META-ANALYSIS

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Unveiling the environmental drivers of intraspecific body size variation in terrestrial vertebrates

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Abstract

Aim: Whether intraspecific spatial patterns in body size are generalizable across species remains contentious, as well as the mechanisms underlying these patterns. Here we test several hypotheses explaining within-species body size variation in terrestrial vertebrates including the heat balance, seasonality, resource availability and water conservation hypotheses for ectotherms, and the heat conservation, heat dissipation, starvation resistance and resource availability hypotheses for endotherms.

Location: Global.

Time period: 1970–2016.

Major taxa studied: Amphibians, reptiles, birds and mammals.

Methods: We collected 235,905 body size records for 2,229 species (amphibians = 36; reptiles = 81; birds = 1,545; mammals = 567) and performed a phylogenetic meta-analysis of intraspecific correlations between body size and environmental variables. We further tested whether correlations differ between migratory and non-migratory bird and mammal species, and between thermoregulating and thermoconforming ectotherms.

Results: For bird species, smaller intraspecific body size was associated with higher mean and maximum temperatures and lower resource seasonality. Size–environment relationships followed a similar pattern in resident and migratory birds, but the effect of resource availability on body size was slightly positive only for non-migratory birds. For mammals, we found that intraspecific body size was smaller with lower resource availability and seasonality, with this pattern being more evident in sedentary than migratory species. No clear size–environment relationships were found for reptiles and amphibians.

Main conclusions: Within-species body size variation across endotherms is explained by disparate underlying mechanisms for birds and mammals. Heat conservation (Bergmann's rule) and heat dissipation are the dominant processes explaining biogeographic intraspecific body size variation in birds, whereas in mammals, body size clines are mostly explained by the starvation resistance and resource availability hypotheses. Our findings contribute to a better understanding of the mechanisms behind species adaptations to the environment across their geographic distributions.

1 | INTRODUCTION

Macroecological patterns can help elucidate the ecological and evolutionary mechanisms driving variation in species traits, like body size (Smith & Lyons, 2011). Bergmann's rule is one of the most noteworthy of these patterns. Bergmann's rule posits that endothermic species tend to have larger body sizes in northern latitudes, and smaller body sizes in southern latitudes, resulting in a latitudinal cline from colder to warmer climates. Bergmann (1847) hypothesized that because larger-bodied species have a lower surface-to-volume ratio, this could limit heat loss in cold environments (heat conservation hypothesis). Despite decades of research on thermoregulation as the main mechanism underlying body size clines in vertebrates, the validity of Bergmann's rule remains disputed with mixed support both at the interspecific (support: Clauss et al., 2013; rejection: Geist, 1987) and intraspecific level (support: Ashton, 2002; Ashton et al., 2000; rejection: Riemer et al., 2018; Rosenzweig, 1968). Consequently, several alternative hypotheses have been formulated to explain body size variation across environmental gradients (see Table 1; Blackburn et al., 1999), but there is still little consensus on which environmental factors matter the most and how their relevance varies across species with different behavioural and physiological traits. For example, high maximum temperature can also be a constraint in endotherms. The heat dissipation hypothesis predicts that smaller animals should reside in warmer and wetter climates as evaporative cooling is less effective (James, 1970). Alternatively, latitudinal size clines may be explained by the resource availability hypothesis, which suggests that animal body size has a positive relationship with primary productivity, as high resource availability may allow animals to grow to a larger size (Blois et al., 2008; McNab, 2010). Additionally, a large body size can be beneficial in highly seasonal environments, where larger individuals can cope with longer food shortage periods due to a higher fat content (i.e., starvation resistance hypothesis; Blackburn et al., 1999; Lindstedt & Boyce, 1985; McNab, 2010). However, the validity of the starvation resistance hypothesis is still unclear when applied to explain variation within species, because individuals with larger mass may also have a greater energy expenditure, which is disadvantageous during periods of food deficit (McNab, 1971).

