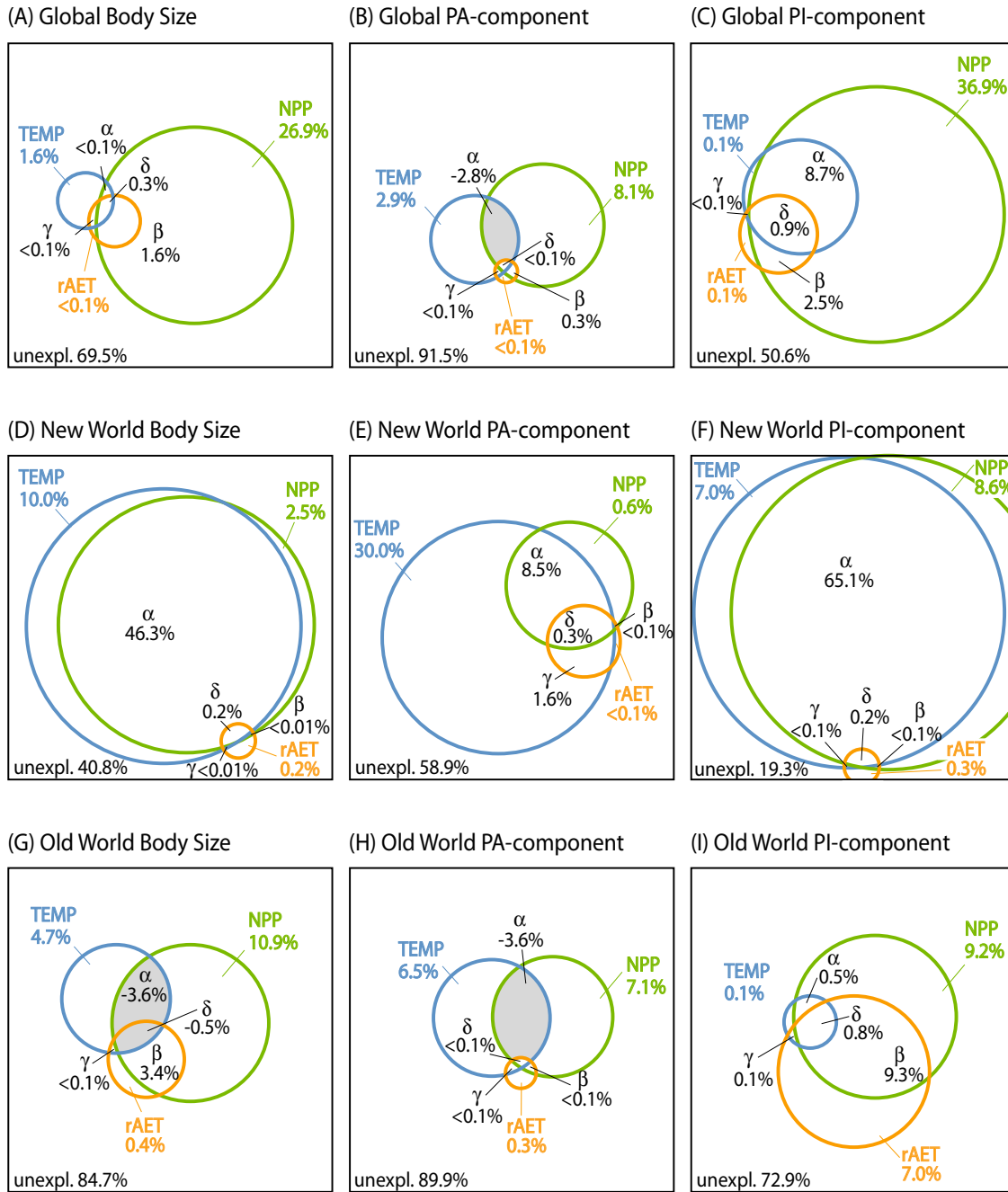
even though the relative contribution of seasonality (i.e. rAET) was marginal in all cases (Figure 3A–H), its independent and overlapping relationships with productivity were larger for the Old World PI component, probably reflecting the selection of larger sizes in deserts. Overall, environmental models were stronger for mean PI than for mean PA in the global context ( $r^2 = 0.494$  versus  $r^2 = 0.085$ ), in the New World ( $r^2 = 0.807$  versus  $r^2 = 0.175$ ), and in the Old World ( $r^2 = 0.270$  versus  $r^2 = 0.101$ ). In all cases productivity and its collinear association with temperature are the main correlates, with the portion of the body size gradient independent of familial phylogenetic relationships. As expected, none of these results were affected by spatial autocorrelation in the full data (Figure S4).

