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Research Article

Body size variation of world's living terrestrial vertebrates in the Cenozoic

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Abstract Body size is among the key subjects in macroecology and macroevolution with important implications for conservation. Two major rules have been proposed to explain how body size changes over evolutionary time (Cope's rule) and across temperature gradients (Bergmann's rule). To date, however, the applicability of both rules to global terrestrial vertebrates (tetrapod) remains elusive. Here, using the newly available data, we comparatively examined the temporal variation in species body size of the world's extant tetrapod species (tetrapoda as a whole) and of each class, amphibians (Amphibia), reptiles (Reptilia), mammals (Mammalia), and birds (Aves), through the Cenozoic Era. When all four classes were considered together, the species' body size had increased over time and was negatively correlated with global surface temperature. However, separate analyses on each of the four classes showed that reptiles and mammals tended to support Cope's rule, while birds and amphibians did not. Also, we found no clear difference in temporal body size variation between endothermic and ectothermic species. Overall, the support for Bergmann's rule was much stronger than that for Cope's rule. Future research using more complete and compatible body size data from fossils is needed to better understand how species' body size evolves over time and across space.

Key words: Bergmann's rule, body size, climate change, Cope's rule, macroevolution, tetrapod.

1 Introduction

Understanding how species' body size evolves (i.e., macroevolutionary trends) and how environmental conditions may affect body size can help interpret multiple macroecological and biogeographic patterns and processes. To date, Cope's rule (also called Depéret's rule) (Cope, 1896; Roy et al., 2024) and Bergmann's rule (Bergmann, 1847) dominate related literature and are increasingly gaining attention. Cope's rule mostly describes that lineages of organisms tend to increase in body size over evolutionary time following a perceived intrinsic factor or benefit (i.e., bigger body is better) (Hone & Benton, 2005), while Bergmann's rule describes spatial patterns (body size is larger in colder places or higher latitudes due to an extrinsic effect of temperature—heat preservation, a well-established notion linked to the surface-to-volume ratio of body). Thus, while Cope's rule reflects the endogenic factors of lineages of organisms, Bergmann's rule describes how the environment (exogenic drivers) may shape a species' body size. Cope's rule could be perceived as supported when at least one of the following three phenomena is observed: (1) the "founder effect" due to the small size of the earliest species (ancestors) that form the taxon or clade (Padian & Chiappe, 1998), (2) the larger size of later-diverging species (Alroy, 1998; Raia et al., 2012), and (3) the higher survival rate of larger species over time (Sanisidro et al., 2023).

By definition and in practice, Cope's rule could only be tested using temporal (e.g., fossil or living species with geological age) data (Baker et al., 2015). In contrast, Bergmann's rule could be tested across both temperature and temporal gradients, although, to date, it has almost exclusively been tested using spatial data (e.g., across latitudes) (Meiri & Dayan, 2003). While these two rules describe variation in body size over different types of gradients, the links between the two and testing each are complicated by a common factor: global temperature change (Hunt & Roy, 2006). Temperature is directly related to testing Bergmann's rule but indirectly confounded with testing Cope's rule using historical data, as Cope's rule describes body size variation through evolutionary scale, for example, during the global climate cooling period in the Cenozoic (since early Eocene). To date, some studies support Cope's rule (Alroy, 1998; McShea, 2000; Kingsolver & Pfennig, 2004), while others do not (Arnold et al., 1995; Jablonski, 1997). Relatively, at least partly due to data availability, Bergmann's rule has gained broader attention and stronger support than Cope's rule (but see Ashton & Feldman, 2003).