Bergmann's rule has also been investigated in ectotherms (Adams & Church, 2008; Olalla-Tárraga et al., 2006; Pincheira-Donoso & Meiri, 2013; Vinarski, 2014). It has been argued that the heat conservation hypothesis does not explain body size variation in ectotherms, as a lower surface-to-volume ratio would not only reduce heat loss, but also heat gain, which is disadvantageous for ectotherms that do not internally regulate body temperature (Cushman et al., 1993; Vinarski, 2014). Yet, the heat balance hypothesis predicts that some ectothermic species with better thermoregulation ability may still follow Bergmann's rule (Olalla-Tárraga & Rodríguez, 2007; Zamora-Camacho et al., 2014). This is the case for reptiles and anurans, which can thermoregulate behaviourally through, for example, basking or moving to microhabitats with suitable temperatures (Adolph, 1990; Cowles & Bogert, 1944; Hutchison & Dupré, 1992). As such, thermoregulators can maintain a relatively constant body temperature; therefore, the improved heat conservation from a larger body size may outweigh the resulting decrease in heating rate. On the contrary, ectotherms that do not behaviourally thermoregulate (i.e., thermoconformers), including caudatans, are expected to benefit from smaller body sizes in colder climates due to the increased ability to take in heat, therefore exhibiting the converse of Bergmann's rule (Blanckenhorn & Demont, 2004; Feder, 1982; Hutchison & Dupré, 1992; Liu et al., 2018; Mousseau, 1997; Olalla-Tárraga et al., 2010; Olalla-Tárraga & Rodríguez, 2007). Other hypotheses that explain ectotherm body size variation are the seasonality hypothesis and the water conservation hypothesis. The first posits that individuals are smaller in areas with a shorter growing season, as a decreased development time can reduce the body size of ectotherms (Mousseau, 1997). The second postulates that amphibian body size will increase in drier environments as a smaller surface-to-volume ratio reduces water loss. Both hypotheses have received mixed support (e.g., Ficetola et al., 2010 and Slavenko & Meiri, 2015 rejected the seasonality and water conservation hypotheses; Gouveia & Correia, 2016 supported the water conservation hypothesis; Valenzuela-Sánchez et al., 2015 supported the seasonality hypothesis), suggesting that other mechanisms may explain the observed body size variations (e.g., resource availability; Olalla-Tárraga et al., 2006).

Large-scale body size patterns may result from a combination of multiple factors, with the most important mechanism differing across regions or species (Correll et al., 2016; Meiri & Thomas, 2007; Rodríguez et al., 2008). For example, interspecific variation in mammalian body size is more influenced by temperature in colder climates than in warmer ones, where the best predictor is seasonality in plant production (Rodríguez et al., 2008). In addition, certain species traits may also affect adherence to Bergmann's rule and other hypotheses behind geographic body size variation. For example, migratory bird species have been found to follow Bergmann's rule less than sedentary species do, possibly because they avoid extreme winter temperatures and therefore would not benefit from better heat conservation (Ashton, 2002; Mainwaring & Street, 2021; Meiri & Dayan, 2003). Similarly, differential exposure to environmental conditions in migrating and sedentary mammals could result in less selection pressure on intraspecific body size in migrating mammals escaping harsher conditions in the winter, but this has been largely unexplored. Additionally, thermoregulating ectotherms are

TABLE 1 Overview of hypotheses that may explain geographic body size patterns among amphibian, reptile, bird and mammal species

Hypothesis	Relevant taxa	Mechanism	Proxy variable	Expected relationship	Source
Heat conservation (Bergmann's rule)	Endotherms	Smaller surface-to-volume ratio minimizes heat loss in cold temperatures. Larger organisms may also carry more insulation	Mean temperature (MeanT)	Negative: body size decreases with increasing temperature	Blackburn and Hawkins (2004); Blois et al. (2008); Correll et al. (2016); Kamilar et al. (2012); Olalla-Tárraga et al. (2006); Riemer et al. (2018); Rodríguez et al. (2008)
Heat dissipation	Endotherms	Larger surface-to-volume ratio helps smaller individuals stay cool in warm and dry environments, by enhancing evaporative cooling	Maximum temperature (MaxT)	Negative: body size decreases with increasing temperature	Blois et al. (2008); Correll et al. (2016)
Starvation resistance	Endotherms	Larger individuals can better withstand resource shortages in more seasonal environments	Seasonality: annual standard deviation of net primary productivity (NPP_{sd})	Positive: body size increases with increasing seasonality (NPP_{sd})	Blackburn et al. (1999); McNab (2010)
Resource availability	All taxa	Greater food availability allows individuals to reach a larger size	Mean net primary productivity (NPP)	Positive: body size increases with increasing productivity (NPP)	Schiaffini (2016); Zhang et al. (2012)
Heat balance	Thermoregulating ectotherms (reptiles and anurans)	Enhanced heat conservation benefits organisms with good thermoregulating abilities	Mean temperature (MeanT)	Negative: body size decreases with increasing temperature	Ficetola et al. (2010); Olalla-Tárraga and Rodríguez (2007)
	Thermoconforming ectotherms (caudatans)	Faster heating rate benefits organisms with limited thermoregulating abilities	Mean temperature (MeanT)	Positive: body size increases with increasing temperature	Ficetola et al. (2010); Olalla-Tárraga and Rodríguez (2007)
Seasonality	Ectotherms	Longer growing seasons allows ectotherms to grow to a larger size	Annual NPP_{sd}	Negative: body size decreases with increasing seasonality (NPP_{sd})	Liu et al. (2018); Mousseau (1997); Olalla-Tárraga and Rodríguez (2007)
Water conservation	Amphibians	Smaller surface-to-volume ratio creates a greater desiccation tolerance in dry areas	Mean precipitation (MeanP)	Negative: body size decreases with increasing precipitation (MeanP)	Ficetola et al. (2010); Olalla-Tárraga and Rodríguez (2007); Slavenko and Meiri (2015)

expected to follow Bergmann's rule, while thermoconforming ectotherms are expected to follow the converse, due to differences in behavioural thermoregulation (Olalla-Tárraga et al., 2010; Olalla-Tárraga & Rodríguez, 2007).

