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Bergmann's rule in global terrestrial vertebrates

Qinfeng Guo[1,*], Hong Qian[2], Pengcheng Liu[3], Jian Zhang[4]

[1]USDA FS – Southern Research Station, 3041 E. Cornwallis Road, Research Triangle Park, NC 27709, United States
[2]Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, United States
[3]Center for Global Change and Complex Ecosystems, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
[4]School of Life Sciences, Sun Yat-Sen University, Guangzhou 510275, P. R. China

[*]Corresponding author. USDA FS – Southern Research Station, 3041 E. Cornwallis Road, Research Triangle Park, NC 27709, United States. E-mail: qinfeng.guo@usda.gov

ABSTRACT

To date, whether Bergmann's rule, initially developed for individual species or closely related taxa, can be applied to broader taxa remains elusive. Using global distribution data for birds, mammals, reptiles, and amphibians, both species- and assemblage-based, we examined the role of species richness and related climate variables in shaping body size patterns across the globe and the Northern Hemisphere only and whether the temperature–body size relationship had a phylogenetic signal. The results show that when species in all four classes were combined, body size increased with latitude but declined with temperature, consistent with Bergmann's rule. Each group showed somewhat unique patterns but was mostly consistent with Bergmann's rule. The body size–temperature relationships were not constrained by phylogenetic relatedness. Warmer places had both large and many small-bodied species, whereas cold places had proportionally more large species. The temperature-dependent variations in body size have important implications for macroecology under climate change.

Keywords: assemblage; body size; latitude; taxonomic scale; tetrapod

INTRODUCTION

Body size has long been among the key terms and subjects in ecology and biogeography, with many ecological and evolutionary consequences and implications for conservation (Peters 1986, Bonner 2007, Noonan *et al.* 2020). The original work of macroecology mainly focused on how species divide food and other resources within and across spatial and temporal scales (Brown 1995). Following the main tenets of this subfield, macroecological patterns are driven primarily by species diversity (or richness) and the abundance of each component species, which are closely related to body size and range size (Brown and Maurer 1989, Brown 1995, Gaston and Blackburn 1996).

Among the few most important, oldest, and yet frequently debated rules (or 'laws') in ecology and evolutionary biology is Bergmann's rule (Bergmann 1847). This rule states that individuals of the same species or closely related taxa (clades) are larger in cooler than in warmer climates (Meiri and Dayan 2003). The primary reasoning behind this rule is that large body size increases the volume-to-surface ratio, thus maximizing metabolic heat retention in animal bodies. In the past, Bergmann's rule has been commonly tested using body size data of individuals or populations within a species (Ashton and Feldman 2003, Adams and Church 2008) or mean species body size data among target species (Clauss *et al.* 2013). The rule has been mostly supported by studies of some taxa of birds and mammals (He *et al.* 2023) but rejected in studies of other taxa or groups such as small-sized mammals (Meiri and Dayan 2003) and lizards and snakes (Ashton and Feldman 2003). However, it has never been clear how general the rule may be applied to all species of tetrapods (i.e. all four classes of birds, mammals, amphibians, and reptiles combined) (Kingsolver and Huey 2008).

Most previous studies testing Bergmann's rule have focused on smaller taxonomic groups (e.g. snakes) and/or a particular region (e.g. North America) (Blackburn and Gaston 1996, Ten Caten *et al.* 2023). Such studies found inconsistent results (Meiri and Dayan 2003, Ten Caten *et al.* 2023) partly because the spatial and/or taxonomic scales do not cover the full, or a large portion of, potential underlying ecological or environmental gradients (Guo *et al.* 2023). Earlier studies found differences or inconsistencies between (i) warm- and cold-blooded species (see references in Olalla-Tarraga *et al.* 2011) and (ii) different subgroups (some follow while others do not follow the rule). Many earlier studies based on specific regions or smaller species groups found

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no support for Bergmann's rule, even though the rule may be at work.

Bergmann (1847) stated that the rule should exist among closely related species. However, when inconsistency is continuously observed in new studies, ecologists and biogeographers would like to know to what (taxonomic) level the close relatedness is relevant in terms of the degree following Bergmann's rule (i.e. individuals within a species, species in a genus, family, suborder, order, class, or even all terrestrial vertebrates). One potential approach to answering such questions is to combine all the species in these hierarchical taxonomic scales for analysis. In other words, whether Bergmann's rule may apply depends on what suborders or subgroups (and the proportion of each in the assemblage) are included in the analysis. In addition, it is expected that if a species or a species group only occurs in limited latitudes (or short ecological gradients), the chances of finding that they follow Bergmann's rule would probably be small. However, larger species groups (broader taxonomic scope) often occupy larger geographical areas and cover longer environmental gradients, thus having a greater chance of supporting Bergmann's rule (Ashton and Feldman 2003).

Previous studies have shown that many ecological and functional traits, including body size, are phylogenetically constrained (Qian and Zhang 2014, Johnson *et al.* 2023). For example, in the mammalian class, the body sizes of different species within the family Canidae, to which dogs belong, are more similar to each other than to those of species in the family Elephantidae, to which elephants belong (Etard *et al.* 2020). However, whether the relationship of body size to latitude or temperature is phylogenetically constrained (i.e. whether more closely related lineages have more similar relationships of body size to latitude or temperature) has rarely been examined (de Queiroz and Ashton 2004).

