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LETTER

Global biogeography and ecology of body size in birds

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Abstract

In 1847, Karl Bergmann proposed that temperature gradients are the key to understanding geographic variation in the body sizes of warm-blooded animals. Yet both the geographic patterns of body-size variation and their underlying mechanisms remain controversial. Here, we conduct the first assemblage-level global examination of 'Bergmann's rule' within an entire animal class. We generate global maps of avian body size and demonstrate a general pattern of larger body sizes at high latitudes, conforming to Bergmann's rule. We also show, however, that median body size within assemblages is systematically large on islands and small in species-rich areas. Similarly, while spatial models show that temperature is the single strongest environmental correlate of body size, there are secondary correlations with resource availability and a strong pattern of decreasing body size with increasing species richness. Finally, our results suggest that geographic patterns of body size are caused both by adaptation within lineages, as invoked by Bergmann, and by taxonomic turnover among lineages. Taken together, these results indicate that while Bergmann's prediction based on physiological scaling is remarkably accurate, it is far from the full picture. Global patterns of body size in avian assemblages are driven by interactions between the physiological demands of the environment, resource availability, species richness and taxonomic turnover among lineages.

Keywords

Adaptation, Bergmann's rule, birds, body mass, ecological rules, taxonomic turnover.

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INTRODUCTION

In 1847, Karl Bergmann argued that species of homeotherms living in colder climates are larger than their relatives living in warmer ones (Bergmann 1847), a hypothesis that is now known as 'Bergmann's rule'. Bergmann's argument was based on simple laws of physiological scaling: larger-bodied species have smaller surface-area-to-volume ratios, thereby increasing heat conservation in colder climates. Conversely, smaller-bodied species have larger surface-area-to-volume ratios, thereby promoting cooling in warm, humid areas (Hamilton 1961; James 1970). Because latitude provides a reasonable surrogate for decreasing temperature (Blackburn *et al.* 1999), Bergmann's rule is commonly discussed as a relationship between large body size and both low temperature and high latitude.

Despite much research, both the pattern and mechanism that Bergmann proposed remain controversial (James 1970; McNab 1971; Yom-Tov & Nix 1986; Geist 1987; Cousins 1989; Blackburn *et al.* 1999; Meiri & Dayan 2003). Several studies of both endotherms and ectotherms have questioned the generality of both the pattern and mechanism of Bergmann's rule (reviewed by Blackburn *et al.* 1999; Chown & Gaston 1999; Meiri & Dayan 2003; Meiri & Thomas 2007; Chown & Gaston 1999). Furthermore, Rosenzweig (1968) argued that body size increases with increasing resource availability, rather than with decreasing temperatures. He claimed that low productivity sets a limit to the body sizes animals can achieve. Increased seasonality and low predictability of environmental conditions were likewise thought to select for large body size (Lindsey 1966; Boyce 1978; Geist 1987) because larger animals can survive starvation longer than smaller ones, especially when under cold stress (Calder 1974; Zeveloff & Boyce 1988).

The increasing availability of animal distribution data has led to assemblage- or grid-cell-based examination of body-size distributions, which involves averaging the body sizes of all species within a cell (Blackburn & Gaston 1996; Ramirez *et al.* 2008). However, within species or lineages, size clines between assemblages can only be fully linked to classical explanations for Bergmann's rule if higher-level processes are not prevalent. For example, species richness may influence body-size gradients if the shape of body-size frequency distributions changes with latitude (Cardillo 2002). Furthermore, body-size gradients of assemblages may also be determined by a phylogenetically non-random set of species, rather than by selection on body size *per se*. For example, some major body plans may be phylogenetically constrained, and may only persist in certain environmental conditions. If these are associated with particular body sizes (e.g., all penguins are large and all are marine), then size distributions may change between different regions because of lineage turnover rather than because of direct selection for size. Additionally, body-size distributions consistent with lineage turnover may be expected if, for example, ancestral colonizations of high latitudes were by large-bodied taxa that subsequently diversified *in situ* (Blackburn *et al.* 1999; Meiri & Thomas 2007), or if small-bodied taxa have been extirpated from colder regions. Patterns of migration may also drive gradients of body size (Blackburn & Gaston 1996). If migratory species tend to be large-bodied, a positive relationship between body size and latitude is expected in summer, but if migratory species tend to be small-bodied, this same positive relationship would instead be expected in winter. The latter effect has been demonstrated in New World birds, by showing that the latitudinal trend in body size was much stronger when based on wintering than on breeding ranges of species (Ramirez *et al.* 2008).

One of the key reasons that biogeographical patterns of body size in general, and Bergmann's rule in particular, have remained controversial is that tests have been limited with respect to the geographical area that they cover, the taxa they include, the explanatory variables and spatial patterns considered, and the statistical methods used. Here we combine newly compiled databases on the body masses of 8270 bird species and the global geographic distribution of all living bird species (Orme *et al.* 2005, 2006) to explore global patterns of avian body size and their environmental and ecological correlates across grid cells (Gaston *et al.* 2008), and to test for consistent geographic gradients in body size within higher taxa.

We generate maps of the global distribution of avian body size based on breeding ranges (Orme *et al.* 2005, 2006) and use them to test whether there are consistent trends with respect to latitude, temperature or temporal resource stability. We begin by testing whether species richness alone can explain body-size patterns, then test whether (1) body size increases with decreasing temperature (Bergmann 1847), productivity (Rosenzweig 1968) or variability in productivity (Lindsey 1966; Calder 1974; Boyce 1978; Zeveloff & Boyce 1988); (2) median body sizes are lower in more species-rich assemblages (Brown & Nicoletto 1991; Cardillo 2002; Meiri & Thomas 2007); (3) island assemblages are characterized by intermediate body sizes (Clegg & Owens 2002); (4) latitudinal size clines are stronger once migration is accounted for (Hamilton 1961; Meiri & Dayan 2003) and (5) different biomes are characterized by unique size–temperature relationships. Finally, we test whether the observed body-size trends are explained by adaptation within lineages, as originally proposed by Bergmann, or by latitudinal turnover between lineages.

MATERIALS AND METHODS

Body-size data and mapping

Body masses of 8270 of 9702 species of extant birds were collected from 434 literature sources (online Appendix S1), following the taxonomy of Sibley and Monroe (Sibley & Monroe 1990). Within-species sample sizes, where reported, ranged from 1 to 41 884 (mean 80.6 individuals; median 9). We mapped the body-size data onto gridded species breeding range maps using equal-area cells approximating to a 1° scale (Orme *et al.* 2005, 2006). We calculated median body mass across all species within grid cells to obtain the global distribution of avian body size. We also identified the genera, families and orders represented in each cell and calculated the median masses at each taxonomic level from the median mass of all species within each taxon.

We calculated the number of species in each cell falling into each of the quartiles of the distribution of body size across bird species (under 15.5 g; 15.5–36.9 g; 37.0–138.8 g; over 138.8 g) in order to reveal differences in the distributions of large- vs. small-bodied species. We calculated linear models of biome differences in the relationship between body size and latitude using the biome occupying the largest land area within each cell (Olson *et al.* 2001). These models used the mean of $\log_{10}$ median body mass within latitudinal bands to remove longitudinal autocorrelation in the model. Similar models for island vs. continental assemblages used only those cells that contained only island or only continental landmass, therefore omitting many continental coastal cells. Species richness was recorded as the number of species in each cell for which body-size data were available.

Body size and species richness

Body-size gradients may result from non-random addition of small-bodied species in more species-rich areas (Cardillo 2002). To examine whether such a mechanism can explain the geographic distribution of avian median masses, we generated a null body-size distribution by drawing species without replacement from the species pool 1000 times for each observed value of cell species richness. The probability of drawing a species was weighted by its range size such that large-ranged species were more likely to be drawn than small-ranged species. The 95% confidence intervals of the expectations from this randomization were then compared to the relationship between median $\log_{10}$ body mass within each cell and the observed total species richness (Orme *et al.* 2005).

Environmental data

Environmental variables were selected for their potential bearing on the mechanisms suggested to explain Bergmann's rule, and we therefore used measures of temperature, primary productivity, degree of seasonality and the year-to-year variability of resources.