Bergmann's original hypothesis (1847) dealt with interspecific body size variation, which has been widely studied (Blackburn & Hawkins, 2004; Carotenuto et al., 2015; Clauss et al., 2013; Geist, 1987), but the mechanism was later argued to be mostly relevant at the intraspecific level (James, 1970; Rensch, 1938), particularly because many of the species considered by Bergmann turned out to be races after a major systematic revision of the taxonomy (Meiri, 2011). There has been little consensus on the generality of Bergmann's rule at the intraspecific level (support: Ashton, 2002 for birds; Meiri & Dayan, 2003 for mammals; rejection: Geist, 1987 for the wolf; Riemer et al., 2018 for mammals and birds). Additionally, many intraspecific studies investigate Bergmann's rule in one or a few species, highlighting the need for more large-scale studies with a broader taxonomic representativeness (Blois et al., 2008; Correll et al., 2016; James, 1970; Kubo & Takatsuki, 2015; L'Heureux & Cornaglia Fernández, 2015; Schiaffini, 2016; Yom-Tov et al., 2010; Zhang et al., 2012). Two such large-scale studies report contrasting results, indicating support for the heat conservation hypothesis in chelonians but a converse relationship in squamates (Ashton & Feldman, 2003), and no strong support in endotherms (Riemer et al., 2018). Yet, other plausible hypotheses underlying intraspecific body size variation remain unexplored (see Table 1).

The aim of this study was to investigate intraspecific body size variability of terrestrial vertebrates on a global scale across environmental gradients (climate, primary productivity and seasonality). We tested the full array of hypotheses described in the literature for ectotherms (amphibians and reptiles) and endotherms (birds and mammals), including the heat balance, seasonality, resource availability and water conservation hypotheses for ectotherms, and the heat conservation (i.e., Bergmann's rule), heat dissipation, starvation resistance and resource availability hypotheses for endotherms (Table 1). Support for these hypotheses may differ between taxa due to differences in selection pressures. For example, amphibian body size variation may depend on water availability more so than temperature (Gouveia & Correia, 2016). While it might be advantageous for birds and mammals to have a smaller size in warmer areas due to a greater surface-to-volume ratio, this high ratio would lead to a greater desiccation rate in amphibians, resulting in dehydration. Further, we investigate if intraspecific body size – environmental gradient relationships are influenced by migratory behaviour in birds and mammals (migratory versus resident), and thermoregulation in ectotherms (thermoregulators versus thermoconformers). We expected clines to be weaker in migratory birds and mammals as they overwinter in areas with milder temperatures and greater food availability. We also hypothesized that at the intraspecific level, thermoregulating ectotherms follow Bergmann's rule, while thermoconforming ectotherms follow the converse (Olalla-Tárraga & Rodríguez, 2007).

2 | METHODS

2.1 | Species body size data

We obtained most of our data from the public database VertNet, a vast compilation of vertebrate biodiversity records from natural history collections worldwide (Constable et al., 2010; Guralnick & Constable, 2010). We downloaded separate datasets for amphibians, reptiles, birds and mammals from http://vertnet.org/resources/datatoolscode.html (Bloom, 2016a, 2016b, 2016c, 2016d). Each data point represents the body size of a single individual, or the average of several individuals, measured at a specific georeferenced location. The original dataset included a total of 2,365,482 records for amphibians, 2,691,446 for reptiles, 5,934,806 for birds and 4,345,250 for mammals. The dataset was later supplemented with body size measurements from published literature found using the following search terms on the Web of Science in February 2019: "mammals", "birds", "body size", "body mass", "reptiles", "amphibians", "body length", "SVL", "body size variation", "geographic variation". Searches were performed using Boolean terms combining one or more terms (e.g., "body size" AND "mammals"; "SVL" AND "amphibians"). We included papers that reported body mass measurements for birds and mammals, snout–vent length (SVL) measurements for reptiles and amphibians, and the spatial coordinates where animals were captured. We retrieved 26 studies, three of which were included in the final dataset after checking for the criteria below. A full list of the data sources is found in Supporting Information Appendix S1. Of these records, we only used those georeferenced with a precision of 10 km or less. We also removed records of juveniles and records collected before 1970 in order to match the time period of the available environmental data. For each species, body size was averaged within 10×10 km cells. We limited our analysis to species with five or more cells to ensure that each species had a sufficient sample size and environmental variation for the analysis.