In this study, we use body size data for global terrestrial vertebrates to test if Bergmann's rule exists at the superclass (all terrestrial vertebrates, mostly Tetrapoda) level. We do this using species- and assemblage-based datasets separately. We hypothesize that while inconsistent patterns have been observed in different terrestrial vertebrate groups as recently revealed (e.g. Ashton and Feldman 2003, He *et al.* 2023, Johnson *et al.* 2023), when all terrestrial vertebrates are considered together, the pattern would follow Bergmann's rule, but the pattern may be moderate. [This is because all species together in the tetrapods cover much broader latitudinal or temperature gradients than any single class, providing ideal conditions to show Bergmann's rule; but at the same time, since ectotherms (which may not follow the rule as strongly as endotherms do) are included in analysis, the overall support may be reduced to some degree (Zamora-Camacho *et al.* 2014).] We also examine whether the relationship of body size to latitude or temperature is phylogenetically constrained.

Testing whether a 'rule' originally developed with certain restrictions could be applied to one or all three categories (within species, among closely related species, and all species in large taxonomic groups) is still a major task in macroecology. Previously, de Queiroz and Ashton (2004) evaluated species-level heritability and early origination of Bergmann's rule based on the phylogenetic signal in body size of 352 tetrapod species. To our knowledge, no study has examined the applicability of Bergmann's rule for all global terrestrial vertebrates as one taxonomic unit (i.e. the superclass Tetrapoda) including the vast majority of the species of the unit. In addition to the inconsistency and controversy among studies focusing on smaller groups and/or particular regions, it is useful to test how broadly Bergmann's rule may be applied, for instance, to much larger groups such as Tetrapoda and at the global or hemispheric scale. We expect that when smaller groups are taken together for consideration, the evidence that supports or rejects Bergmann's rule that is observed in smaller individual groups may not be enhanced because large groups often include some small groups that follow Bergmann's rule and other small groups that do not, which would cancel opposing patterns otherwise conspicuous in either case. After detecting any possible broad patterns, we then examine how climate (mean annual temperature and mean annual precipitation) and species richness may affect the body size of terrestrial vertebrates.

We adopt two commonly used approaches to test the applicability of Bergmann's rule, i.e. the species- (Ashton and Feldman 2003) and assemblage-based (Olson *et al.* 2009, Mähn *et al.* 2023) methods. The first is straightforward and most commonly used. The second approach is based on the fact that when all land surface of the globe is divided into equal-area grids, most species (except for extremely rare species with very small ranges) will share grids, especially among neighbouring grids, and thus to some degree all grids would be interconnected. Also, species composition in the grids may not be 'random', and to some extent it is determined by biotic interactions such as competition, mutualism, species infestations (e.g. by diseases, insects, and pathogens), and predation, following the 'assembly rule' (Cody and Diamond 1975). In other words, there are reasons that proportionally more species with large body sizes can be concentrated in colder places, i.e. not simply through random immigration or dispersal. In addition, previous studies confirm that patterns of body size variation in response to climate at the individual species level could be transferred or reflected to the community level (Millien *et al.* 2006). For these reasons, but especially for comparisons with the species-based approach (e.g. Mähn *et al.* 2023), the assemblage-based approach (Olalla-Tárraga *et al.* 2010) is commonly used in related studies.

MATERIALS AND METHODS

This study included species in four terrestrial vertebrate classes or tetrapods (i.e. birds, mammals, reptiles, and amphibians). We used both species- and assemblage-based data. For the species-based dataset, the species range maps of birds were obtained from BirdLife International (2021) and those of the other three vertebrate classes from IUCN (2022). For each species, only its breeding distribution range was considered in this study. We obtained the body size data (mass, g) from Wilman *et al.* (2014), Pincheira-Donoso *et al.* (2019), Etard *et al.* (2020), Pincheira-Donoso *et al.* (2023), and Johnson *et al.* (2023). However, it should be noted that, unlike birds and mammals for which body weight is measured directly, for amphibians and reptiles, mass is usually calculated from snout to vent length (SVL; Santini *et al.* 2018) based on an established conversion formula, rarely

from direct measurements. Nevertheless, the body sizes of all species used in this study are in grams. This study included all species of terrestrial vertebrates for which geographical distribution and body size data are available from the afore-cited literature (24 236 in total, birds = 8251, mammals = 4414, reptiles = 6740, amphibians = 4831), which accounts for about two-thirds of the extant species of terrestrial vertebrates worldwide.

In the assemblage-based dataset, the global terrestrial regions were divided into 300 × 300-km grid cells based on the Mollweide (equal-area) projection. After excluding grid cells with < 50% of land or no terrestrial vertebrate species, a total of 1469 grid cells were included in this study. We recorded the number of species in each grid cell and calculated the mean body size (mass in g) for the grid cell. Bergmann's rule has often been described using latitude (mainly as a surrogate of temperature). However, it is widely recognized that latitude per se has little biological meaning; it is a surrogate of the environment, particularly temperate (Rosenzweig 1995). Accordingly, we related body size to latitude in one set of analyses in order to facilitate comparison of the results of this study with those of related studies based on latitude on the one hand; our main analysis examines the relationship between body size and temperature on the other hand.