Mean annual temperature was determined using monthly temperature data averaged across the period 1961–1990, recorded at a 10-min resolution (New *et al.* 2002). The same data were used to calculate the annual amplitude in temperature as the mean intra-annual temperature range across years. Productivity was measured by the Normalized Difference Vegetation Index (NDVI) using monthly $\log_{10}$-transformed remotely sensed NDVI averages across the period 1982–1996 at 0.25° resolution (The International Satellite Land-Surface Climatology Project Initiative II 2004). We included seasonality (absolute value of the difference between the October–March mean and the April–September mean), and the inter-annual coefficient of variation of NDVI.

We used additional environmental variables estimating habitat heterogeneity as covariates for similar reasons as species richness, that is, as median body mass may be influenced by habitat turnover independently of the climate predictors of interest. Habitat heterogeneity was estimated as the number of land-cover types occurring in a grid cell, computed using remotely sensed data for the 12-month period between April 1992 and March 1993 at 30-arcsec resolution with types classified following the Global Ecosystems 100 category land-cover classification (Olson 1994a,b). Elevation range (maximum minus minimum elevation) was used as an alternative estimate of habitat heterogeneity, calculated from 30-arcsec resolution data (United States Geological Survey 2003). Finally, using the same data source, we tested the fit of mean elevation, as elevation (like latitude) is not strictly an ecological predictor but a spatial one that is allied to a number of climatic gradients we explicitly test. Nevertheless, we wished to establish its relative importance among single-variable models only (see below). Data for each environmental variable were re-projected and re-sampled to the same equal-area grid as the geographic range data.

Spatial analyses

We used $\log_{10}$ median body mass as the response variable in our environmental models and included quadratic and linear terms as predictors to test for nonlinear associations. Because richness could either drive size patterns or respond to similar environmental conditions as size, we ran two sets of models: including and excluding species richness as a covariate. In both sets of models, the $\log_{10}$ land area in each cell was also included as a predictor. To remove extremes of variation in land area that might dominate and/or distort environmental model results, grid cells with less than 50% landcover were omitted from the final dataset.

In addition to fitting non-spatial ordinary least squares (OLS) regressions, we fitted spatial generalized least squares (GLS) regressions using SAS version 9.1.3 (Littell *et al.* 1996) to test the fit of environmental predictors while accounting for spatial non-independence. The latter models included multiple exponential spatial covariance terms fitted independently within each biogeographic realm using a realm-specific range parameter (ρ), or distance over which autocorrelation between grid cells is observed to occur, as estimated from semi-variograms of OLS regression residuals.

For both OLS and GLS model sets, we first ran single-variable models of both linear and quadratic forms of the environmental parameters. We then used a backwards removal procedure from the full model (excluding mean elevation, see above) to arrive at a minimum adequate model (MAM). The removal of predictor terms was based on the maximum decrease in AIC, hence the maximum increase in overall model fit, for the removal of each remaining term. We stopped removing terms when no term deletion further decreased AIC. While this does not achieve a best-fit model set in the same way as a full model selection procedure using all combinations of predictors, the latter was not computationally feasible given the numbers of predictor variables involved and the computational intensity of GLS regression. Nevertheless, our method is the next best option for incorporating some beneficial elements of an information-theoretic approach to our model building. We used tolerance levels (Quinn & Keough 2002) to exclude the possibility of serious collinearity (tolerances > 0.1) in all models.

In order to determine the relationships between $\log_{10}$ median body mass and each of our predictors, as indicated by the spatial GLS multipredictor model results, we plotted values predicted from the parameter estimates of the predictor in question against the linear term for that predictor, while holding all other predictors at their mean values. We compared the relationships predicted by GLS MAMs that include and exclude species richness.

Within-taxon analyses

To examine whether adaptation within lineages or turnover between lineages drives body-size clines, we regressed species' body masses on the median temperature in their breeding ranges within genera, families and orders (484 genera, 102 families and 23 orders with five or more species). We tested for the existence of an overall negative size–temperature relationship across taxa at each of these levels using a meta-analysis. Using Fisher's Z-transformation of r and weighting by taxon species richness, we pooled the estimated correlation coefficients (r) within each taxonomic level and tested whether the weighted common correlation (Z_+) differed from zero (Hedges & Olkin 1985).

Migratory effects

We used data from 2789 bird species for which we had data on migratory habits to examine the role of migration in generating the observed body-size gradients. We included only species with breeding and wintering ranges that could be assigned unambiguously to either tropical–subtropical or to temperate–polar regions. Unambiguously sedentary or migrant species were identified, along with other species exhibiting some range movements (nomads, partial migrants or elevational migrants). We divided the species into body-size quartiles and used chi-squared tests to test for the dependence of body size and migratory behaviour in both tropical–subtropical and temperate–polar regions.

RESULTS

Global maps of avian body size

Bird assemblages exhibit a strong, global, latitudinal gradient in body size (Fig. 1a,e) with large masses being associated with higher latitudes. The median body mass of species within cells increases with absolute latitude both globally and within the northern and southern hemispheres respectively (Table 1). Although there is a consistent latitudinal gradient in body size (Fig. 1e), there is considerable variation within latitudes (Fig. 1a). Latitudinal patterns of median body mass within biomes (Olson *et al.* 2001) show marked differences (Fig. S1a) in both slope ($F_{13,753} = 10.1$, $P < 0.0001$) and intercept ($F_{13,766} = 39.7$, $P < 0.0001$). For example, species assemblages breeding in the tundra have markedly larger body sizes given their latitude and, whilst showing considerable variation, Mediterranean forest assemblages reverse the overall trend, with larger body sizes at low latitudes. In addition, island assemblages (Fig. S1b) have larger median body sizes than those of mainland assemblages at similar latitudes ($F_{1,271} = 115.7$, $P < 0.0001$) and median body size increases more rapidly with increasing latitude on islands ($F_{1,270} = 6.2$, $P = 0.014$). These relationships often show considerable differences between the northern and southern hemispheres (Fig. S1).

Species richness and body size

Species-rich cells generally have right-skewed body-size distributions (Cardillo 2002; Meiri & Thomas 2007) and usually occur in tropical areas (Orme *et al.* 2005) (Fig. 2a) whereas species-poor cells, which tend to occur at high latitudes, on islands and in deserts (Orme *et al.* 2005), are characterized by less-skewed distributions and larger median sizes (Cardillo 2002; Meiri & Thomas 2007).

Maps of the proportion of total species richness in cells falling into the lowest and highest quartiles of the species body-size distribution (Fig. 2b,c respectively) show that small-bodied species are over-represented in many species-rich regions (Orme *et al.* 2005), and under-represented in species-poor regions (e.g. islands, deserts and polar regions). In contrast, large-bodied species are over-represented in tundra regions. The correlation between the skew in body-size distributions and the number of species in the lowest body-size quartile ($r = 0.73$) is stronger than the equivalent relationship in the highest quartile ($r = 0.56$).

Random community assembly models, however, fail to capture the true relationship between median body size and species richness (Fig. 2d). Simulations weighted by range