There are several metrics in the literature that have been employed to measure body size, including mass, length, and skeletal measurements (e.g., cranial greatest length). In this study, body size was reported as mass for endotherms and SVL for ectotherms, as these are the metrics most widely reported in the VertNet database for mammals and birds, and reptiles and amphibians, respectively. Mass is a good indicator for endotherms because it accounts for body fat – an essential factor in heat conservation and starvation resistance (McNab, 2010). For ectotherms, SVL is a more commonly available measure, particularly in the case of amphibians, where body mass can vary widely within the individual depending on body condition, reproductive status and dehydration, potentially adding substantial noise to geographic body size patterns (Boback & Guyer, 2003; Pincheira-Donoso & Meiri, 2013; Santini et al., 2018). Using allometric regressions to convert length to body mass equivalents is possible (e.g., Feldman et al., 2013; Meiri, 2010; Santini et al., 2018), but since we are calculating Spearman rank correlations between size and environmental factors per species, using allometrically derived body mass estimates would yield identical results (see

Data analysis). Hereafter, 'body size' refers to body mass in birds and mammals and SVL in amphibians and reptiles.

2.2 | Environmental variables

For each georeferenced body size measurement we extracted the values of environmental variables representing the different proposed drivers (Table 1). Rationale for the use of these variables is provided in Supporting Information Appendix S2. We retrieved raster maps for mean annual precipitation (MP), mean annual temperature (MeanT) and maximum annual temperature (MaxT) from WorldClim version 2.0 at a resolution of 5 arcminutes (http://worldclim.org; Fick & Hijmans, 2017). These variables were average values from 1970–2000. Mean annual net primary productivity (NPP) data ($g/m^2/day$) were taken from the US National Aeronautics and Space Administration (NASA) Earth Observatory at https://neo.gsfc.nasa.gov/archive/geotiff.float/MOD17A2_M_PSN/. We used the mean of all monthly raster maps for NPP (2000–2016, 6 arcminutes resolution) to test resource availability. To investigate the starvation resistance and seasonality hypotheses, we calculated the standard deviation of NPP (NPP_{sd}) for each available year and then averaged them.

2.3 | Data analysis

To test the hypotheses, we ran phylogenetic meta-analyses to test the consistency of the correlation between body size and potential predictor variables across many species while weighting by the statistical power of each correlation and controlling for phylogenetic relatedness (e.g., Hillebrand & Azovsky, 2001; Santini et al., 2018; Weber et al., 2017). We calculated weighted Spearman's rank correlation coefficients for each species, relating body size (i.e., body mass in endotherms and SVL in ectotherms) to each environmental variable (Table 1). We used the Spearman's rank-order test so that nonlinear monotonic relationships could be detected. Correlations were weighted by the log_{10}-transformed number of individuals within each cell plus 1 (to avoid $n = 1$ being weighted as zero) to account for the unequal sample size across cells. That is, some body size values were based on one or few specimens per cell, whereas others were based on many and were thus more representative of the average body size of the local population. Then, we transformed these correlation coefficients into Fisher's z-scores to normalize the sampling distributions using the formula: $\frac{\log((1+r)/(1-r))}{2}$, where r is Spearman's correlation coefficient. We also calculated sampling variances as $Vz = \frac{1}{n-3}$, so that species with a larger sample size (number of cells) would have more weight in the analysis (Borenstein et al., 2009). While using a minimum number of five cells is necessary to calculate a meaningful correlation, small-sample correlations are given less weight in the analysis as they are corrected by the inverse of the sampling variance. Next, we used the z-scores and variances to fit a mixed-effects meta-analysis to the species correlations for each hypothesis.