#### SPECIES RICHNESS, PHYLOGENETIC INERTIA, AND PHYLOGENETIC NICHE CONSERVATISM

Although species richness has been hypothesized to represent a primary driver of global body size gra-

dients (Olson *et al.*, 2009), and correlations of richness with both mean body size ( $r = 0.493$ ) and mean PI ( $r = 0.627$ ) were also moderately strong in our data, partial regressions indicated that most of the variation associated with species richness is collinear with that associated with climate, whether for body size gradient (Figure 4) or mean PI (Figure 5). Therefore, the independent relationships of species richness and body size were virtually absent in both the phylogenetic and non-phylogenetic components (all  $r^2 < 0.021$ ; Figures 4, 5), and we cannot conclude unambiguously that biotic interactions associated with the number of potential competitor species have influenced the spatial body size gradients of birds.

Most of the variation in the spatial body size gradient was independently accounted for by phylogeny, suggesting strong phylogenetic inertia at all extents (Figure 4). Variable levels of covariation between phylogeny and environment suggest substantial niche conservatism of body size in the New World, but much less so in the Old World.



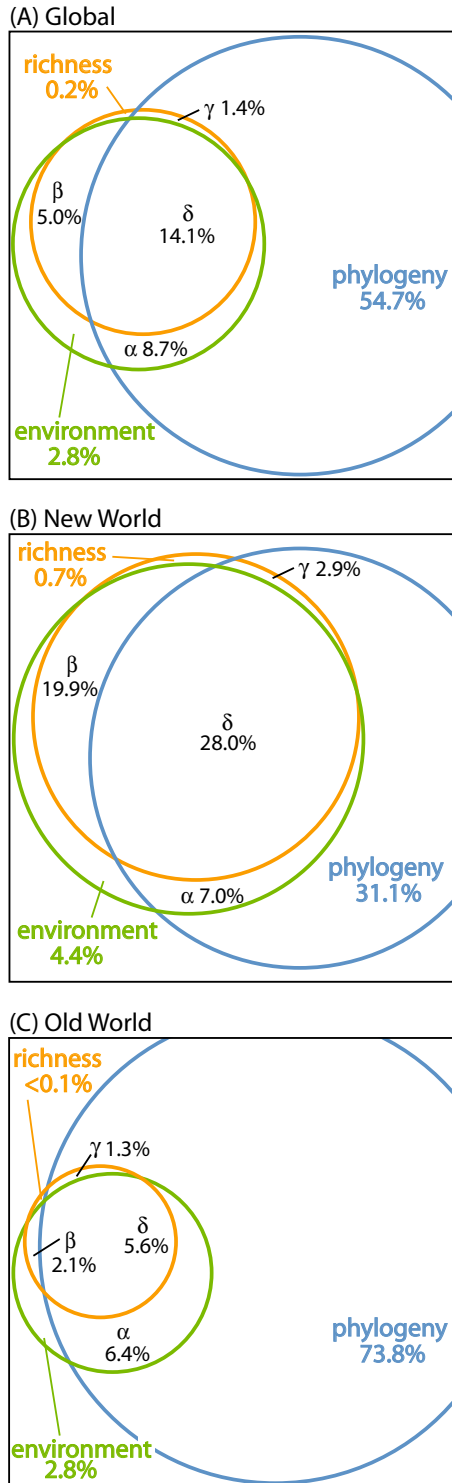
**Figure 3.** Venn diagrams for environmental three-way partial regressions showing the independent and overlapping relationships of mean annual temperature (TEMP), net primary productivity (NPP), and seasonal range in actual evapotranspiration (rAET), and variation in mean log<sub>10</sub> body size, mean PA, and mean PI globally (A, B, C), for the New World (D, E, F), and for the Old World (G, H, I). Lower case Greek letters indicate overlapping proportions of variation of TEMP and NPP ( $\alpha$ ), NPP and rAET ( $\beta$ ), TEMP and rAET ( $\gamma$ ), and among the three variables ( $\delta$ ). Regions shaded in grey indicate negative values resulting from interactions among variables.