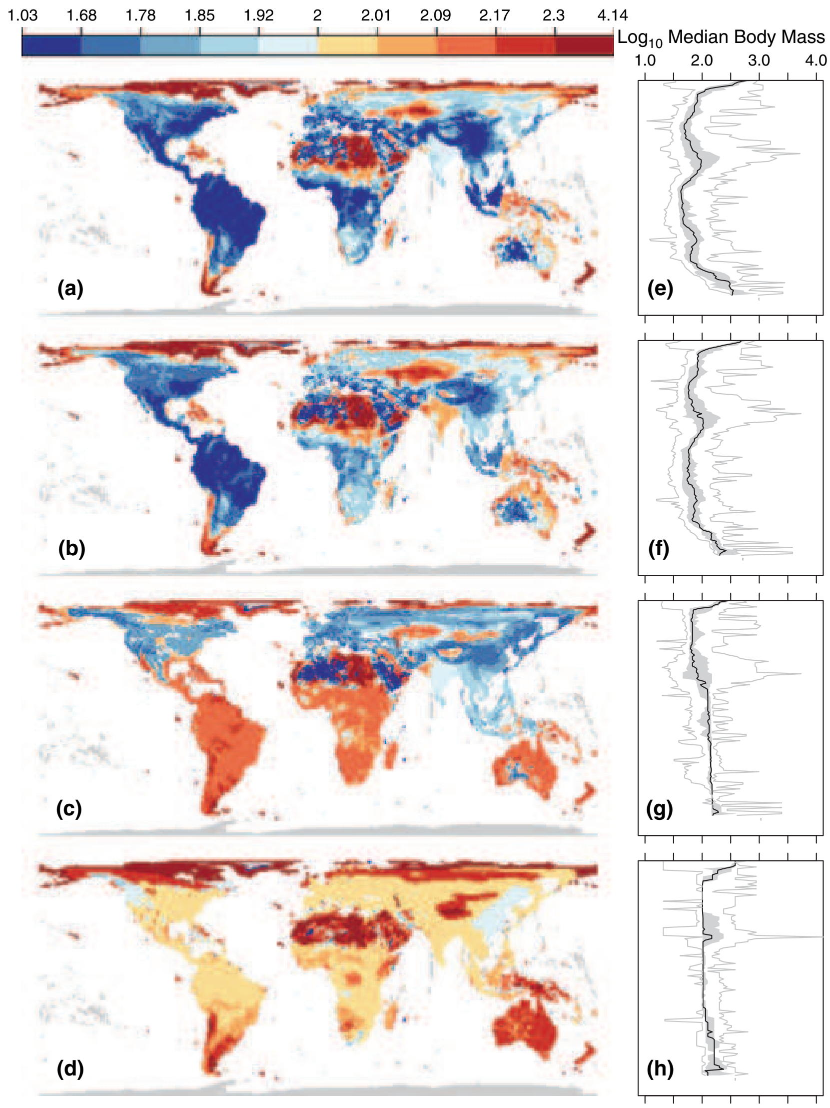

Figure 1 Global distribution of avian body sizes. The median $\log_{10}$ body mass within grid cells is shown for: (a) species, (b) genera, (c) families and (d) orders. In the case of higher taxa (b, c, d), the values shown are the median of the median masses of all taxa of that rank occurring in each grid cell (c). The four maps share a common colour scale. In addition, the plots shows the corresponding median $\log_{10}$ body mass within latitudinal bands for species (e), genera (f), families (g) and orders (h). In plots (d–f), grey shading shows the interquartile range and dashed lines show the minimum and maximum of values of cells within latitudinal bands.

size describe the associations between median size and species richness at some medium richness values (between *c.* 200 and 300 species) relatively well, but they poorly capture both the observed small median body sizes at high species richness, and the large median sizes observed in species-poor cells. Thus, other mechanisms are needed to explain the geographic distribution of median body sizes.

Environmental drivers of avian body size

Multivariate MAMs based on spatial GLS regression showed considerably lower AIC values compared with equivalent OLS models fitting the same predictors (Table 2), as well as with OLS MAMs achieved using backwards removal (Table S1), indicating that the GLS models were a consistently more accurate description of variability in body mass. Spatial MAMs show significant associations between median body size and species richness, temperature and resource availability. Species richness was the most important predictor of size in the spatial MAM. Other variables in the model predicting large body size were (in decreasing order of importance) low mean annual temperature, intermediate temperature amplitude, low elevation range, high inter-annual variability of productivity and high overall productivity (NDVI, only when controlling for species richness) (Table 2 and Fig. 3, see also Fig. S2). Mean productivity was the only predictor for which direction of slope was reversed when not controlling for species richness (excluding richness, the relationship is negative at most productivity values). While seasonality in productivity was maintained both in MAMs that did and did not fit species richness, it was only statistically significant in the former case, and even here, it had minor effects (Table 2). Spatial GLS and non-spatial OLS models that fitted each environmental predictor in

Table 1 Slopes, standard errors and correlation coefficients from linear models of absolute latitude as a predictor of median body mass within cells for species, genera, families and orders

Taxonomic level	Slope	SE	*R*	d.f.
Species				
Both hemispheres	0.0100***	0.00090	0.686***	139
Northern hemisphere	0.0066***	0.00092	0.643***	74
Southern hemisphere	0.0190***	0.00110	0.906***	63
Genera				
Both hemispheres	0.0071***	0.00067	0.671***	139
Northern hemisphere	0.0049***	0.00081	0.574***	74
Southern hemisphere	0.0130***	0.00077	0.899***	63
Families				
Both hemispheres	−0.0003	0.00082	−0.034	139
Northern hemisphere	−0.0015	0.00078	−0.220	74
Southern hemisphere	0.0048***	0.00100	0.508 ***	63
Orders				
Both hemispheres	0.0048***	0.00045	0.671***	139
Northern hemisphere	0.0047***	0.00060	0.673***	74
Southern hemisphere	0.0059***	0.00056	0.795***	63

Significance is indicated as: $^{***}P < 0.001$.

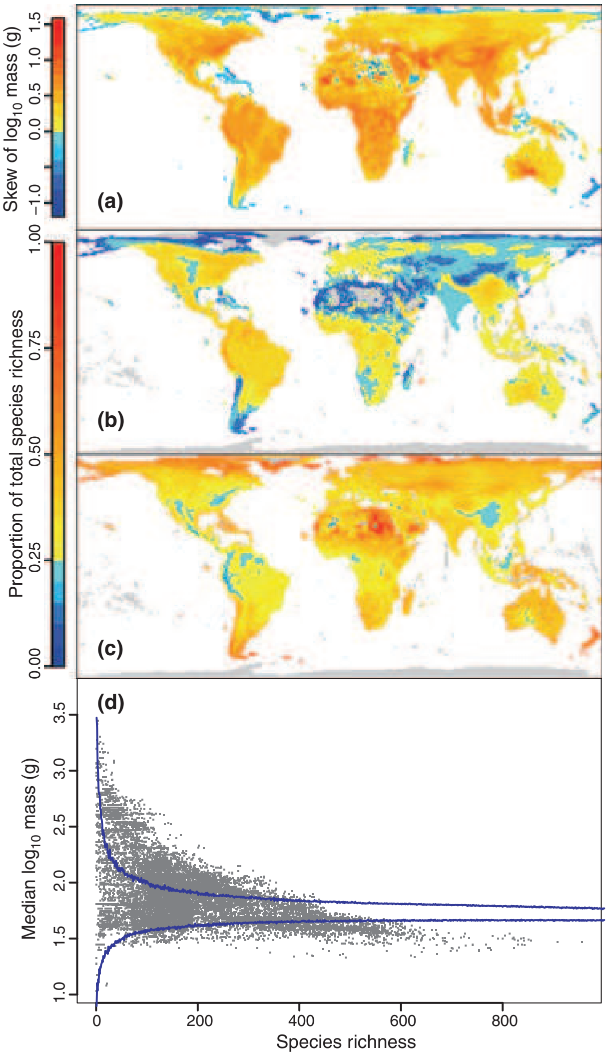

Figure 2 Global distribution of skewness in $\log_{10}$ body mass (a) along with species richness of cells using species in the first (b) and fourth (c) quartiles of the avian body-mass distribution as a proportion of total species richness. The distribution of median mass in cells with respect to total species richness (d). Predicted 95% confidence intervals are also shown on expectations from a range-weighted randomization model (see Materials and methods).

isolation (while also controlling for species richness) gave broadly similar results to the spatial MAMs (Tables S2 and S3 respectively). Our analyses suggest that variation in species richness is the most influential variable affecting the median body size within grid cells. Variation in temperature is the main environmental correlate of avian body-size distributions, after controlling for species richness and spatial autocorrelation. We found a hump-shaped relationship between size and seasonality, as well as support for the hypothesis that resource availability has an important influence on the geographic distribution of bird body sizes (Fig. 3; Geist 1987; Blackburn *et al.* 1999; Meiri & Dayan 2003).

Within-taxon analyses

To ascertain whether assemblage-level size clines result from adaptation within lineages (Bergmann 1847) or from turnover between lineages (Blackburn & Gaston 1996; Blackburn *et al.* 1999), we tested whether the associations between body size and environmental factors were also present when comparing species within genera, families and orders, or whether patterns were present only when we examined all birds.