We ran separate models for each taxonomic class and included species and phylogeny as random effects to estimate the non-phylogenetic and the phylogenetic species-level variance (Hadfield & Nakagawa, 2010). The first component accounts for species similarities due to shared ecology while the second accounts for species similarities due to evolutionary history (Cinar et al., 2021). Phylogenetic similarity was accounted for as a variance–covariance matrix, which was derived from synthetic phylogenetic trees from the Open Tree of Life (Hinchliff et al., 2015). Phylogenetic trees were pruned for our species list, single polytomies encountered were dealt with via randomization, and then we estimated branch lengths following Grafen (1989). Each phylogenetic meta-analytical model estimates a grand mean correlation coefficient (Fisher's z) along with the 95% confidence interval of the tested hypothesis. We present the results by back-transforming Fisher's z-scores into Spearman's r for ease of interpretation, which summarize the overall intraspecific patterns detected across species. We did not test for publication bias towards taxa expected to follow Bergmann's rule or towards studies reporting 'statistically significant' results (Gurevitch et al., 2001). This is because the vast majority of our data come from a huge repository (VertNet) that stores data from different museums and sources, and thus consists of primary data that we used to calculate the correlation coefficients between size and each environmental variable. Additionally, most of the newly added data come from studies that did not aim to assess the generality of Bergmann's rule (Supporting Information Appendix S1.2, except for Sun et al., 2017). Because intraspecific patterns in size variation are likely to be stronger for widespread species that experience greater environmental variation (Gaston et al., 2008), we tested whether models including environmental variation as a covariate/moderator were better than the random intercept-only models (null models). We compared both models for each hypothesis using likelihood ratio tests, and included environmental variation as the standard deviation of the environmental factor representing the tested hypothesis (e.g., for the heat conservation hypothesis we regressed the $r_{size\text{-}MeanT}$ correlation coefficient against sdMeanT).

We ran subgroup phylogenetic meta-analyses to investigate which species traits may affect adherence to the different hypotheses (Table 1). For the heat balance hypothesis, we used thermoregulation as a categorical moderator for the MeanT model, comparing thermoregulators (reptiles and anurans) with thermoconformers (caudatans). For migration, we classified bird migratory behaviour into resident or migratory (fully migratory and partial migratory) using the dataset by Eyres et al. (2017). We excluded species classified as nomadic in this dataset because they perform erratic movements and their body size is thus not under selection by the local environmental conditions. Missing information on migratory behaviour was retrieved from the Birds of the World (https://birdsoftheworld.org; Billerman et al., 2020). For mammals we used information from Gnanadesikan et al. (2017), Soriano-Redondo et al. (2020), Bisson et al. (2009) and Animal Diversity Web (https://animaldiversity.org/) to classify them as migratory or resident species.

The data collection and analysis were completed using R version 3.5.0 and RStudio version 1.2.5042 (R Core Team, 2018; RStudio Team, 2016). For handling large tables we used the package 'data.table' (Dowle & Srinivasan, 2017), and for data processing we used 'stringr' (Wickham, 2018) and 'dplyr' (Wickham et al., 2015). To match species names with synonyms we used 'taxize' (Chamberlain & Szocs, 2013). For raster operations we used 'raster' (Hijmans, 2017), 'sp' (Bivand et al., 2013; Pebesma & Bivand, 2005) and 'rgdal' (Bivand et al., 2017). Lastly, we used the package 'metafor' for the meta-analysis, meta-regressions, and z-score transformations (Viechtbauer, 2010), 'ape' for estimating branch lengths and resolving polytomies (Paradis & Schliep, 2018), 'rotl' for building the phylogenies for our species by searching the Open Tree Taxonomy (Michonneau et al., 2016; Rees & Cranston, 2017) and retrieving the phylogenetic relationships from the Open Tree of Life (Hinchcliff et al., 2015), and 'ggplot2' (Wickham, 2009), 'ggpubr' (Kassambara, 2017) and 'rphylopic' (Chamberlain, 2020) for creating figures.

We report our results using effect sizes, confidence intervals and exact p-values, and use the language of evidence to describe our findings instead of relying on a single cut-off p-value to report a finding as statistically significant or not. We thus employ the terms no ($p > .1$), weak ($.05 < p < .1$), moderate ($.01 < p < .05$), strong ($.001 < p < .01$), very strong ($p < .001$) for certain findings (see Amrhein et al., 2019; Muff et al., 2022).

## 3 | RESULTS

3.1 | Data coverage

Our dataset included 52,026 grid cells with 235,905 size records from 2,229 species, including 36 amphibian, 81 reptile, 1,545 bird and 567 mammal species. The majority of data points were located in North America, although bird and mammal species were spread across all continents except Antarctica (Figure 1). Reptiles and amphibians were scarcer, present mostly in North America, but also in Europe, Africa and Southeast Asia (Figure 1). Our dataset covers 36% (49/135), 76% (140/184), 26% (19/73) and 15% (11/73) of taxonomic families of terrestrial species for mammals, birds, reptiles (squamates) and amphibians, respectively (Supporting Information Figure S4.1). The mean latitudinal range covered by the data was 3.75° for amphibians, 7.58° for reptiles, 21.62° for birds and 16.29° for mammals (Supporting Information Appendix S3), and the average number of 10 km × 10 km cells per species was 9.5 for amphibians, 12.1 for reptiles, 16.5 for birds and 44.8 for mammals.