Many studies related to Cope's rule have targeted mammals mainly because of anthropocentrism and because

they are endothermic (Guo et al., 2024a). However, most related studies have focused on smaller taxonomic groups (i.e., with fewer species), such as woodrats, during the past 25 000 years (Smith et al., 1995), 3321 living mammals (Baker et al., 2015), and 1169 cheilostome bryozoans in the past 150 million years (Liow & Taylor, 2019); all have invoked the biological mechanisms for Bergmann's rule. Based on mammal fossil data, Smith et al. (1995, 2010) show that body size variation with paleotemperature is consistent with Bergmann's rule. Indeed, most terrestrial vertebrates have a lifespan of less than 100 years (Austad & Finch, 2022). Thus, over thousands or millions of generations, if body size is at least partly regulated by temperature, evolutionary changes in body size would be typically shaped by environmental selection.

In the last few decades, studies testing Cope's rule on other terrestrial vertebrates such as birds (Butler & Goswami, 2008), reptiles (Hone & Benton, 2007; Benson et al., 2014), and amphibians have also been on the rise. However, most of these studies still focus on a single taxonomic level, although comparative analyses across taxonomic levels and on much larger taxonomic groups (i.e., with large number of species) are being called for (Gould, 1997; Hone & Benton, 2007). Here, we present quantitative analyses on comprehensive species phylogenetic age (estimated by divergence time) and body size data at both (1) superclass (all living terrestrial vertebrates, i.e., Tetrapoda) and (2) class levels (each of the four classes) and make direct comparisons. We also investigate whether endotherms (birds and mammals) and ectotherms (reptiles and amphibians) show different patterns in terms of body size variation over time. We then discuss possible mechanisms driving the temporal changes in species' body size in relation to Cope's rule and Bergmann's rule.

2 Materials and Methods

This study included all species of terrestrial vertebrates for which body size and divergence time data are available from published sources (24 236 in total, amphibians = 4831, reptiles = 6740, birds = 8248, mammals = 4417). These species account for about two-thirds of all the extant species of terrestrial vertebrates worldwide. Species names from different sources were standardized using the R package U.Taxonstand (Zhang & Qian, 2023; Zhang et al., 2025) and according to The Integrated Taxonomic Information System (https://ITIS.gov) for birds and Catalogue of Life (https://www.catalogueoflife.org/) for mammals, amphibians, and reptiles. We used the species body size data from the same sources as those used in Guo et al. (2024c). The body size data of each species (mass, g) were obtained from Wilman et al. (2014), Pincheira-Donoso et al. (2019), Etard et al. (2020), Johnson et al. (2023), and Pincheira-Donoso et al. (2023).

Because most species lack fossil records that can be used to determine the times of their originations, true species' ages remain unknown. Many studies have used a phylogeny-based approach to estimate ages for species (Davies et al., 2011; Alzate et al., 2025) or higher taxa (e.g., genera and families) (Lu et al., 2018; Ramirez-Barahona et al., 2020). Taxon ages derived from phylogenies are commonly called "phylogenetic age" or "divergence time" (Lu et al., 2018; Ramirez-Barahona et al., 2020). Species ages used in this study are phylogenetic ages of species examined. Specifically, the phylogenetic age of a species was defined as the divergence time of the species in a time-calibrated species-level phylogenetic tree, which was measured based on the length of the tip branch representing the species in a phylogenetic tree, an approach commonly used to estimate taxon age (Lu et al., 2018; Ramirez-Barahona et al., 2020). The estimated divergence time (T) is the stem age and may thus be considered as the maximum age of the species. Time-calibrated phylogenetic trees for amphibians, birds, mammals, and reptiles were obtained from the VertLife website (https://data.vertlife.org) (Jetz et al., 2012; Tonini et al., 2016; Jetz & Pyron, 2018; Upham et al., 2019). Details about how the divergence time or age of each species was derived were described in Guo et al. (2024b).

We used Mann–Whitney tests to examine the difference in body size between each pair of the four terrestrial vertebrate classes. We obtained the global surface temperature for the Cenozoic (the last 66 million years – Myr) from Hansen et al. (2013) and Westerhold et al. (2020). We used simple linear regression to examine the relationships between (1) species richness and time (Ma – million years ago) across the Cenozoic Era, (2) species divergence time (T) and body size, and (3) global surface temperature at species divergence time over the Cenozoic and body size. Body size data were Log_{10}-transformed before analyses.