There was no significant correlation between body size and temperature within the majority of genera (Fig. 4a, 430/484), families (Fig. 4b, 80/104) and orders (Fig. 4c, 15/23). Only 37 genera, 20 families and six orders showed a significant, negative size–temperature association, while 17 genera, four families and two orders showed a significant positive correlation (Fig. 4, Table S4). However, because many lineages contain few species and we are performing multiple tests, we used a meta-analysis to test for an overall trend in the correlations between body size and temperature within genera, families and orders. For genera (Fig. 4d; $Z_+ = -0.109$, $P < 0.0001$) and families (Fig. 4e; $Z_+ = -0.068$, $P < 0.0001$), we found a significant overall negative association between body size and temperature. However, the relationship was not significant for orders (Fig. 4f; $Z_+ = -0.016$, $P = 0.196$).

Table 2 Best-fit multivariate spatial generalized least squares models of global patterns of avian body size in relation to environmental variables

	Including species richness: $AIC_{GLS} = -34\ 018.9$, $AIC_{OLS} = -6232.0$			Excluding species richness: $AIC_{GLS} = -32\ 122.0$, $AIC_{OLS} = -5481.7$		
Predictor	Slope	SE	$F_{1,13941}$	Slope	SE	$F_{1,13942}$
Intercept	3.26	0.064		3.30	0.073	
Log_{10} land area	−0.036	0.012	9.72**	−0.13	0.014	85.50****
Species richness	0.0013	0.000062	459.94****	–	–	–
Sqrt species richness	−0.073	0.0023	1019.34****	–	–	–
Temperature						
Mean annual	−0.026	0.0021	154.73****	−0.041	0.0022	339.54****
Mean annual^2	0.00028	0.000022	155.66****	0.00041	0.000025	276.40****
Amplitude	0.0066	0.00091	51.88****	0.013	0.0011	154.88****
Amplitude^2	−0.00019	0.000024	59.65****	−0.00028	0.000026	115.14****
NDVI						
Log_{10} NDVI	0.56	0.13	17.76****	−0.96	0.14	44.63****
Log_{10} NDVI^2	−1.15	0.41	7.86**	2.53	0.45	31.11****
Log_{10} NDVI seasonality	0.25	0.12	4.55*	0.21	0.13	2.39
Log_{10} NDVI seasonality^2	−1.66	1.02	2.63	−1.32	1.12	1.40
Log_{10} CV NDVI	–	–	–	0.045	0.014	10.76**
Log_{10} CV NDVI^2	0.068	0.011	37.94****	–	–	–
Elevation						
Log_{10} elevational range	–	–	–	0.047	0.012	16.34****
Log_{10} elevational range^2	−0.0030	0.00042	50.62****	−0.016	0.0023	47.14****

Significance is indicated as follows: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$.
NDVI, Normalized Difference Vegetation Index; OLS, ordinary least squares; GLS, generalized least squares; SE, standard error; CV, coefficient of variation.
Models are shown including and excluding species richness as a covariate. The estimated slope and SE are shown along with the F-ratio. AIC values are shown from spatial GLS models and non-spatial OLS models containing the same variables

Between-taxon analyses

Size increases with increasing latitude when all species are considered, and when we use a single, average mass value for all species within genera and all species within orders in each grid cell (Table 1, Fig. 1b,d,f,h). However, for families this is true only in the southern hemisphere (Table 1, Fig. 1g). Thus, the increase in size with latitude is driven, in part, by taxonomic turnover across latitudes: large-bodied genera and orders (and, in the southern hemisphere, also families) replace small-bodied ones at high latitudes. In the northern hemisphere, small-bodied families occupy mainly intermediate latitudes whereas large-bodied families are represented more at both equatorial and polar latitudes (Fig. 1c,g).

Migratory effects

We found that frequencies of migratory behaviour are not independent of body size in either tropical–subtropical ($\chi^2_6 = 31.31$, $P < 0.0001$) or temperate–polar ($\chi^2_6 = 29.79$, $P < 0.0001$) regions (Fig. S3). Small-bodied migratory species were significantly ($Z = 2.95$, $P < 0.0001$) over-represented in temperate and polar regions (Table S5).

DISCUSSION

We found strong support for a global Bergmann's rule in birds, whether framed in terms of latitude or temperature: species living at high latitudes and in cooler climates tend to be larger-bodied than their relatives living at lower latitudes or in warmer climates. The negative relationship between richness and size is not simply reflecting the common influence of temperature and seasonality on both species richness and body size. The association between body size and species richness is the strongest factor affecting size even after the effects of temperature and seasonality are accounted for. While species richness was the strongest predictor of median body size, our weighted null model shows that richness alone underestimates median masses at species-poor cells, and systematically overestimates median masses in species-rich ones. Thus, a combination of community assembly and environmental factors is needed to explain avian body-size distributions.

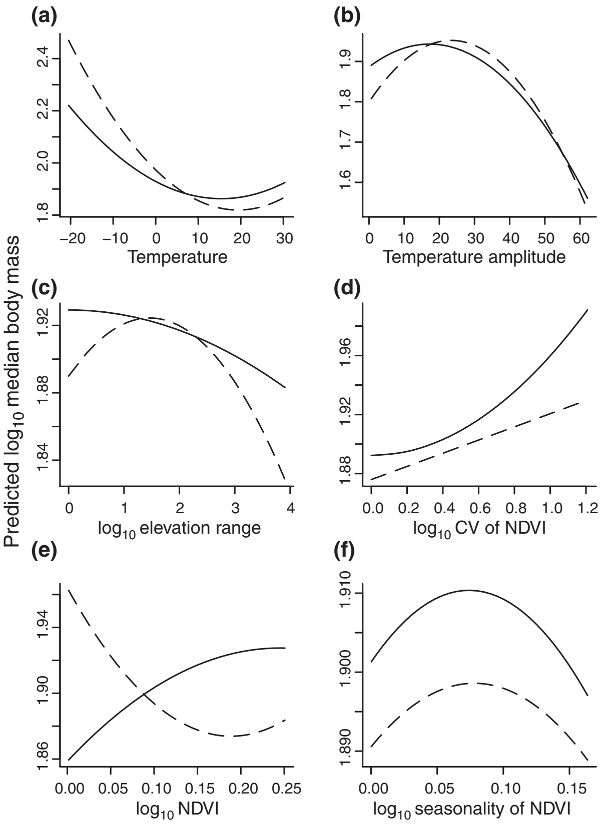

Figure 3 Model predictions of $\log_{10}$ median body mass for cells from minimum adequate generalized least squares models both including (solid lines) and excluding (dashed lines) species-richness terms. Predictions are shown for: (a) mean annual temperature; (b) mean annual amplitude in temperature; (c) $\log_{10}$ elevational range; (d) $\log_{10}$ coefficient of variation in NDVI; (e) $\log_{10}$ NDVI and (f) $\log_{10}$ seasonality in NDVI. The predictions for each variable, including linear and squared terms where necessary, are made whilst holding the other variables fixed at their global means.

Mean temperature, temperature amplitude, inter-annual variability in productivity, and mean productivity were important correlates of size. However, while the positive relationships between size and both inter-annual variability of productivity and mean annual productivity were expected (Rosenzweig 1968), the hump-shaped relationship between body size and temperate amplitude was not (Lindsey 1966; Calder 1974; Boyce 1978; Zeveloff & Boyce 1988).

Our between-assemblage and within-lineage results are broadly consistent with patterns observed at the intraspecific level, in which body-size clines are typically explained by variation in temperature or seasonality (Meiri & Dayan 2003). However, our results indicate that the observed body-size patterns are not only due to adaptation within lineages, but also due to taxonomic turnover across lineages. Although we found strong support for a body size–temperature gradient consistent with Bergmann's rule, it is clear that spatial patterns of avian body size are also driven by forces acting at the between-taxon and assemblage levels (Gaston *et al.* 2008). Notably, body-size gradients are present at taxonomic levels above the species (generic to ordinal levels), indicating that taxon turnover at different levels may at least partly account for the geographic distribution of avian body sizes.