## DISCUSSION

Primary productivity statistically explains most of the global bird body size gradient once phylogenetic relat-

edness is accounted for, in concert with temperature in the New World and with seasonality in the Old World. This challenges the idea that temperature is the primary driver of bird body size across all





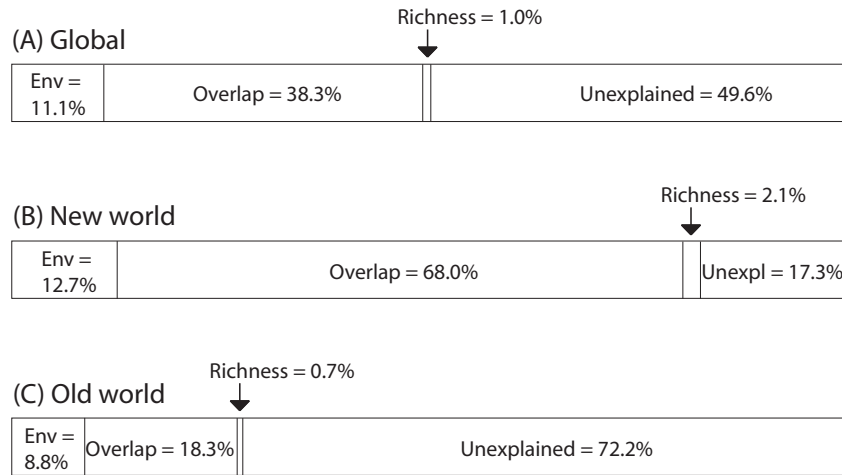
**Figure 4.** Venn diagrams for three-way partial regressions showing the independent and overlapping contributions of environment [i.e. mean annual temperature (TEMP), net primary productivity (NPP), and seasonal range in actual evapotranspiration (rAET) combined], phylogeny, and species richness on explaining the variance in mean  $\log_{10}$  body size globally (A), in the New World (B), and in the Old World (C). The proportion of variation explained independently by phylogeny is interpreted as phylogenetic inertia, whereas the overlapping variation between phylogeny and environment encompasses niche conservatism (*sensu* Desdevises *et al.*, 2003). Lower case Greek letters indicate an overlapping of variation of phylogeny and environment ( $\alpha$ ), environment and richness ( $\beta$ ), phylogeny and richness ( $\gamma$ ), and among the three variables ( $\delta$ ).

tion in the gradient can be predicted by the phylogenetic structure of avian families. This is consistent with previous analyses for birds (Ramirez *et al.*, 2008), carnivores (Gittleman *et al.*, 1996; Diniz-Filho & Tôrres, 2002; Diniz-Filho *et al.*, 2009; Freckleton & Jetz, 2009), *Plethodon* salamanders (Olalla-Tárraga *et al.*, 2010), and with general strong phylogenetic constraints on body size (Freckleton, Harvey & Pagel, 2002; Blomberg *et al.*, 2003). Clearly, future work focused on body size patterns, such as Bergmann's rule, will need to consider phylogenetic structure in the data as either a pattern or a process.

#### PATTERNS OF MEAN PA, PHYLOGENETIC INERTIA, AND NICHE CONSERVATISM

To the extent that phylogenetic inertia operating independently of environmental drivers and niche conservatism, generating covariance between the trait and environmental gradients (Desdevises *et al.*, 2003; Diniz-Filho & Bini, 2008), can be partitioned by partial regression methods, our results potentially identify phylogenetic inertia at the family level as the dominant component on the global level. Additionally, there is clear spatial variation in the relationships between the phylogenetic component of body size and environment: in regions with cold climates, mean PA shows moderately strong relationships with temperature in the New World (see Figure 2E). Even though current climatic conditions could not have influenced phylogenetic patterns generated over evolutionary time, contemporary climate can serve as an indicator of past climatic events (i.e. glaciated regions in the Pleistocene are still cold). Given that most of Canada was under a kilometre of ice during the most recent ice age, the current body size gradient in the northern half of North America is consistent with a pattern of recolonization following glacial retreat, suggesting a link between body size and dispersal ability that is

latitudes, as suggested by previous analyses where phylogenetic effects had not been considered. However, higher-level phylogenetic relationships explain a substantial proportion of the global bird body size gradient: up to two-thirds of the total varia-



**Figure 5.** Partial regression showing the relative contributions of environment [i.e. mean annual temperature (TEMP), net primary productivity (NPP), and seasonal range in actual evapotranspiration (rAET) combined] and species richness to the variation in mean values of the non-phylogenetic (PI) component of body size globally (A), in the New World (B), and in the Old World (C).

also phylogenetically conserved at the family level. There are a number of potential reasons why the relationship might partially occur in the Old World (see Figure 2F), which was not as extensively glaciated, but we lack the data to evaluate them. Irrespective, the patterns suggest a leading role for temperature on the phylogenetic structure of body size in areas with very cold climates. Olson *et al.* (2009) studied the relationships between temperature and body size variation within taxonomic levels, finding a general negative correlation for genera and families. However, they did not evaluate climatic variability across regions, which might explain the weakness of their associations of within-taxon body size with temperature.