We used Blomberg's K (Blomberg et al., 2003) to assess the phylogenetic signal of body size variation among species in the four classes of vertebrates. In addition to using ordinary least squares (OLS) model to assess the relationships of body size with divergence time and global temperature at the diversification time, we also used models accounting for phylogenetic relatedness among species to assess the relationships of body size with divergence time and global temperature at the diversification time. Specifically, we used Pagel's λ model, the Brownian motion model, and the Ornstein–Uhlenbeck model (Ho & Ané, 2014a, 2014b). The phylogenetic tree including the four groups of the terrestrial vertebrates was assembled based on the backbone of the four groups of the terrestrial vertebrates (Hedges et al., 2015), and individual phylogenetic trees of amphibians, birds, mammals, and reptiles were obtained from the VertLife website (Jetz et al., 2012; Tonini et al., 2016; Jetz & Pyron, 2018; Upham et al., 2019). We used the R function "phylosig" in the R package "phytools" (Revell, 2012) to assess the phylogenetic signal and the R function "phylolm" in the R package "phylolm" (Ho & Ané, 2014a) to conduct the phylogeny-based models.

3 Results

Most of the extant terrestrial vertebrate species (four classes: amphibians, reptiles, birds, and mammals) examined in this study were formed in the Cenozoic (from the Paleocene to the present). On average, amphibians had the longest divergence time, followed by reptiles, birds, and mammals. However, the species body size followed the

exact opposite order. In other words, at the class level, the group with the shortest divergence time had the largest body size (in all Mann–Whitney rank sum tests between each pair of the four classes, $P < 0.001$; Fig. 1, Table S1). The skewness in species body size frequency distributions (FDBS) was significant at both the superclass level (skewness for all tetrapods = 1.43) and within each of the four classes. The skewness increased from the class with a longer divergence time to that with shorter divergence time (i.e., 0.416, 0.575, 0.858, and 0.991 for amphibians, reptiles, birds, and mammals, respectively; Fig. 1).

Despite differences in the overall species richness (the number of species) among the four classes, species diversity in all classes was negatively correlated with species divergence time (in all cases, $P < 0.001$), except for species with very short divergence times (Figs. 2A, S1). However, different groups (classes) showed different patterns. For example, the peaks of rates of cladogenesis for amphibians, reptiles, birds, and mammals appeared to be around 7–10, 3–6, 2–4, and 1 million years ago (Ma), respectively (Fig. S1; Table S1).

Overall, the body size of the world's terrestrial vertebrates (when all four classes were considered together) increased during the Cenozoic Era (Table 1; Figs. 1, 2A, 3). During most of this period, the global climate was cooling (Fig. 2A). The results were consistent with Cope's rule, as the body size of species increased over time (i.e., the period used in this study; Fig. 2A). Across all tetrapods, linear regression revealed a negative relationship between the global ambient temperature of a species at the time when the species evolved and the body size of the species when all four classes were considered ($r = -0.27$, $P < 0.001$), that is, during the same period when terrestrial vertebrate species were formed (Table 1; Fig. 2B). This negative relationship appears to be consistent with Bergmann's rule. Simple linear regressions (ordinary least squares models) of body size on