Island assemblages have larger median sizes than expected from their latitude alone. This may be a manifestation of the negative correlation between cell species richness and median body size (Brown & Nicoletto 1991; Cardillo 2002; this study). The body size of bird species has been shown to shift following the colonization of islands, due to ecological processes related to feeding, competition and heat balance (Clegg & Owens 2002) – a finding supporting the idea that the larger body sizes we observed on islands are at least partly adaptive. While it has been claimed that size evolution on islands drives species towards medium sizes (Clegg & Owens 2002; but see Gaston & Blackburn 1995), we note that the cut-off between large and small sizes in that work (Clegg & Owens 2002) (321.4 g) is well within the largest body-size quartile in our global dataset (over 138.8 g). The large median body sizes observed on islands may also be due, in part, to the number of seabirds that breed there (Gaston & Blackburn 1995). Most species comprising typical 'seabird' families (i.e. Phaethontidae, Sulidae, Phalacrocoracidae, Spheniscidae, Procellariidae, Fregatidae) are large and breed partly or exclusively on islands. Island patterns would probably have been even stronger before the large recent extinction event following human colonization of most oceanic islands around the world, where mostly large-bodied birds went extinct (Blackburn & Gaston 2005; Steadman 2006).

Body-size distributions may differ between areas of high and low species richness because of factors related to community assembly (Brown & Nicoletto 1991; Meiri & Thomas 2007), rather than by direct adaptation to lower temperatures. Alternatively, species richness may represent a trade-off between body size and abundance: if resources are limiting, then given that abundance decreases with increasing size, an area can either support many small, abundant species or few large, rare ones (Cousins 1989; Blackburn & Gaston 1996). Thus, species richness may be a consequence rather than a driver of body-size distributions. At present, we cannot readily distinguish between these possibilities. Greve *et al.* (2008) found that the body size in high-richness areas fell within the bounds of their null distributions. The discrepancy between these and our results is likely to be due to regional (South Africa) vs. global effects. Specifically, variation in global rates of speciation, extinction and immigration is expected to generate phylogenetically non-

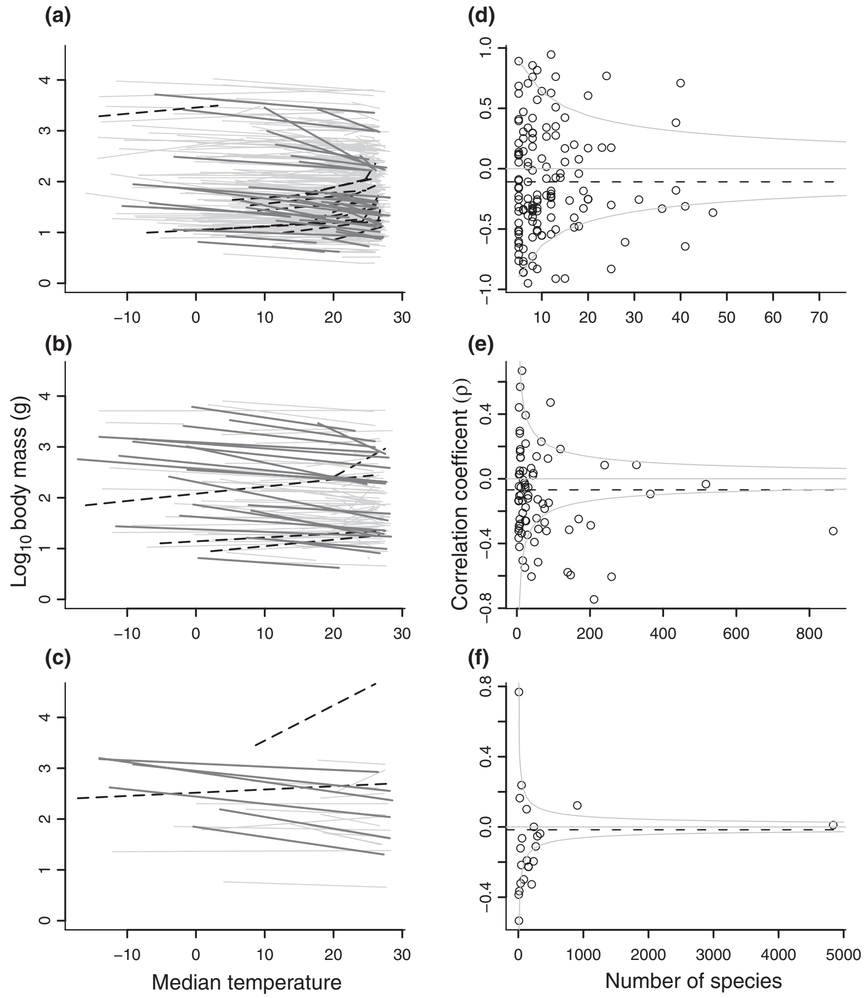

Figure 4 Body mass vs. median temperature for species within (a) genera, (b) families and (c) orders of birds. Each line represents a family or order with colours denoting significant slopes in the direction predicted by Bergmann's rule (dark grey), significant slopes in the opposing direction (dashed) and non-significant slopes (light grey). Transformed effect sizes vs. sample sizes for the relationship are also shown for (d) genera, (e) families and (f) orders along with the results of meta-analysis across taxa.

random species distributions, whereas at regional and local scales the phylogenetic pattern is probably much weaker. Furthermore, the range of variation in environmental variables in regional assemblages may be insufficient to drive strong patterns of geographic size variation (Meiri *et al.* 2007).

Most genera, families and orders did not show significant body size–temperature gradients, even when their geographical distributions encompassed large temperature variation (Fig. 4). This may be due to the large number of small-bodied species that migrate away from cold and seasonal regions when not breeding (Fig. S3). It can also reflect adaptations other than body size that increase fitness in harsh climates such as communal roosting (Marsh & Dawson 1989; Cartron *et al.* 2000; McKechnie & Lovegrove 2002). Interestingly, we found that large-bodied migratory or nomadic species were over-represented in warm climates, potentially supporting a hypothesis (Hamilton 1961; James 1970) that large-bodied taxa are at a disadvantage in tropical conditions (Table S5).

Taken together, global distributions of avian body masses are not simply reflections of processes at and within the species level. While environmental variables, in particular temperature, are certainly important determinants of body-size distributions, they cannot account by themselves for the whole, richly textured, pattern. Non-random patterns of community assemblage and geographic variation in the phylogenetic affinities of co-occurring taxa are also important drivers of global body-size distributions.

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SUPPORTING INFORMATION

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

Figure S1 Predicted trends in mean $\log_{10}$ body mass, averaged within latitudinal bands, with absolute latitude from linear models (a) within biomes and (b) comparing continental and island cells.

Figure S2 Global maps of the main environmental predictor variables: (a) mean annual temperature, (b) mean seasonality of NDVI and (c) inter-annual coefficient of variation in NDVI.

Figure S3 Proportional prevalence of different migratory behaviours (resident – dark grey; other – medium grey; migrant – light grey), categorized by body-size quartile and preference for tropical–subtropical (a) or temperate–polar (b) regions of the globe.

Table S1 Best-fit multivariate non-spatial ordinary least squares models of global patterns of avian body size in relation to environmental variables.

Table S2 Spatial generalized least square regression results of linear and quadratic relationships between avian body size and key environmental variables across grid cell values

Table S3 Non-spatial ordinary least squares regression results of linear and quadratic relationships between avian body size and key environmental variables across grid cell values.

Table S4 Significant relationships between median temperature of bird species ranges and body size within extant genera, families and orders containing more than four species.

Table S5 Chi-squared tests for differences in migratory behaviour between bird species in (a) tropical–subtropical and (b) temperate–polar climates.

Appendix S1 List of references for avian body sizes, organized by document type.