Several previous studies showed that minimum temperature (e.g. the mean temperature of the coldest month) and temperature seasonality might have a stronger association with species distributions or measures of life history traits than mean annual temperature (MAT) (e.g. Johnson *et al.* 2023). However, the three temperature-related variables are strongly correlated (the absolute value of Pearson's correlation coefficient is often greater than 0.9, based on the CHELSA dataset at https://chelsa-climate.org/bioclim), and many studies on body size have solely used MAT (e.g. He *et al.* 2023). Here, in addition to using MAT in our primary analyses, we also reported the relationships of body size with the mean temperature of the coldest month and temperature seasonality. To assess the possible contributions of precipitation, we also included annual precipitation (AP) and precipitation seasonality in our study. We obtained climate data from CHELSA (Karger *et al.* 2017). The mean value of each variable was calculated for each grid cell using data at 30-arc-second resolution. For a given climatic variable, its mean value for each species was calculated using all the grid cells in which the breeding range of the species was present.

To test Bergmann's rule, we first used the body size data in the species-based dataset with body size and centroid latitude. We then used the assemblage-based data with the mean body size of all species in the grid cell. The unique feature here was that we included all living species of terrestrial vertebrates for which geographical distribution and body size data are available, and the links between latitude and body size were examined at a global scale.

We examined latitude–body size correlations (Pearson's r) (i) across the entire globe (using the absolute latitude) and (ii) within the Northern Hemisphere and Southern Hemisphere, separately, for comparative purposes. To assess whether the relationship between body size and latitude (or temperature) is phylogenetically constrained, we calculated Pearson's correlation (r) between body size and latitude (or temperature) for species within each family. To achieve more robust results that could also support the observations at the global scale, this analysis only included the Northern Hemisphere and only included those families that each had more than 50 species in the Northern Hemisphere. In this analysis, the reason why we focused on the Northern Hemisphere was mainly due to greater gradients of latitude and temperature in this hemisphere than in the Southern Hemisphere (see Supporting Information Fig. S1); and the reason why we selected families with 50 species in the Northern Hemisphere was to maximize the robustness of the result of the analysis by balancing the average length of gradients of temperature and the sample size of the analysis (on the one hand, selecting families with a smaller number of species per family would include more families and thus increase sample size but would include shorter gradients of latitude and temperature, which may reduce the robustness of the result of the analysis; on the other hand, selecting families with a larger number of species per family would increase the length of the gradients on average, which would benefit the test of Bergmann's rule, but would reduce statistical power due to reduction of the number of families and thus sample size of the analysis).

A total of 63 families were included in this analysis (14 for amphibians, 27 for birds, nine for mammals, and 13 for reptiles). We extracted a family-level phylogenetic tree including these families from the 'Tree of Life' reported by Hedges *et al.* (2015) and used Pagel's λ (Pagel 1999) to assess whether Pearson's correlation between body size and temperature has a phylogenetic signal using the function phylosig in the package phytools (Kembel *et al.* 2010). A value of 0 indicates a random distribution of Pearson's correlation with respect to the phylogeny (i.e. no phylogenetic signal), whereas a value of 1 indicates that the distribution of Pearson's correlation values across the phylogeny matches expectations under the Brownian motion model and is strongly constrained by phylogenetic relatedness. In addition to assessing the phylogenetic signal for all 63 families of vertebrates as a whole, we also assessed the phylogenetic signal for families in each class separately, using the phylogenetic tree only, including the families of the class under investigation.

We used general linear regression, Pearson's correlation analysis, and structural equation modelling (SEM) to explore the direct and indirect effects of key biotic (species richness) and abiotic (MAT and AP) variables on body size based on grid data. We used the R package 'lavaan' (cran.r-project.org/web/packages/lavaan) to conduct SEM and the package Spatial Analysis in Macroecology (www.ecoevol.ufg.br/sam) to conduct simultaneous autoregressive error models. Log_{10} transformation of original data was performed where appropriate.

RESULTS

Globally, despite the major differences in mean body size and many other life history aspects among global terrestrial vertebrate species, when all species were combined in analysis, Bergmann's rule seemed at work; that is, species body size was larger at higher latitudes, regardless of whether the data were analysed using the species- or assemblage-based approach.

Patterns derived from species-based data

For all terrestrial vertebrate species examined in this study, the latitudinal trends in body size in species-based data followed Bergmann's rule (Fig. 1). Regression analyses using absolute latitude revealed that tetrapods showed clear latitudinal trends across the globe in supporting Bergmann's rule (r = .11, P < .0001). Analyses using data from the Northern and Southern Hemispheres separately also showed similar results (r = −.16, P < .0001, and r = .02, P = .022, respectively) (Fig. 1A).

Body size had a significant negative relationship with MAT (global: r = −.10, P < .0001). While both hemispheres exhibited similar trends, the relationship in the Southern Hemisphere was not significant (Northern Hemisphere: r = −.16, P < .001; Southern Hemisphere: r = −.01, P = .21; Fig. 1B).

At the species level and global scale (i.e. across both Northern and Southern Hemispheres), global curve fitting and loess smoothed curves showed that species of tetrapod seemed to show some level of support for Bergmann's rule (Fig. 2). Small-sized species were mostly found at lower latitudes (or warmer places) whereas large-sized species were found at both lower and higher latitudes (i.e. across much broader latitudinal extents; Mann–Whitney Rank Sum Test on 200 smallest vs. 200 largest species, T = 45 919, P < .001; Fig. 2).