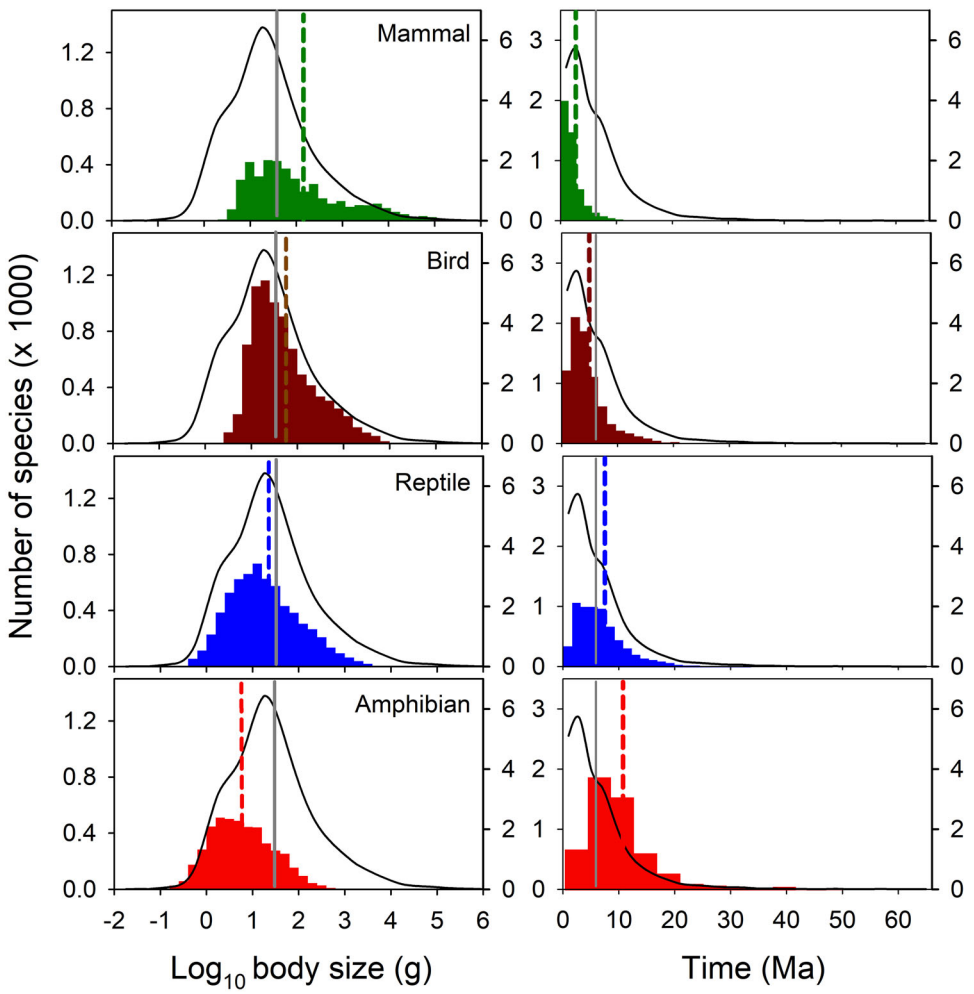

Fig. 1. Frequency distribution of species' divergence time (Ma) and Log_{10} body size (g) of the four classes of the world's living terrestrial vertebrates in comparison with that for all tetrapods represented by the dark gray curve. The vertical dashed line represents the mean for each class and the solid vertical line is the mean for all tetrapods. At the class level, the class with a longer divergence time has a smaller body size. Shapiro–Wilk tests show skewness of both Log_{10} body size ($W = 0.744$, $P < 0.001$) and divergence time ($W = 0.563$, $P < 0.001$) at both the superclass level (all tetrapods) and within each class (in all cases, $P < 0.001$).