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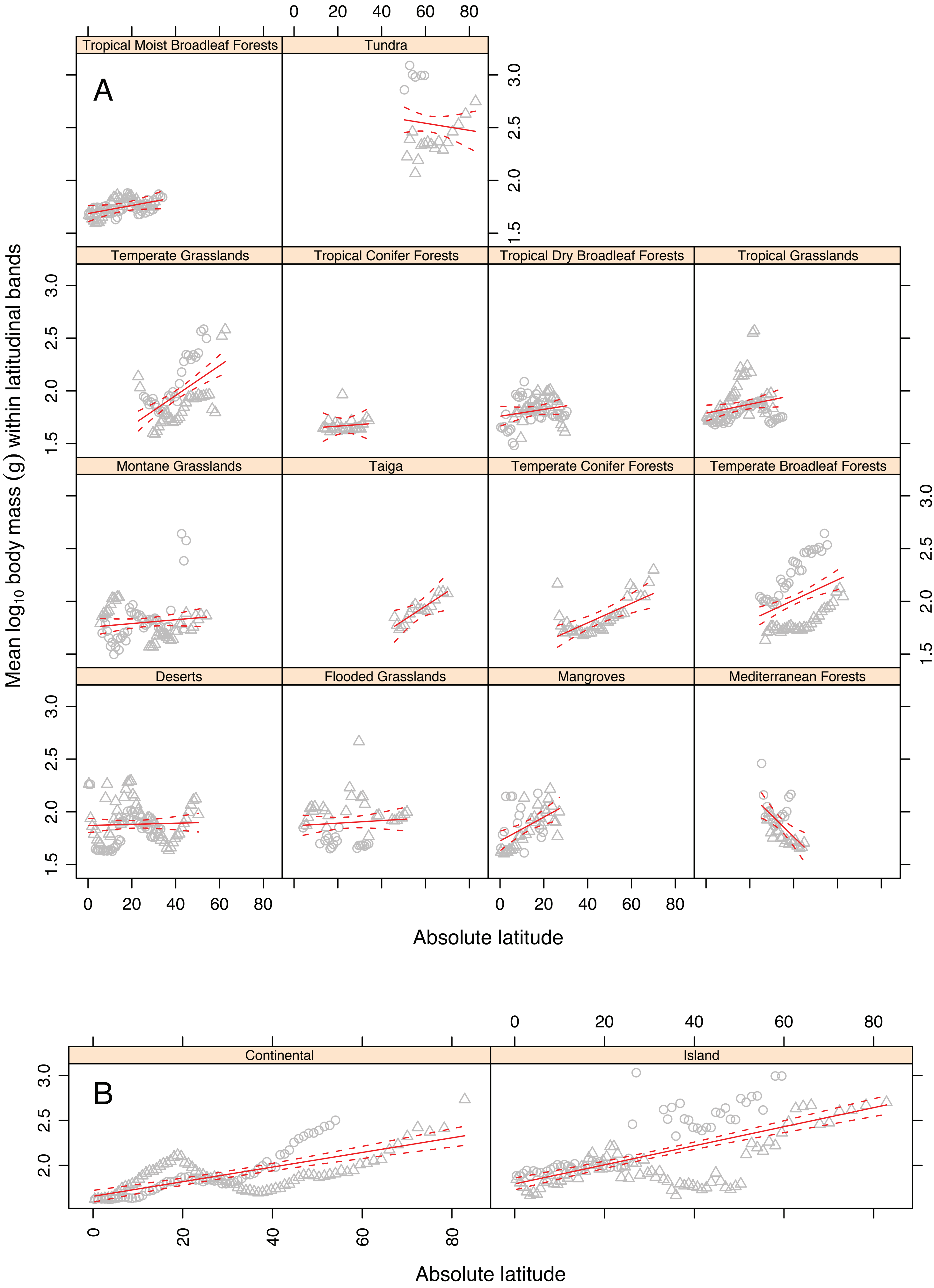
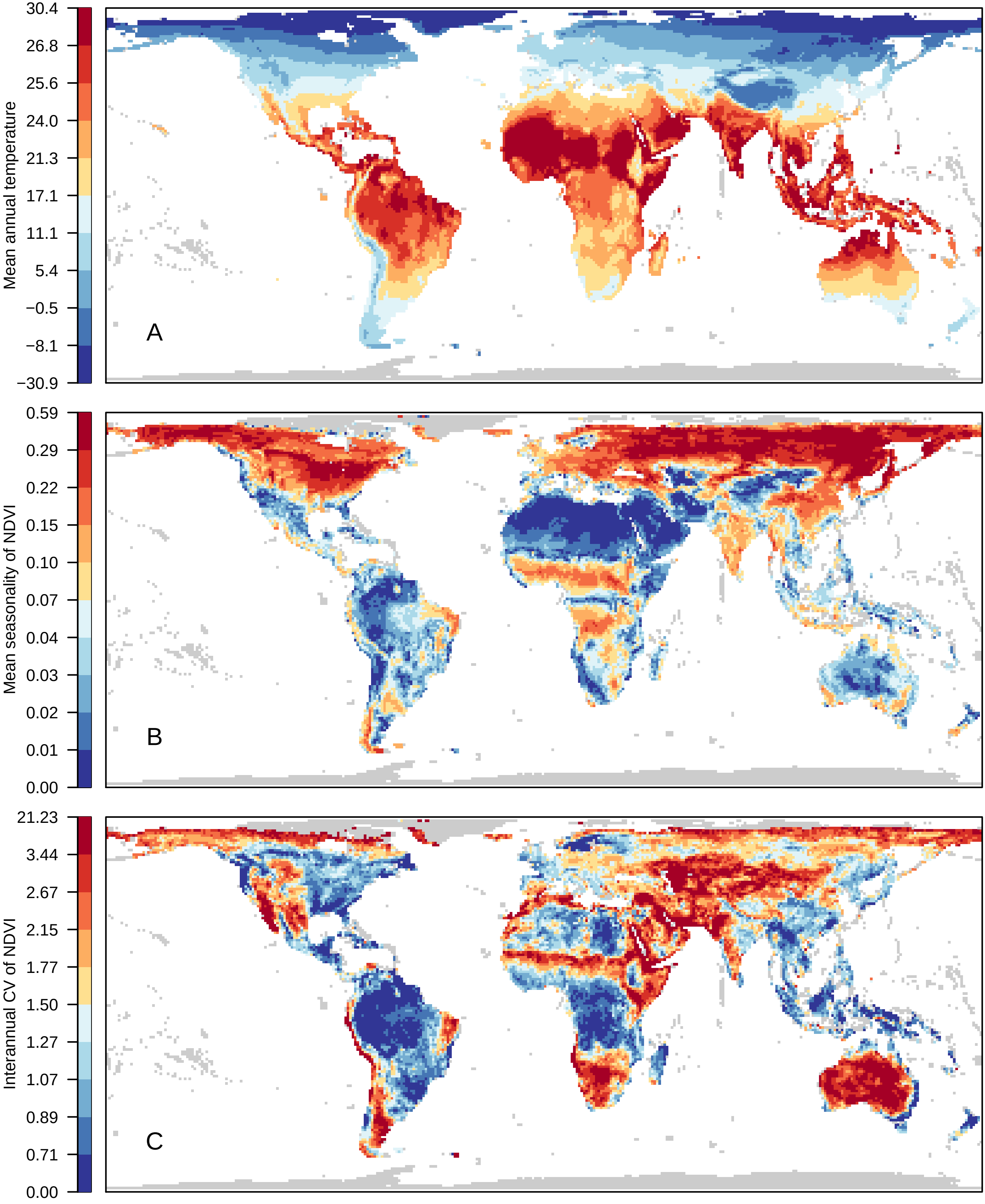
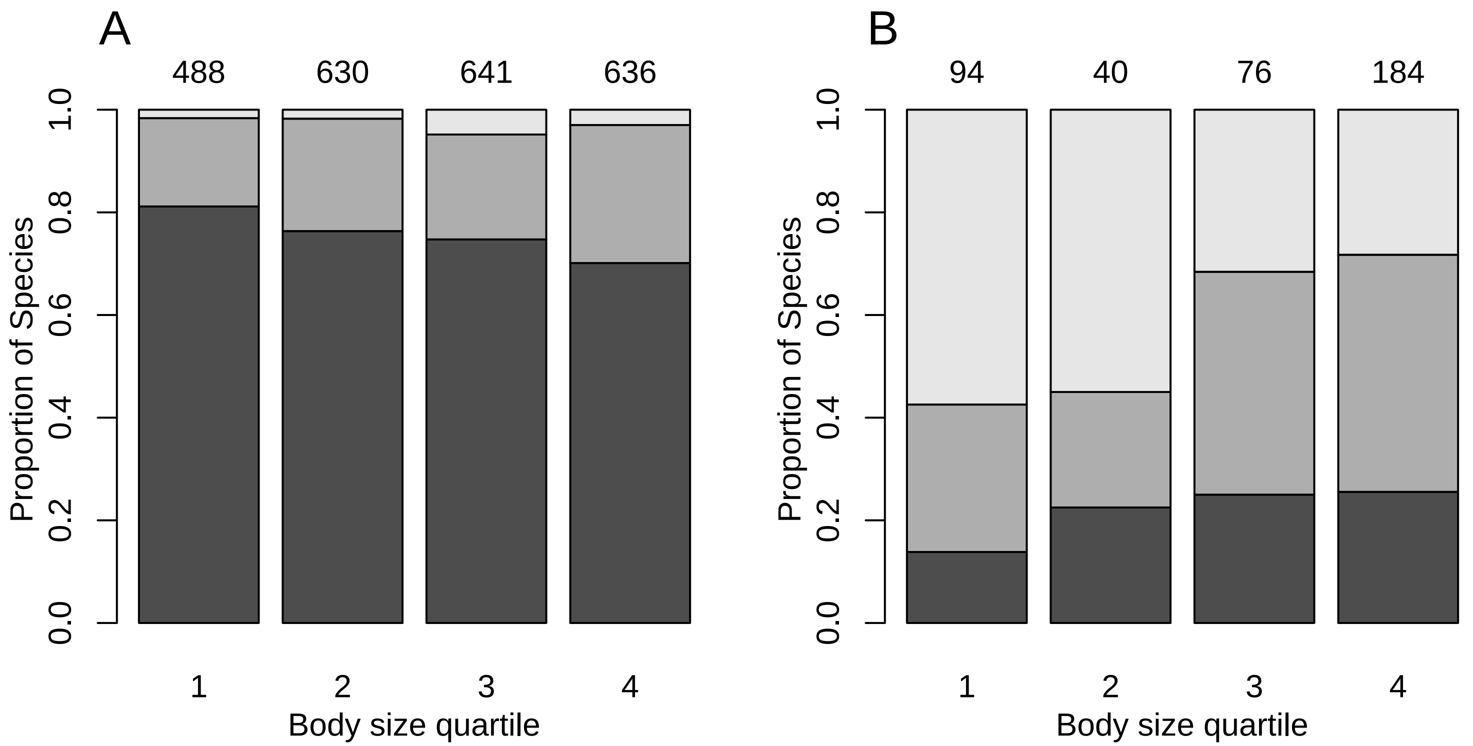