Patterns derived from assemblage-based data

Using assemblage-based data that included all global terrestrial vertebrates, body size had a significant relationship with MAT (global: r = −.29, P < .001; Northern Hemisphere: r = −.30, P < .001). In addition, the assemblage-based latitudinal trends in body size were also clear (global: r = .28, P < .001; Fig. 3). Assemblage-based data from the Northern Hemisphere showed a similar latitudinal pattern (r = .19, P < .001). Spatial autocorrelation made little contribution to our observed patterns. For example, when body size and MAT were both standardized to zero mean and unit variance, the standardized coefficient derived from an ordinary least square (OLS) model was very similar to that derived from a spatial autoregressive (SAR) error model (−.288 vs. −.296, respectively; P < .001 in both cases).

The results from SEM showed that MAT and AP directly and negatively affected the mean body size of terrestrial vertebrates (Fig. 4).

Phylogenetic signal

The relationship (Pearson's r) between body size and temperature varied greatly among the 63 selected families across the four vertebrate classes (Pearson's r ranging from −.51 to .32; Fig. 5). Support for Bergmann's rule was found in 40 families. When all 63 families were included in an analysis assessing phylogenetic signal in the relationship between body size and temperature, Pagel's λ on Pearson's r was .00007. When the families of the four classes of terrestrial vertebrates were analysed separately, Pagel's λ was < .0001 in all four cases. The fact that Pagel's λ was close to zero in all five cases indicates that the relationship between body size and temperature is not constrained by phylogenetic relatedness among different lineages (i.e. families in this study).

DISCUSSION

General and hemispherical patterns

We have observed some strong evidence supporting Bergmann's rule when all terrestrial vertebrates are analysed together. This is similar to a few recent studies that focus on other organisms (e.g. insects) or smaller vertebrate groups with inconsistent results (e.g. Ten Caten *et al.* 2023) especially when different analytical approaches are used. Unlike most previous studies focusing on smaller species groups (from a genus or family to an order), this study focuses on a much larger taxonomic scale (all tetrapods). When target taxonomic groups are small (e.g. orders, families, the groups within each class), the exceptions to the 'rule' would inevitably increase. This has appeared in our study when analysing the 63 selected families. This is mostly because, in general, smaller groups have small sample sizes (the number of species and/or grids) and are likely to occupy smaller latitudinal extents, and thus shorter environmental gradients. For this reason and to be eco-evolutionarily meaningful, large taxonomic groups should be used to test most ecological rules. Nevertheless, even

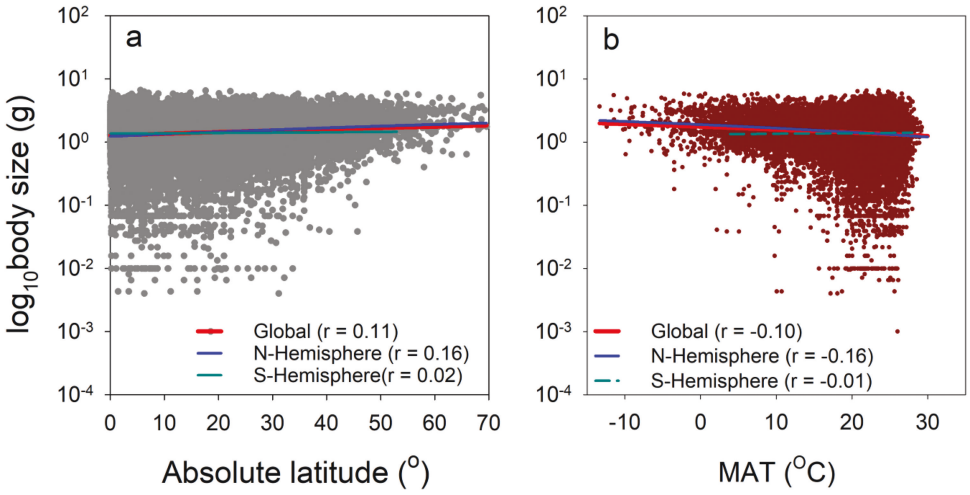

Figure 1. Latitudinal trends in body size of all terrestrial vertebrates (each dot is a species). The latitudinal trends show that many small-sized species are lacking at high latitudes, partly because of Bergmann's rule and the fact that high species richness at low latitudes needs to include many small-sized species.

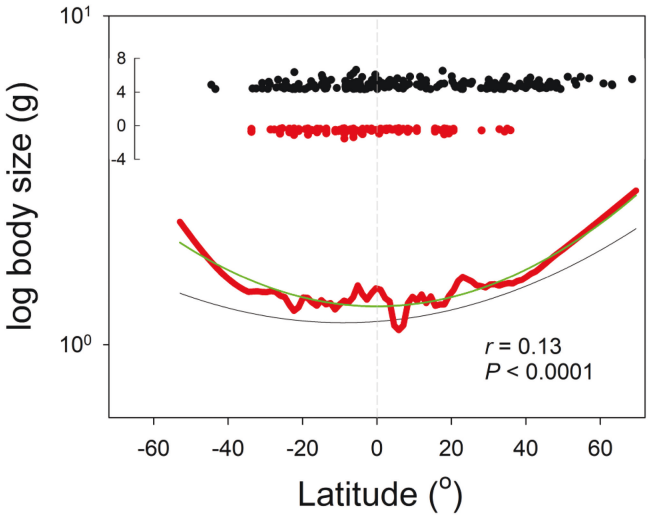

Figure 2. Comparison in species-based latitudinal variation in body size of terrestrial vertebrates across the globe and between Northern and Southern Hemispheres (each dot is a grid). The red line represents loess smoothed curves (sampling proportion = 0.1) based on bandwidth using nearest neighbours, the green line is the global fitting polynomial regression curve, and the grey line represents the second-order regression curve (r = .13). Red and black dots in the inset panel represent the latitudinal distribution of the 200 smallest and 200 largest terrestrial vertebrate species, respectively.

in family-level lineages, our study showed that most of the analysed families support Bergmann's rule.