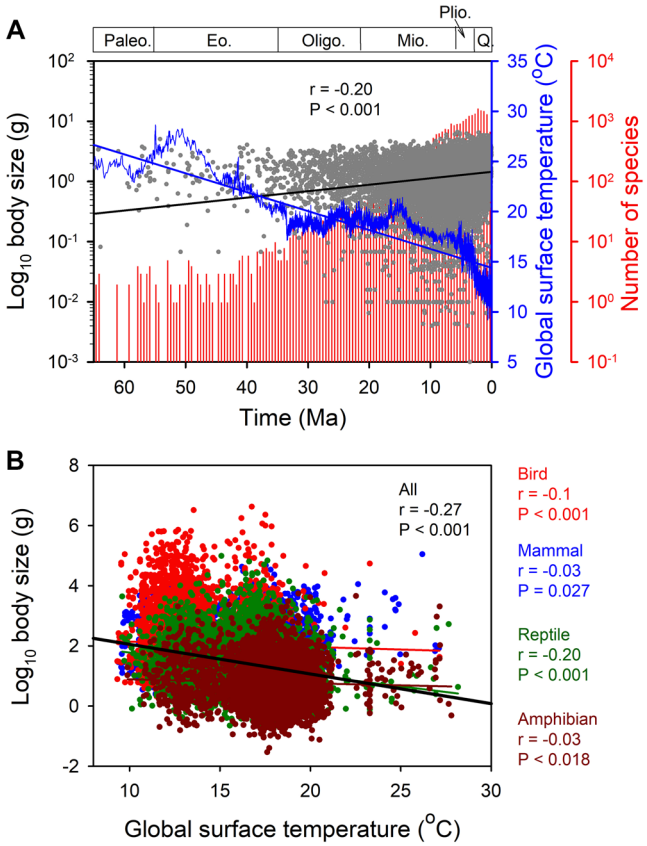

Fig. 2. Relationships of body size with species divergence time, global surface temperature variation, and species diversity. (**A**) Species divergence time (Ma) and global surface temperature variation (Ts), species diversity (the number of species), and Log_{10} body size (g) of the world's living terrestrial vertebrates (a total of 24 236 species in the superclass Tetrapoda) over the Cenozoic. Red vertical lines (bars) represent the number of species. (**B**) Negative relationship between the global surface temperature at the time when a species formed and the body size of the world terrestrial vertebrates at both superclass (the black line) and class levels. Note that species > 66 Myr were excluded from the analysis. Each dot represents a species.

Table 1 Results of regressions of Log_{10} body size (g) of global terrestrial vertebrates against divergence time (Ma) or global surface temperature (°C) at the divergence time based on an ordinary least squares (OLS) model, Pagel's λ (PL) model, the Brownian motion (BM) model, and the Ornstein–Uhlenbeck (OU) model with an ancestral state to be estimated at the root

	Divergence time				Global temperature			
Model	Coefficient	Std. Error	*t*	*P*	Coefficient	Std. Error	*t*	*P*
OLS	−0.178	0.006	−30.74	<0.001	−0.247	0.006	−43.29	<0.001
PL	<0.001	0.004	0.10	0.918	−0.007	0.003	−2.25	0.024
BM	0.117	0.012	9.62	<0.001	−0.379	0.004	−92.03	<0.001
OU	0.003	0.007	0.38	0.706	−0.336	0.004	−75.20	<0.001

Body size data were Log_{10}-transformed, and time and global temperature were z-score-transformed (mean = 0, SD = 1).

time and global temperature showed similar results, that is, body size increased over time and with cooling global temperature (Table 1).

The phylogenetic signal of body size was low (Blomberg's K = 0.239 on average across the four classes of vertebrates). The results of our phylogeny-based models were generally consistent with those of the ordinary least squares model when the global temperature at the divergence time was considered (e.g., coefficient was negative and significant in all four models; Table 1), but were variable when the divergence time was considered (e.g., the coefficient was not significant in two of the three phylogeny-based models, and was significant and positive in the other phylogeny-based model; Table 1).

When the four classes were considered separately, different classes showed different patterns in temporal body size evolution, although the temporal diversity patterns were similar and body size was negatively related to global