A
B
Tropical Moist Broadleaf Forests
Tundra
Temperate Grasslands
Tropical Conifer Forests
Tropical Dry Broadleaf Forests
Tropical Grasslands
Montane Grasslands
Taiga
Temperate Conifer Forests
Temperate Broadleaf Forests
Deserts
Flooded Grasslands
Mangroves
Mediterranean Forests
Continental
Island
Mean $\log_{10}$ body mass (g) within latitudinal bands
Absolute latitude
0 20 40 60 80
1.5 2.0 2.5 3.0



Mean annual temperature
30.4
26.8
25.6
24.0
21.3
17.1
11.1
5.4
−0.5
−8.1
−30.9
A
Mean seasonality of NDVI
0.59
0.29
0.22
0.15
0.10
0.07
0.04
0.03
0.02
0.01
0.00
B
Interannual CV of NDVI
21.23
3.44
2.67
2.15
1.77
1.50
1.27
1.07
0.89
0.71
0.00
C



A
488
630
641
636
Proportion of Species
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
Body size quartile
B
94
40
76
184
Proportion of Species
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
Body size quartile

Supplementary Table S1: Best-fit multivariate non-spatial OLS models of global patterns of avian body size in relation to environmental variables. Models are shown a) including and b) excluding species richness as a covariate. The estimated slope and standard error (SE) are shown along with the F-ratio. Significance is indicated as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$.

Predictor	Slope	se	$F_{1,13940}$	Slope	se	$F_{1,13942}$
	a) Including species richness: AIC_{OLS} =-6305.4			b) Excluding species richness: AIC_{OLS} =-5481.7		
Intercept	5.171	0.144		6.148	0.144	
Log_{10} Land Area	-0.571	0.036	257.76****	-0.843	0.035	577.28****
Species richness	0.00037	0.000068	28.79****	-	-	-
Sqrt Species richness	-0.0305	0.0021	216.98****	-	-	-
Temperature						
Mean annual	-0.036	0.0012	959.33****	-0.043	0.0015	801.07****
Mean annual^2	0.00037	0.000014	729.37****	0.00045	0.000018	619.46****
Amplitude	-0.0065	0.00034	372.48****	0.0032	0.00068	22.11****
Amplitude^2	-	-	-	-0.00017	0.000013	173.68****
NDVI						
Log_{10} NDVI	-0.533	0.186	8.24**	-2.35	0.160	214.91****
Log_{10} NDVI^2	-1.203	0.649	3.43*	2.179	0.615	12.57***
Log_{10} Seasonality	1.455	0.184	62.77****	1.392	0.191	52.95****
Log_{10} Seasonality^2	-3.558	1.261	7.96**	-3.412	1.328	6.60*
Log_{10} CV NDVI	0.126	0.0177	50.52****	-0.063	0.016	15.61****
Log_{10} CV^2 NDVI	-	-	-	-	-	-
Landcover variability	0.0019	0.00043	19.23****	-	-	-
Elevation						
Log_{10} Elev. Range	0.239	0.028	72.65****	0.319	0.0275	135.35****
Log_{10} Elev. Range^2	-0.062	0.0054	132.26****	-0.080	0.0052	235.82****

Supplementary Table S2: Spatial GLS regression results of linear and quadratic relationships between avian body size and key environmental variables across grid cell values. Models contain either only linear values (L), only quadratic values (Q), or both linear and quadratic forms (LQ). Associated degrees of freedom were either 13,950 in the case of (L) and (Q) or 13,949 (LQ). The model for each variable with the best AIC is shown in bold. All analyses controlled for cell land area, as well as species richness (range of slopes: 0.00128 – 0.00145, range of standard errors: 0.000058 – 0.000061) and the square root of species richness (range of slopes: -0.079 – -0.073, range of standard errors: 0.00209 – 0.00223). Significance levels are indicated as in Table 2.

Predictor	Terms	AIC	Slope	se	F
Log_{10} Elevation Range	L	-33876.9	-1.5E-02	2.0E-03	56.66****
	Q	**-33882.5**	-3.3E-03	4.0E-04	65.85****
	LQ	-33878.2	1.7E-02	9.5E-03	3.21
			-6.6E-03	1.9E-03	12.11***
Log_{10} Mean Elevation	L	-33981.4	-4.2E-02	3.3E-03	161.93****
	Q	-33994.9	-8.5E-03	6.4E-04	179.40****
	LQ	**-33999.0**	6.8E-02	2.1E-02	10.04**
			-2.1E-02	4.1E-03	27.01****
Temperature	L	-33817.0	4.6E-07	3.0E-04	0.00
	Q	-33812.2	6.9E-06	3.3E-06	4.42*
	LQ	**-33950.4**	-2.2E-02	1.8E-03	158.94****
			2.5E-04	1.9E-05	162.71****
Temperature Amplitude	**L**	**-33830.3**	1.4E-03	3.8E-04	12.91****
	Q	-33814.4	2.0E-05	9.7E-06	4.26*
	LQ	-33818.4	3.6E-03	8.9E-04	16.50****
			-6.0E-05	2.3E-05	7.76**
Log_{10} NDVI	L	-33827.2	-2.8E-02	3.5E-02	0.62
	Q	**-33829.9**	-1.1E-01	1.2E-01	0.95
	LQ	-33827.6	5.1E-02	1.1E-01	0.20
			-2.7E-01	3.8E-01	0.53
Log_{10} Seasonality of NDVI	L	-33835.3	1.2E-01	5.6E-02	4.58*
	Q	-33835.8	4.1E-01	5.1E-01	0.65
	LQ	**-33841.8**	3.3E-01	1.1E-01	8.54**
			-2.2E+00	1.0E+00	4.61*
Log_{10} CV of NDVI	L	-33841.5	3.9E-02	9.2E-03	17.67****
	Q	**-33842.9**	3.8E-02	8.7E-03	19.22****
	LQ	-33837.6	5.8E-03	2.8E-02	0.04
			3.3E-02	2.6E-02	1.59
Landcover Variability	**L**	**-33816.6**	1.4E-04	1.8E-04	0.65
	Q	-33809.5	3.5E-06	6.0E-06	0.34
	LQ	-33796.8	4.1E-04	5.2E-04	0.60

	-9.6E-06	1.8E-05	0.29

Supplementary Table S3: Non-spatial OLS regression results of linear and quadratic relationships between avian body size and key environmental variables across grid cell values. Models contain either only linear values (L), only quadratic values (Q), or both linear and quadratic forms (LQ). Associated degrees of freedom were either 13,956 in the case of (L) and (Q) or 13,955 (LQ). The model for each variable with the best AIC is shown in bold. All analyses controlled for cell land area, as well as species richness (range of slopes: -0.00017– 0.00046, range of standard errors: 0.000054 – 0.000066) and the square root of species richness (range of slopes: -0.0385 – -0.0178, range of standard errors: 0.00153– 0.00197). Significance levels are indicated as in Table 2.