3.2 | Intraspecific body size patterns

We did not find evidence for any of the hypotheses we tested in ectotherms (resource availability, seasonality, water conservation;
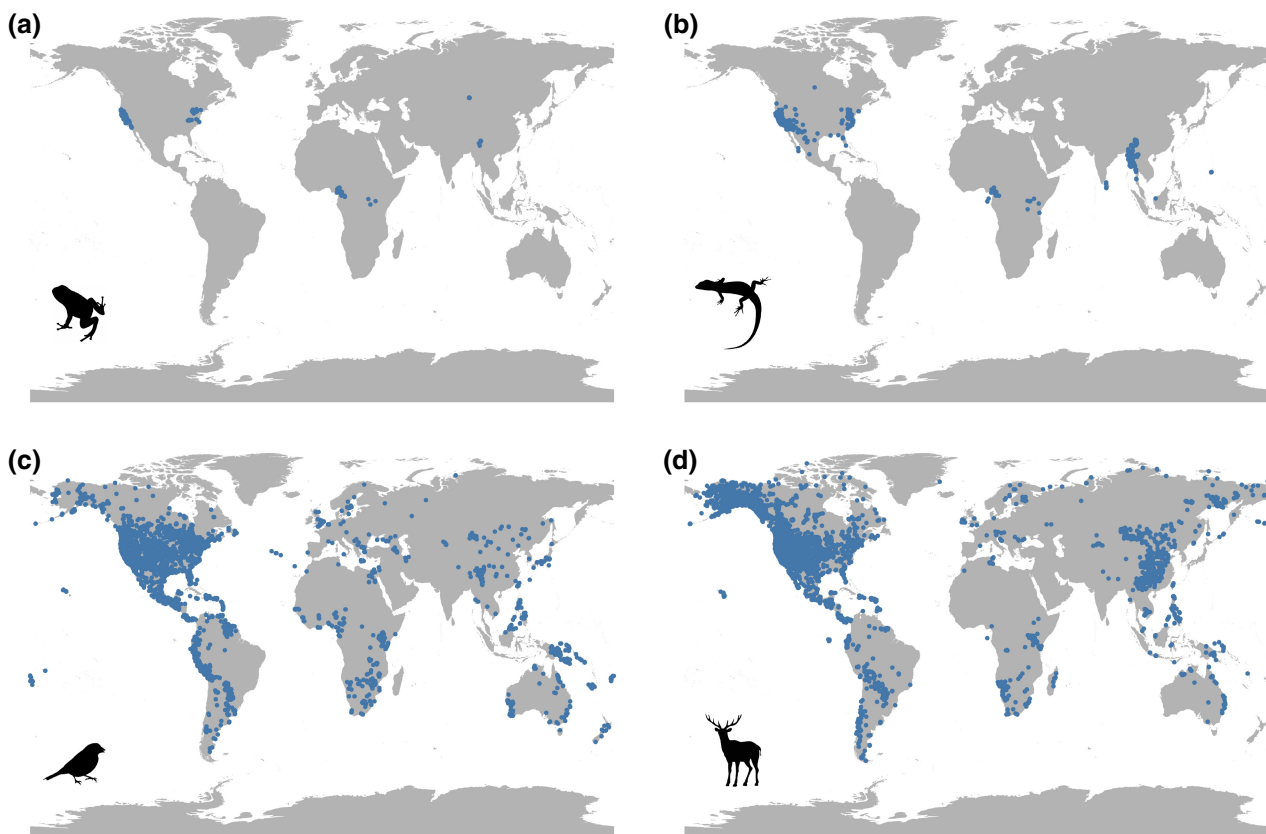
FIGURE 1 Geographic distribution of the body size records retrieved from the VertNet database and published literature for (a) amphibians, (b) reptiles, (c) birds and (d) mammals
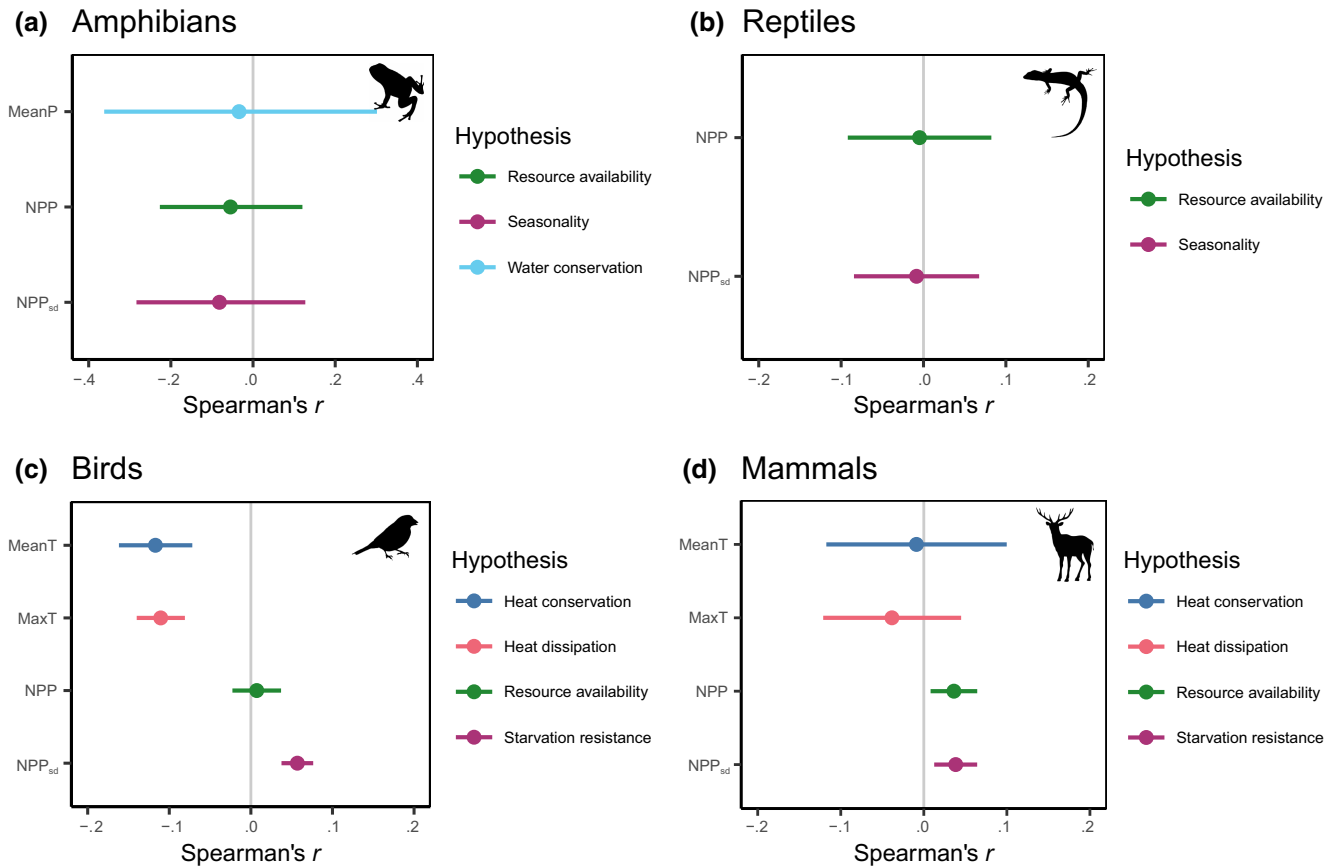
FIGURE 2 Effect sizes (points) of the meta-analyses of correlation coefficients between body size and each environmental predictor for (a) amphibians (*n* = 36), (b) reptiles (*n* = 81), (c) birds (*n* = 1,545) and (d) mammals (*n* = 567). Horizontal lines indicate the 95% confidence intervals. Environmental variables include mean annual temperature (MeanT), maximum annual temperature (MaxT), mean annual precipitation (MeanP), mean annual net primary productivity (NPP) and the annual standard deviation of NPP (NPP$_{sd}$). Colours indicate the corresponding hypotheses