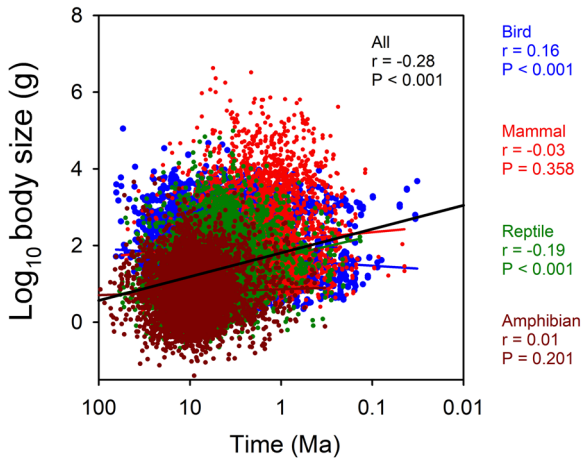

Fig. 3. Relationships between divergence time (Ma) and Log_{10} body size (g) of world's living terrestrial vertebrates in the Cenozoic Era (all tetrapods vs. individual groups: amphibians, reptiles, birds, and mammals).

surface temperature for each of the four classes (Fig. 2B). For example, the body size of reptiles increased significantly ($r = 0.19$, $P < 0.001$), but birds showed a significant decline in body size over time ($r = -0.16$, $P < 0.001$; Figs. 3, S1). Also, mammals showed an increasing trend in body size over time, while amphibians showed an opposite trend (in both cases, $P > 0.05$; Fig. S1). When endotherms (birds and mammals) and ectotherms (reptiles and amphibians) were analyzed separately and comparatively, we found that both groups of species showed similar patterns in terms of species diversity increase and body size decline over time (in all cases, $P < 0.001$; Fig. S2).

4 Discussion

Overall, we found a few similarities in variation in diversity and body size of the four groups of terrestrial vertebrates worldwide over time and taxonomically scale-dependent patterns from individual class to superclass (i.e., across all four classes). For example, species diversity of all tetrapod superclass and in each of the four classes increased over time and was negatively correlated with species divergence time. However, the differences in body size variation over time and among the four classes or across the whole spectrum of global living vertebrates are more striking. Given the fact that all classes follow Bergmann's rule based on spatial data (Guo et al., 2024c) and temporal data (this study), we mainly discuss the possible drivers behind these observed patterns regarding the applicability of Cope's rule.

4.1 Global (superclass)- versus clade (class)-level patterns

Throughout the entire Cenozoic Era, when all four classes were analyzed together, the species' body size increased over time and was negatively correlated with global surface temperature. These patterns seem to follow both Bergmann's rule (external temperature effects on the volume-to-surface ratio of the body) and Cope's rule (time effect and evolutionary consequence due to genuine biological causes; Cope, 1896; Roy et al., 2024).

However, although the observed patterns at both superclass and class levels generally follow Bergmann's rule (see also Guo et al., 2024c based on data across spatial temperature gradients), not all classes follow Cope's rule. Specifically, reptiles show strong support to Cope's rule, followed by mammals, but birds and amphibians show reverse trends, consistent with preliminary observations by Stanley (1973). Despite the common belief that endothermic and ectothermic species would respond differently to temperature change, we found no clear difference in body size evolution between them. We currently do not have satisfying answers regarding the underlying causes.

4.2 Possible mechanisms for the differences among classes

In our study, both mammals and reptiles seem to follow Cope's rule, consistent with most previous studies (Alroy, 1998; Hunt & Roy, 2006; Smith et al., 2010; Benson et al., 2014; Baker et al., 2015). Several possible reasons could help explain our observed patterns. First, the dominant driving force could be the long-term falling global temperature during the same time, following Bergmann's rule (Fig. 2B) (Clavel & Morlon, 2017). There is indeed enough and increasing evidence to show the temperature effect on body size (Smith et al., 2010; Raia et al., 2012), and such an effect could be similar on both endothermic and ectothermic species. Using temporal data, the present study reveals that all four classes support Bergmann's rule.