Testing and explaining within-species body size patterns seem more straightforward but difficult for species with highly restricted ranges (i.e. rare species) due to the short temperature gradient within their ranges (e.g. many cases in the Southern Hemisphere; Supporting Information Fig. S1) (Guo *et al.* 2023). In general, although both within- and among-species patterns show a certain level of support for Bergmann's rule, it seems that within-species patterns are stronger than those found among species, at least for mammals (Ashton *et al.* 2000). Among-species comparisons include species- and assemblage-based approaches, each offering unique insights and having advantages and disadvantages. The former uses the species' centroid latitude to represent the species' latitude; thus, species with very large ranges (usually with large body sizes) may have a midlatitude around 20–40° but may occur across most latitudinal zones. This could obscure true among-species latitudinal patterns in body size. The assemblage-based approach can test whether species in a cold area (at a high latitude) have larger body sizes than those in a warm area (at a low latitude). Because these two approaches are complementary to each other, using both approaches in our study has enabled us to reach more robust conclusions.

Possible causes

In general, the warmer places (e.g. tropics) have both large and many more small-bodied species, whereas cold places at higher latitudes have proportionally more large species. Such a latitudinal difference in body size distribution itself could be partly responsible for the overall global assemblage-based patterns. Additionally, not only could different species groups within a large taxon show different patterns in body size–MAT (or latitude) relationships, as shown in our analysis using the 63 individual families, but within the same large taxon, species with small body sizes could also show different patterns from those with large body sizes. For example, Meiri and Dayan (2003) found that small-sized mammals are somewhat less likely to follow Bergmann's rule than larger mammals (but see McNab 1971, Ashton *et al.* 2000, Clauss *et al.* 2013).

For several reasons, some earlier studies do not support Bergmann's rule. First, many earlier studies using short latitudinal extents (although some small groups only cover small extents) found no support for Bergmann's rule, even though the rule may be at work. Second, it may be true that some subgroups in a taxonomic class follow Bergmann's rule while others do not, as shown in our analysis based on the 63 families of terrestrial vertebrates. Whether a large group follows the rule depends on what subgroups are included in the study. Third, it is possible that the mechanisms underlying Bergmann's rule may well be operating in certain situations (McQueen *et al.* 2022), but due to opposing or off-setting effects, the evidence for the rule may have been overshadowed or cancelled. For example, in species-rich habitats or under warm conditions, not all species can have large sizes simply due to competitive exclusion (they may consume similar food or prey of similar sizes) and, consequently, some species are forced to have smaller sizes (McNab 1971, Liu *et al.* 2023).

In addition to the aforementioned factors (reasons), the comparison between this study and several earlier findings raises other key questions regarding testing Bergmann's rule (and other ecological and evolutionary 'rules') that need to be addressed in future studies. First, the effects of temperature on body size could be explored in multiple ways, and using different temperature measures (see below) could lead to somewhat different conclusions (Table 1). Like many related biotic variables, the body size of the same species could show different responses to daily (daytime vs. nighttime), monthly (the warmest vs. the coldest), seasonal (winter vs. summer or temperature in wet vs. dry seasons), and annual (mean or extreme) temperatures. Second, some studies use seasonality or variation in temperature (e.g. daily, seasonal, annual, decadal) and find it more important than mean temperature (e.g. Johnson *et al.* 2023). Yet, across latitudes, seasonality is inversely related to temperature (Sobel 2012); that is, colder places or higher latitudes usually show greater seasonality than the tropics (Conover 1992), and seasonality in temperature itself also has various measures and meanings (Chown and Klok 2003) and can also be used in different ways (e.g. the differences between the warmest and the coldest months in a year). For example, Wang *et al.* (2011) found that the relationship between the mean temperature of the warmest month and a biological metric (e.g. species richness) is much weaker compared to the mean temperature of the coldest month or quarter. Our study shows that the strength of the relationship between body size and the mean temperature of the coldest month is very similar to that of body size with MAT in the world's terrestrial vertebrates (Table 1).

In the past, environmental variables such as temperature, seasonality, precipitation, and resource availability, among others, have been used to explain the latitudinal body size patterns (Ashton and Feldman 2003, Mähn *et al.* 2023, Guo *et al.* 2024).