Table 1), with all size–environment relationships having correlation coefficients close to zero or wide confidence intervals (Figure 2a,b; Supporting Information Figures S4.4 and S4.5, Table S4.1). Birds exhibited negative relationships between body size and mean and maximum temperature [$r_{size-MeanT}$ = −.118; 95% confidence interval (95CI): −.163 − −.072, *p* < .001; and $r_{size-MaxT}$ = −.111; 95CI: −.141 − −.081, *p* < .001], a positive, albeit weaker, relationship with NPP$_{sd}$ ($r_{size-NPPsd}$ = .057; 95CI: .038 − .076, *p* < .001) and no relationship with NPP ($r_{size-NPP}$ = .007; 95CI: −.023 − .037, *p* = .636; Figure 2c; Supporting Information Table S4.1). In mammals, there was no evidence of a relationship between body size and mean or maximum temperature ($r_{size-MeanT}$ = −.009, 95CI: −.118 − .100, *p* = .873; $r_{size-MaxT}$ = −.038, 95CI: −.122 − .045, *p* = .367; Figure 2d; Supporting Information Table S4.1). Yet, there was moderate evidence for a positive relationship between size and NPP ($r_{size-NPP}$ = .036, 95CI: .008–.064, *p* = .011), and strong evidence for a positive size–NPP$_{sd}$ relationship ($r_{size-NPPsd}$ = .038, 95CI: .014–.066, *p* = .004; Figure 2d; Supporting Information Table S4.1). Models that included environmental variation as a covariate were not better than the null models (Supporting Information Table S4.2). The only exceptions are the size–MaxT and the