Second, across all species in tetrapod, the overall increase in body size over time is also likely because more species in classes with larger body sizes emerge after those with smaller sizes through the Cenozoic Era (e.g., Alroy, 1998; Bokma et al., 2016). This could be seen by the relative positions with different ages and body sizes of the four classes in the two-dimensional age—body size space: Amphibians have the longest divergence time but the smallest body size, followed by reptiles and birds (in the middle), while mammals have the shortest divergence time but the largest smallest body size, forming the overall negative age—body size relationship for world's living tetrapods (Fig. 3; Table S1; see also Guo et al., 2024b). However, while we know that larger-bodied species tend to have longer generation time or longevity (Etard et al., 2020), we have no solid data to show whether larger-bodied species survive much longer than small-bodied species over the same geological time, but see Hone & Benton (2005).

Third, for each specific class, the initial size (or founder effect) would be very different or unique, depending on which ancestor group the specific new class originated from. The initial size when a new class is formed could lead to either a larger or a smaller size (passive diffusion) (Raia et al., 2012; Benson et al., 2018). However, if the initial size is already very large, subsequent generations could become small because of the trade-offs or balance between costs and benefits. This might help explain the pattern found for birds (Fig. S1). Ultimately, the decline in birds' body size could be because some early birds evolved from small bipedal dinosaurs, which were large, so their initial size would be large (Padian & Chiappe, 1998). Yet, because of biomechanical and energetic constraints and especially because most

bird species rely on flying, birds cannot evolve to become larger (Hone & Benton, 2007).

Fourth, during the same period, compensatory growth (including across trophic) in body size among the four classes (as reflected by the shifts in peak body size over time) in relation to niche availability and competition might have taken place. For mammals, Alroy (1998) proposed that the extinction of large terrestrial vertebrates such as dinosaurs at the Cretaceous–Tertiary (or K-T) boundary, which separates the age of reptiles and the age of mammals, opened up the larger end of the body size spectrum for occupation by mammals. Also, the smaller size of one class (or more classes) over a certain geological period might have been "compensated" by the larger size of other classes in terms of space use and diet preference related to limited niche availability (Benson et al., 2014), and vice versa (Fig. 2), or complementary niche evolution (Benson et al., 2014; Roy et al., 2024). In other words, all four classes cannot have their largest possible sizes at the same time due to inter- and within-class competition for space and resources (e.g., ecosystem primary production) and/or phylogenetic/energetic constraints (Alroy, 1998; Kelt & Van Vuren, 1999; Benson et al., 2014; Jiangzuo et al., 2024; Roy et al., 2024).

Fifth, there could be several other responsible or contributing factors for which we currently have no quality data to perform related analyses. These factors may be associated with flight-related biomechanical constraints in birds, or eco-physiological limitations in amphibians, or their integration with evolutionary opportunity windows. However, there is no evidence that our observed patterns are due to deficiency in data completeness or sampling bias, as our data set includes quality body size data of almost all extant species.

Finally, the role of species diversity remains unclear, again mainly because of its consistently increasing trend but divergent patterns in the species age—body size relationships among the four classes (Fig. S1). In a community with many large animals, species of smaller body size could use different niches with many other benefits, such as higher production rates and less food and space requirements, among others (Arnold et al., 1995; Senthilnathan, 2023; Roy et al., 2024). This could counter the argument regarding the advantages for being large. Future work should separate the interplay among the perceived mechanisms behind Cope's and Bergmann's rules across both space and time. For example, more work is needed to quantify the relative effects of temperature and evolution corresponding to Bergmann's and Cope's rules. A key question related to Bergmann's rule is how long it may take for a species to adjust or change its body size in response to climate change (temperature cooling or warming). Of course, the answer to this question would be species-specific and likely reflect the differences between endotherms and ectotherms (Fig. S2), but it could also be size-dependent (Table S1; Figs. 1, 3).