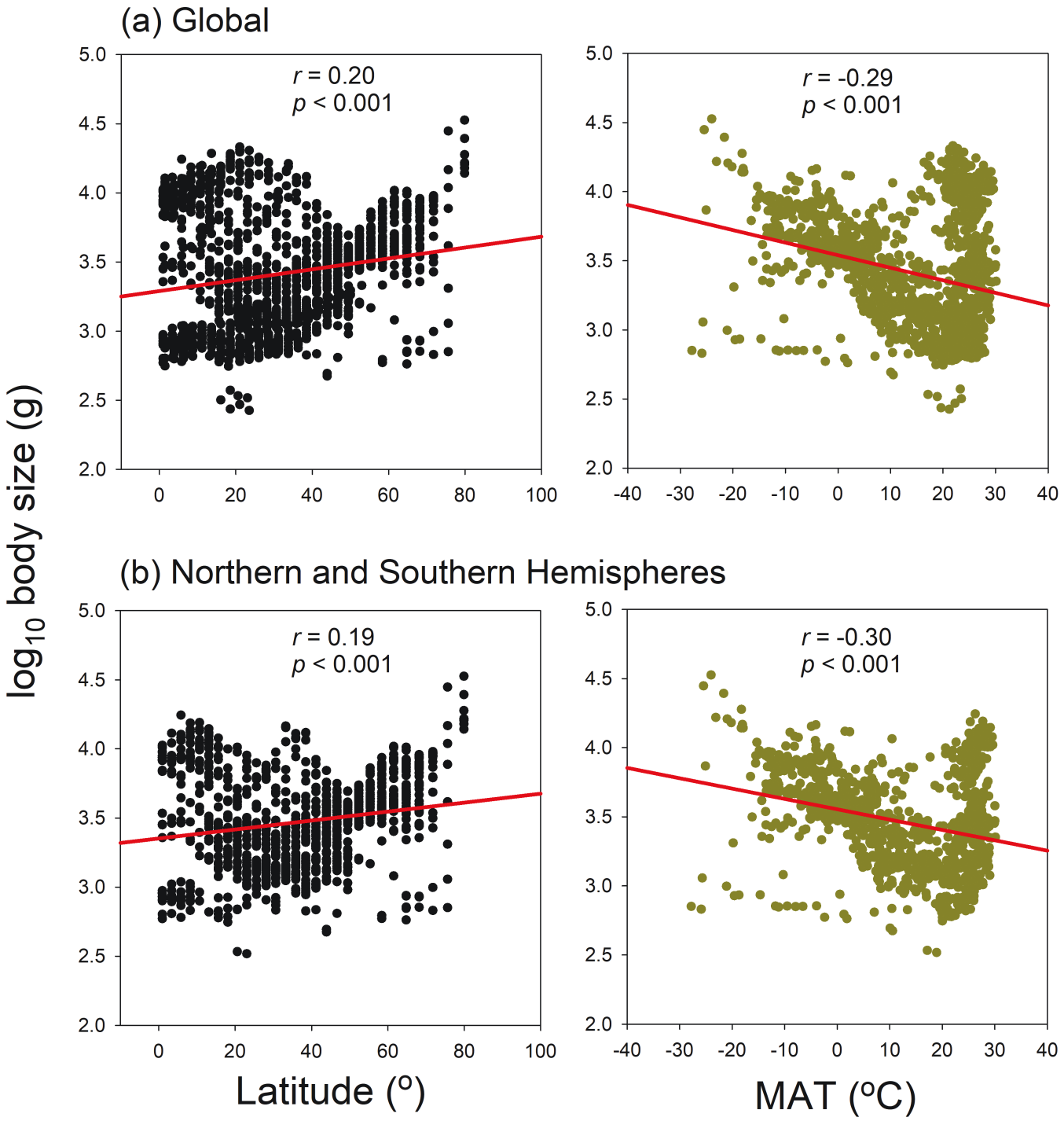

Figure 3. Assemblage-based global patterns of body size of the world's terrestrial vertebrates and relationships with mean annual temperature (MAT) across the globe (A) and Northern Hemisphere (B). Each dot represents a grid.

However, the selected climate (or environmental) variables are often interrelated to each other and latitude; thus, it is difficult to determine which one is more important. Biologically, competition and prey size have also been used, but we particularly stress the role of competition; that is, when species richness is high, even though the environmental conditions may favour large species, not all species can have large sizes simply because of competition (Olson *et al.* 2009, Lyons and Smith 2013). In such environments, being small could have advantages to avoiding competition with large species by consuming abundant smaller prey or different resources that large species may not prefer (i.e. niche differentiation). The generally negative relationship between richness and body size may help explain the differences in the body sizes of tropical species. To test this hypothesis, future studies could examine the size differences of the same species in species-rich versus species-poor habitats.

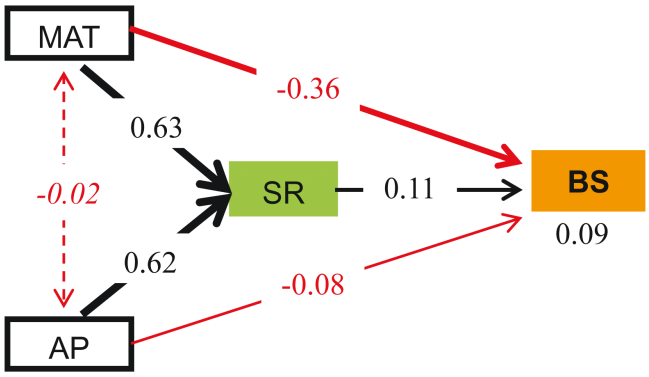

Figure 4. Direct and indirect relationships among climatic variables (mean annual temperature and annual precipitation, i.e. MAT and AP, respectively) and biotic variables (species richness and mean body size, i.e. SR and BS, respectively) based on results from structural equation modelling (SEM). AP, SR, and BS were $\log_{10}$-transformed.