#### THE NON-PHYLOGENETIC COMPONENT AND HYPOTHESES FOR BODY SIZE

Approximately a third of the variance in bird body size gradient is independent of the phylogenetic relationships among families. However, evaluating processes such as the heat conservation hypothesis proposed by Bergmann (1847) requires removing the influence of phylogenetic relatedness in order to assess responses of species to environmental clines, which unfortunately we can only partially do in the absence of a species-level supertree.

Globally, the non-phylogenetic responses of species body size to environment appear to be fundamentally driven by decreasing primary productivity (see Figure 3C). Thus, our results are inconsistent with the resource availability hypothesis (Rosenzweig, 1968), as mean body size is negatively correlated with

primary productivity. Despite collinearity between the relationships of temperature and productivity with body size, temperature is not a strong predictor of body size across all climates, which is a pattern also known for mammals (Rodríguez *et al.*, 2006, 2008). Nevertheless, major differences between the New and Old worlds indicate that non-phylogenetic patterns are not easy to interpret.

The strong collinearity between productivity and temperature makes interpretation of the patterns in the PI component in the New World difficult (see Figure 3F). This is unavoidable because in the New World the least productive areas are primarily the coldest. In contrast, non-phylogenetic patterns in the Old World are associated with productivity, either its annual value (NPP) or the degree of seasonality (rAET), and there is almost no association with temperature (see Figure 3I). This reflects that the Old World contains extensive non-polar deserts (with low productivity and high temperatures), and also a more seasonal climate outside of those desert areas. The pattern of larger body sizes in areas of low productivity is clear, not only in the most extensive deserts but also in smaller ones, including the Namibian and Kalahari deserts in Africa, and the Kara-Kun and Takla Makan deserts in Asia (see Figure 1C). Thus, although all associations between body size and environment are weak, the resistance to starvation hypothesis (Calder, 1984; Lindstedt & Boyce, 1985; Cushman *et al.*, 1993) is most consistent with the patterns in the Old World (Geist, 1987; Zaveloff & Boyce, 1988). At the very least, the heat conservation hypothesis can be dismissed across the Old World (see Figure 2B, J).

Our results partially contradict Olson *et al.* (2009), who identified temperature as the strongest predictor of body size and concluded that productivity plays a secondary role. We found that once family-level phylogenetic autocorrelation is removed, productivity explains substantially more of the variance in the body size gradient. Our results cannot be directly compared with those of Olson *et al.* (2009), as the goodness of fit of their models or the independent relationships of their predictors with body size were not reported. Our modelling approach also had a different goal: our primary goal was not to predict body size values given environmental conditions, but to assess the degree to which phylogenetic structure constrains the bird body size gradient, and to evaluate how environment is associated with phylogenetic and non-phylogenetic components of global body size patterns.

### CONCLUSIONS

A major aspect of our analysis is that it is unlikely that a single, global explanation for bird body size gradients exists, whether in a phylogenetic or non-phylogenetic context. Although the New World shows a clear Bergmann-like gradient in both North and South America, body size patterns in the Old World are complex (see Figure 1A) and largely independent of major environmental gradients (see Figure 2). Although identifying the sources of this geographic complexity will not be easy, we agree with Olson *et al.* (2009) that it will almost certainly require a detailed understanding of the deep evolutionary history of the major bird clades and geographic patterns of diversification. The phylogenetic signal in body sizes is very strong, even given that we may have underestimated its strength by excluding any autocorrelation below the family level. After removing the family-level autocorrelation we find that decreasing productivity in conjunction with decreasing temperature (in the New World) or increasing seasonality (in the Old World) are most closely associated with body size gradients. Although hypotheses for body size gradients are often viewed as mutually exclusive alternatives, it is likely that resistance to starvation and heat conservation are both in operation, albeit in different parts of the world. On the other hand, we find no evidence that biotic interactions associated with species richness patterns have any independent effect on bird body size patterns, but given that richness is itself strongly influenced by climate, disentangling their contributions is challenging. Despite over 160 years of research on body size gradients, we still do not have a clear picture of the drivers of global body size patterns, but at least we are developing a clearer picture of what we are trying to explain.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

**Figure S1.** Comparison between branch lengths and node counting as methods of measuring the phylogenetic distances among bird families.

**Figure S2.** Phylogenetic correlograms showing Moran's *I* coefficients for the body size of 122 bird families.

**Figure S3.** Comparison of results from PVR with PGLS.

**Figure S4.** Tests of the potential influence of spatial autocorrelation on the coefficients of 12 environmental OLS regression models.

**Table S1.** Bird species checklist and their body masses.

**Table S2.** List of references used to obtain bird body masses.

**Table S3.** Comparison of phylogenetic signals in body size between family, genus and species levels for the New World mammals.

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