Overall, the perceived mechanisms behind Cope's rule (e.g., a larger body is better for competition) seem to be difficult to prove. Also, similar to many related studies, especially those dealing with Cope's rule, our work clearly has limitations, as we do not have complete fossil data. It is particularly challenging to incorporate both fossil and living data into one study, especially given the scope here dealing with all terrestrial vertebrates (tetrapods) for which fossil data are largely unbalanced among the four classes. First, in most cases, fossil data are likely incomplete or biased, and, in most cases, only large-bodied species (e.g., ≥10 kg) were included in the analysis. Second, there are no standard methods to measure the body sizes of fossil species. As a result, for the same extinct taxa, body sizes estimated with different methods can vary greatly. For example, the body size for extinct mammals Castoroides is 213 kg based on Stirton's (1965) estimate, but is 60–100 kg based on Reynolds' (2002) estimate, which differs by a factor of over 2. Because body sizes of different extinct species have been commonly estimated with different methods, using body sizes of different extinct species estimated with different methods would likely create bias. Third, although there are numerous fossil records for extinct animals, many animal lineages do not have estimated body sizes, and the data with estimated body sizes are biased toward certain lineages. Thus, use of estimated body sizes for fossil taxa in our study could create another level of bias. Finally, body size is measured differently for fossils and for living individuals (actually, in the literature, some body size data for fossils are inferred from extant species); therefore, body size data could not be used consistently across the same data set as we used here. For all these major reasons, we have to limit our work to extant or living species.

In sum, species diversity in all four classes of terrestrial vertebrates increased with time, but different classes show different patterns over geological time. Although the general patterns in body size variations of all tetrapods in the last 66 Myr seem to follow both Cope's and Bergmann's rules, the argument for supporting the latter may be stronger, as it has a solid biological mechanism that has gained much broader support in the literature (Gould, 1997; Jablonski, 1997; Roy et al., 2024). The benefit of being large, claimed behind Cope's rule, appears to be soft, given the benefits and drawbacks of being large or small in body size (Arnold et al., 1995; Senthilnathan, 2023). Although we are not able to separate the mechanisms behind Cope's rule from those behind Bergmann's rule, the possible effect of global temperature cooling cannot be ignored in interpreting the increase in body size of newer species in the Cenozoic Era (Raia et al., 2012). Our findings have implications for species conservation (related to extinction), as climate warming may lead to a decline in the body size of certain species groups, which is closely linked to abundance and range size (Smith et al., 2010; Herrera et al., 2022; Guo et al. 2025). Future studies are needed to explore how fast species may alter their size in response to temperature change, such as anthropogenically induced global warming.

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Author Contributions

QG initiated the research, JZ and HQ collected data, QG, HQ, and JZ analyzed the data, QG wrote the manuscript, and all authors contributed to the writing of the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

Data Availability Statement

All data used in this study have been published. Sources and links of the data have been provided in the manuscript, that is, https://www.iucnredlist.org (global terrestrial vertebrates), http://datazone.birdlife.org/home (birds), https://doi.org/10.6084/m9.figshare.10075421 (terrestrial vertebrates), https://doi.org/10.6084/m9.figshare.c.3306933.v1 (birds and mammals), www.amphibianbiodiversity.org (amphibians), and http://www.columbia.edu/~mhs119/Sensitivity+SL+CO2 (global surface temperature).

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.70038/suppinfo:

Fig. S1. Changes in species diversity (the number of species) and the relationships between species divergence time (Ma) and Log_{10} body size (g) for each of the four classes of global terrestrial vertebrates over the Cenozoic. Red vertical lines (bars) represent the number of species. Solid and dashed lines represent significant and nonsignificant relationships, respectively. Each dot represents one species.

Fig. S2. Changes in species diversity (the number of species) and the relationships between species divergence time (Ma) and Log_{10} body size (g) for global endotherms (birds and mammals) vs. ectotherms (reptiles and amphibians) over the Cenozoic. Red vertical lines (bars) represent the number of species. Each dot represents one species.

Table S1. Comparisons of the species phylogenetic age or divergence time (Ma, million years ago) and Log_{10} body size (g) among the four classes of terrestrial vertebrates and all tetrapods in the Cenozoic Era (the last 66 million years). Log_{10} body size refers to Log_{10}-transformed body size.