The role of phylogeny

Our study showed that the relationship between body size and temperature (and thus latitude) is not constrained by phylogenetic relatedness among different lineages of tetrapods. This finding appears inconsistent with that of de Queiroz and Ashton (2004) who showed that there is a significant phylogenetic signal for the relationship between body size and latitude when data from 352 tetrapod species were analysed. However, because our study examined Bergmann's rule among species within family (i.e. interspecific) whereas their study examined Bergmann's rule among individuals within species (i.e. intraspecific), the results of these two studies may not be comparable.

We should point out that the effects of phylogenetics on body size could also be examined in different ways, and there is still a lack of consensus regarding how phylogeny or phylogenetics should be used in ecological studies (Tucker *et al.* 2017). For example, whether and how phylogenies (e.g. which matrices) are included in the analysis as a covariate or random factor in the models is still debatable. If a selected phylogeny is included as a random variable, the resulting relationships of body size to temperature reflect the 'residual', not actual, relationships after accounting for the variation of body size caused by different evolutionary histories among different species. If the relationship between body size and latitude or temperature remains significant after accounting for phylogenetic relatedness among species, this implies that the relationship between body size and latitude or temperature supporting Bergmann's rule is robust to the effect of phylogenetic relatedness among species, as shown in He *et al.* (2023) for global birds and mammals. However, if the result is derived from an analysis in which phylogeny is included as a covariate or random factor and is not significant, the result may not be used as evidence to reject Bergmann's rule. This is partly because the 'rule' is designated to explain the relationship between body size and latitude or temperature for closely related individuals (e.g. individuals within a species) or closely related taxa and partly because body size has a strong phylogenetic signal. When the variation of body size caused by phylogenetic relatedness is statistically accounted for in an analysis, the actual relationships between body size and latitude or temperature naturally become much weaker or do not exist because the relationship predicted by Bergmann's rule might have been masked by strong phylogenetic relatedness in body size among species.

Thermal adaptation and eco-physiological consequences

In contrast to the original intent of Bergmann's rule formulated for endotherms that need smaller surface-area to volume ratios (or larger body size) to preserve heat in colder environments, accumulative evidence shows that some ectotherms also follow the rule, although to a lesser degree (Ashton and Feldman 2003, Audzijonyte *et al.* 2020). This may explain the overall support for Bergmann's rule when all species of tetrapod with 12 665 (52%) endotherms and 11 571 (48%) ectotherms were assessed. As different world regions are warming up differently and and species in each region show varying adaptabilityability (King *et al.* 2020, McQueen *et al.* 2022), the global and regional patterns in species body size may change accordingly. For example, species in the arctic region and high mountain tops may be drastically affected by a faster pace of climate warming, and thus body size distribution may be shifted (King *et al.* 2020).

Whether a species group follows Bergmann's rule has significant ecological consequences. Following Bergmann's rule, climate warming may lead to multiple consequences such as: (i) shrinking body size; (ii) more small species (due to the extinction or population reduction of larger coexisting species or predators), or population reduction of larger coexisting species or predators; and (iii) greater dominance of small species in local communities (Tan *et al.* 2021, Verberk *et al.* 2021). If an organism's body size can adapt to climate warming quickly enough (Millien *et al.* 2006, Herrera *et al.* 2022), using latitude to assess the applicability of Bergmann's rule may become less valuable, especially if warming trends are more prominent at higher latitudes (Deutsch *et al.* 2008, Pörtner *et al.* 2022, Liu *et al.* 2023). The changes related to body size distribution are closely associated with intra- and intertrophic interactions such as competition and predator–prey interactions, especially when more large-bodied species may shift towards higher latitudes or altitudes following climate warming (Treasure and Chown 2014). The key question now is whether the new latitudinal trends in body size when species' range shifts are considered still follow Bergmann's rule.

Future directions

Future studies should examine why some species groups follow Bergmann's rule while others do not. For example, although the mechanisms behind the rule are still at work, it is difficult to assess the applicability of the rule if a particular species or species group only has a very small population size (i.e. with very few individuals) or very small ranges and latitudinal extents (Guo *et al.* 2023). Thus, at what level (group size) or taxonomic scales Bergmann's rule may apply and why different kinds of organisms show different patterns should continue to be the focus of related studies. A related question would be how climate change-related range (e.g. poleward) shifts may affect the applicability of Bergmann's rule in the future. Third, future studies need to explore how long it may take for a particular species or species group to vary in body size under projected climate warming and Bergmann's rule.