Predictor	Terms	AIC	Slope	se	F
Log_{10} Elevation Range	L	-4100.0	-0.06567	0.003516	348.86****
	Q	-4137.0	-0.01305	0.000661	390.24****
	LQ	**-4185.6**	0.2098	0.02855	54.03****
			-0.05225	0.005373	94.55****
Log_{10} Mean Elevation	L	-4661.5	-0.1352	0.00442	935.58****
	Q	-4713.4	-0.0257	0.000815	994.73****
	LQ	**-4747.4**	0.2451	0.03942	38.65****
			-0.07068	0.007281	94.23****
Temperature	L	-3881.3	-0.00184	0.00016	132.72****
	Q	-3780.1	-1.00E-05	1.96E-06	39.77****
	LQ	**-5156.8**	-4.04E-02	0.001058	1459.87****
			0.000477	0.000013	1358.17****
Temperature Amplitude	L	-3835.5	0.001475	0.000159	86.55****
	Q	-3944.5	4.20E-05	2.96E-06	204.77****
	LQ	**-4152.5**	-0.00798	0.000535	222.95****
			0.000185	0.00001	342.32****
Log_{10} NDVI	L	-4077.8	-0.7344	0.04098	321.16****
	Q	-4152.7	-3.0625	0.1541	395.19****
	LQ	**-4167.8**	0.6137	0.1482	17.16****
			-5.286	0.5584	89.61****
Log_{10} Seasonality of NDVI	L	-4048.8	0.7165	0.04686	233.78****
	Q	-4028.9	5.1567	0.3563	209.42****
	LQ	**-4051.6**	0.8319	0.168	24.52****
			-0.9132	1.2765	0.51
Log_{10} CV of NDVI	L	-4143.7	0.2455	0.01241	391.1****
	Q	-4083.3	0.2265	0.01249	329.17****
	LQ	**-4165.5**	0.5259	0.05657	86.42****
			-0.2885	0.05678	25.81****
Landcover Variability	**L**	**-3930.1**	-0.00479	0.000357	180.46****
	Q	-3922.8	-1.70E-04	1.30E-05	179.77****
	LQ	-3915.7	-0.00255	0.001199	4.52*
			-0.00008	0.000043	3.84

Supplementary Table S4: Significant relationships between median temperature of bird species ranges and body size within extant genera, families and orders containing more than four species. Taxa in italics show a slope opposite to that predicted by Bergmann's rule. Significance levels are indicated as in Table 1. Passerine taxa are indicated ($^{+}$).

Taxon	N	Slope	Taxon	N	Slope
Genera			Genera (continued)		
Pteroglossus	13-0.128*		*Philydor*+	120.024*	
Porphyrio	5-0.076*		*Grallaria*+	250.030*	
Cercomacra+	9-0.059*		*Chamaeza*+	50.033*	
Euplectes+	16-0.058****		*Myzomela*+	210.036*	
Spizaetus	8-0.050*		*Illadopsis*+	90.048**	
Gallirallus	6-0.045*		*Sarothrura*	80.055**	
Andropadus+	12-0.041*		*Cacicus*+	70.058*	
Campylorhamphus+	5-0.040*		*Amaurornis*	50.217*	
Agapornis	9-0.037*		*Napothera*+	70.217*	
Geositta+	10-0.028*		*Malacopteron*+	60.794*	
Sylvietta+	9-0.027**		Families		
Galerida+	6-0.026*		Megapodiidae	13-0.062*	
Lampornis	5-0.025*		Podicipedidae	20-0.029**	
Apalis+	19-0.022**		Rhinocryptidae+	27-0.028*	
Puffinus	17-0.022*		Corvidae+	517-0.027****	
Malacoptila	7-0.022**		Apodidae	81-0.021**	
Sicalis+	9-0.020*		Spheniscidae	16-0.020*	
Ploceus+	51-0.020*		Sulidae	8-0.020*	
Aulacorhynchus	6-0.017*		Pardalotidae+	58-0.018**	
Pterocles	13-0.017*		Phalacrocoracidae	30-0.015**	
Dendrocopos	21-0.016***		Phasianidae	169-0.014****	
Pachycephala+	26-0.016**		Falconidae	59-0.013*	
Phalacrocorax	30-0.015**		Cisticolidae+	92-0.011*	
Sericornis+	12-0.015*		Laridae	119-0.011***	
Veniliornis	12-0.015*		Accipitridae	211-0.010**	
Metallura	6-0.014*		Alaudidae+	76-0.010***	
Carpodacus+	17-0.013*		Regulidae+	5-0.009*	
Haliaeetus	7-0.011*		Caprimulgidae	67-0.008*	
Charadrius	28-0.010**		Pteroclidae	15-0.008*	
Aegithalos+	5-0.010*		Anatidae	143-0.007**	
Caprimulgus	47-0.010*		Passeridae+	327-0.005***	
Regulus+	5-0.009*		*Sylviidae*+	4510.008***	
Dryocopus	7-0.009*		*Certhiidae*+	870.013**	
Cranioleuca+	17-0.009*		*Scolopacidae*	820.014***	
Progne+	6-0.007*		*Bucerotidae*	480.074*	
Zonotrichia+	5-0.007*		Orders		
Dendroica+	27-0.005**		Coraciiformes	132-0.023*	
Parus+	470.007***		Apodiformes	85-0.020**	
Bradypterus+	150.009*		Gruiformes	156-0.020**	
Pheucticus+	60.010*		Strigiformes	235-0.014**	
Icterus+	240.011*		Galliformes	206-0.014****	
Anser	100.012*		Anseriformes	156-0.006**	
Pipilo+	70.015*		*Ciconiiformes*	9070.006***	
Alcippe+	130.017*		*Struthioniformes*	100.069**	

Supplementary Table S5: Chi-square tests for differences in migratory behaviour between bird species in a) tropical-subtropical and b) temperate-polar climates. The bird species are divided by body-size quartiles (Q1 – Q4). Values are the observed numbers of species in each category and values in italics are the expected numbers. Significant departures from expected values (see Table 1 for levels) were tested using the normal approximation of the standardized Pearson residuals and are shown in bold.

	Q1	Q2	Q3	Q4
a) tropical and subtropical climates ($\chi^2_6 = 31.31$, $p < 0.0001$)				
Resident	396.0	481.0	479.0	446.0
	367.2	*474.0*	*482.3*	*478.5*
Other[1]	**84.0***	138.0	131.0	**171.0****
	106.8	*137.8*	*140.2*	*139.1*
Migrant	8.0	11.0	**31****	19.0
	14.1	*18.2*	*18.5*	*18.3*
b) temperate and polar climates ($\chi^2_6 = 29.79$, $p < 0.0001$)				
Resident	13.0	9.0	19.0	47.0
	21.0	*8.9*	*17.0*	*41.1*
Other[1]	27.0	9.0	33.0	85.0
	36.7	*15.6*	*29.7*	*71.9*
Migrant	**54.0****	22.0	24.0	**52.0***
	36.3	*15.4*	*29.3*	*71.0*

1 – Includes partial migrants, nomads, and elevational migrants

Online Appendix 1 – List of references for avian body sizes, organised by document type.

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