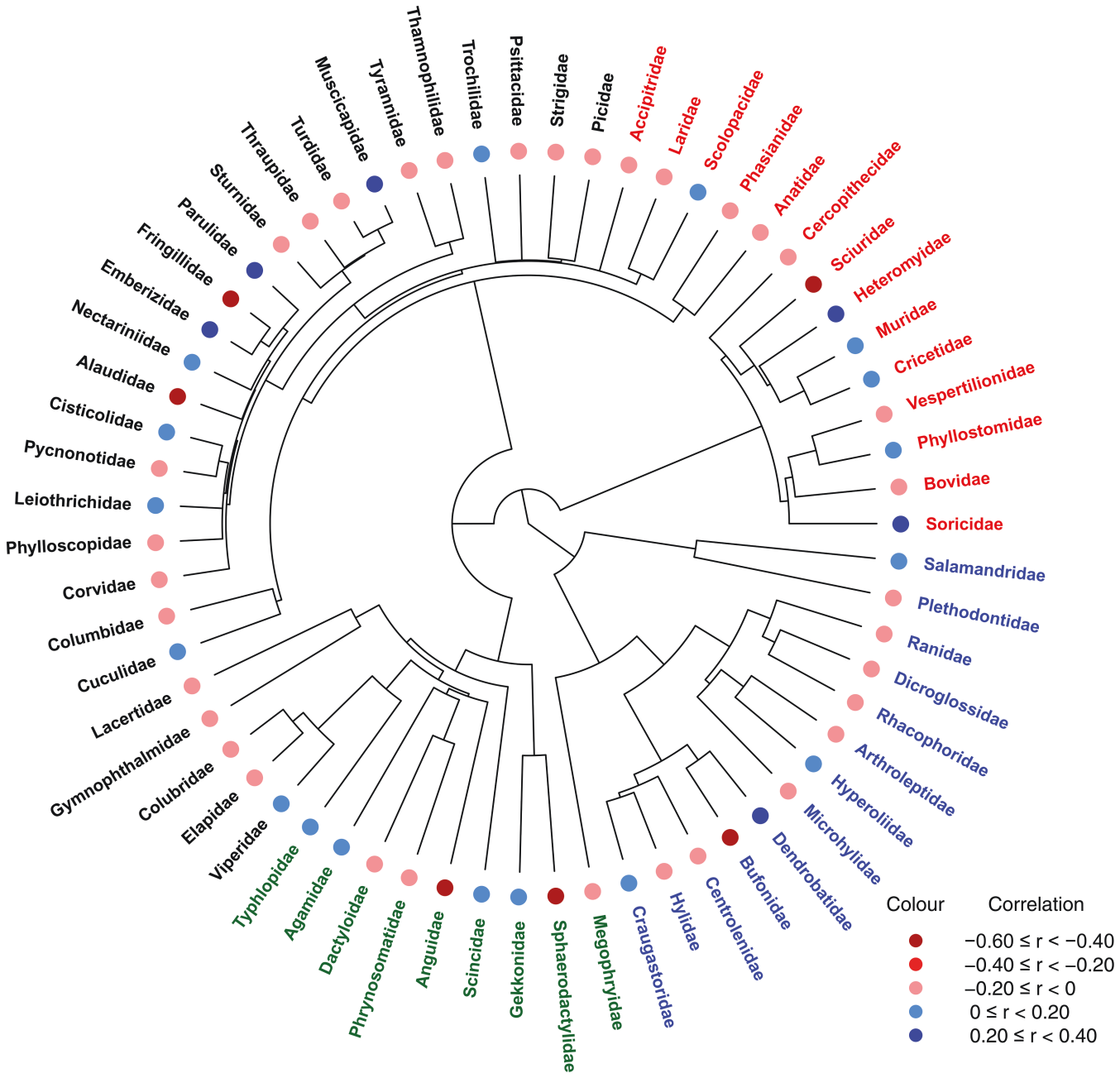

Figure 5. Phylogeny of the 63 families of terrestrial vertebrates used in testing phylogenetic signal in Pearson's correlation coefficient (r) between body size and mean annual temperature. Family names in red, black, green, and blue colours are amphibians, birds, mammals, and reptiles, respectively. Families with dots in the three warm colours are those for which the relationship between body size and temperature is consistent with Bergmann's rule.

Table 1. Pearson's correlation coefficient (r) and P-values for the relationship between log-transformed body size and each of five climatic variables for global terrestrial vertebrates.

Climatic variable	r	P
Mean annual temperature	−.101	<.001
Minimum temperature of the coldest month	−.124	<.001
Temperature seasonality	.134	<.001
Annual precipitation	−.065	<.001
Precipitation seasonality	.018	.005

Note that the five climatic variables are bio1, bio6, bio7, bio12, and bio15, respectively, in the CHELSA climate database (https://chelsa-climate.org/bioclim).

In summary, the body size–latitude (or temperature) relationships in terrestrial vertebrates seem to be consistent with Bergmann's rule. The results derived from species- and assemblage-based datasets are consistent, and the assemblage-based dataset generally reveals stronger latitudinal trends in body size than the species-based dataset. There is little phylogenetic signal in the relationships between body size and temperature among different families of vertebrates. Lower latitudes (or warmer places) support both small- and large-bodied species, but higher latitudes (or cold places) usually host species with larger body sizes. These observations offer new insights into macroecology and have deep implications for conservation, especially under climate change.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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AUTHORS CONTRIBUTIONS

Q.G. initiated the research. J.Z., P.L., and H.Q. collected data. Q.G., H.Q., P.L., and J.Z. analysed the data. Q.G. and H.Q. wrote the manuscript, and all authors contributed to the revision of the manuscript.

DATA AVAILABILITY

Open research: All data used in this study have been published. Sources and links to the data are provided in the manuscript: i.e. https://www.iucnredlist.org, http://datazone.birdlife.org/home, https://doi.org/10.6084/m9.figshare.10075421, https://doi.org/10.6084/m9.figshare.c.3306933.v1, and www.amphibianbiodiversity.org.

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