size–MeanT relationships in birds and the size–MeanP relationship in amphibians (Supporting Information Table S4.2). Evidence for a negative relationship between size–MaxT and increasing variation in maximum temperature was moderate (slope = −.01, 95CI: −.020 − −.001, *p* = .032; Supporting Information Figure S4.2a). However, the relationship between size–MeanT and variation in mean temperature was not conclusive even though the likelihood ratio test indicated that this model was better than the null model (Supporting Information Table S4.2, slope = −.009, 95CI: −.020 −.003, *p* = .133). Furthermore, we found moderate evidence that amphibian species experiencing a wide variation in precipitation regimes across their distribution have a negative correlation between size and precipitation (slope = −.014, 95CI: −.026 − .002, *p* = .028), thereby supporting the water conservation hypothesis.

3.3 | Effects of thermoregulatory and migratory behaviour on body size patterns

We further explored how adherence to Bergmann's rule could differ between ectothermic species with different thermoregulatory

behaviour, and for birds and mammals with different migratory behaviour. We found no evidence that either thermoconformers or thermoregulators adhered to the heat balance hypothesis, with both groups exhibiting large uncertainty around the estimated correlations between body size and mean temperature (thermoconformers: $r_{\text{size-MeanT}} = .202$, 95CI: $-.150 - .553$, $p = .262$; thermoregulators: $r_{\text{size-MeanT}} = .006$, 95CI: $-.108 - .119$, $p = .922$; Supporting Information Table S4.3). Additionally, we found that non-migratory and migratory birds had negative relationships between body size and MeanT and MaxT, and positive relationships between size and NPP_{sd}, but there was no evidence for differences between the two groups for any of these hypotheses (Figure 3a; Supporting Information Table S4.4). However, there was weak evidence of different size–NPP relationships for resident and migratory species [omnibus test of moderators (QM) = 3.69, $p = .055$]. Resident birds showed a positive correlation coefficient ($r_{\text{size-NPP}} = .031$, 95CI: $.017 - .060$, $p = .038$), whereas for migratory birds the size–NPP relationship was flat ($r_{\text{size-NPP}} = -.009$, 95CI: $-.038 - .019$, $p = .524$). In turn, mammals exhibited no differences between migratory and sedentary species for the size–MeanT and size–MaxT relationships, but we found moderate evidence for differences between these two groups for the resource availability (QM = 7.25, $p = .027$) and starvation resistance hypotheses (QM = 8.97, $p = .011$) (Figure 3b; Supporting Information Table S4.4). There was strong evidence of positive size–NPP and size–NPP_{sd} relationships for sedentary species, but not for migratory species (sedentary mammals: $r_{\text{size-NPP}} = .040$, 95CI: $.011 - .069$, $p = .007$ and $r_{\text{size-NPPsd}} = .041$, 95CI: $.014 - .068$, $p = .003$; migratory mammals: $r_{\text{size-NPP}} = -.015$, 95CI: $-.127 - .097$, $p = .795$ and $r_{\text{size-NPPsd}} = .001$, 95CI: $-.103 - .104$, $p = .988$).

4 | DISCUSSION

Here, we investigated the main drivers of environmental size clines in terrestrial vertebrates at the intraspecific level (Table 1). Overall, we found support for the heat conservation, heat dissipation and starvation resistance hypotheses in birds, with the size–temperature relationships being stronger than the relationship between body size and seasonality in resources. In contrast, mammals tended to better follow the resource availability and the starvation resistance hypotheses, although both relationships had small correlation coefficients (Spearman's $r < .1$). In the case of ectotherms, our results suggest that body size–environment relationships are inconclusive and overall highly variable across species as shown by the wide confidence intervals.

We found no evidence that thermoregulating (reptiles and anurans) or thermoconforming ectotherms (caudatans) follow Bergmann's rule, neither the original formulation (negative size–temperature relationship) nor the converse form (positive size–temperature relationship). Although thermoconformers tended to have positive correlation coefficients between body size and mean temperature, this relationship was extremely variable among caudatan species. These findings contradict the heat balance hypothesis, which predicts that thermoregulating ectotherms should follow Bergmann's rule while thermoconforming ectotherms follow the converse, although this hypothesis was formulated at the interspecific level (Olalla-Tárraga & Rodríguez, 2007). There has been mixed support for Bergmann's rule in single-species studies, reporting both Bergmann's clines in anurans and caudatans (Ficetola et al., 2010; Zamora-Camacho et al., 2014) and converse Bergmann's clines in anurans (Cvetković et al., 2009; Liu et al., 2018). However, similar
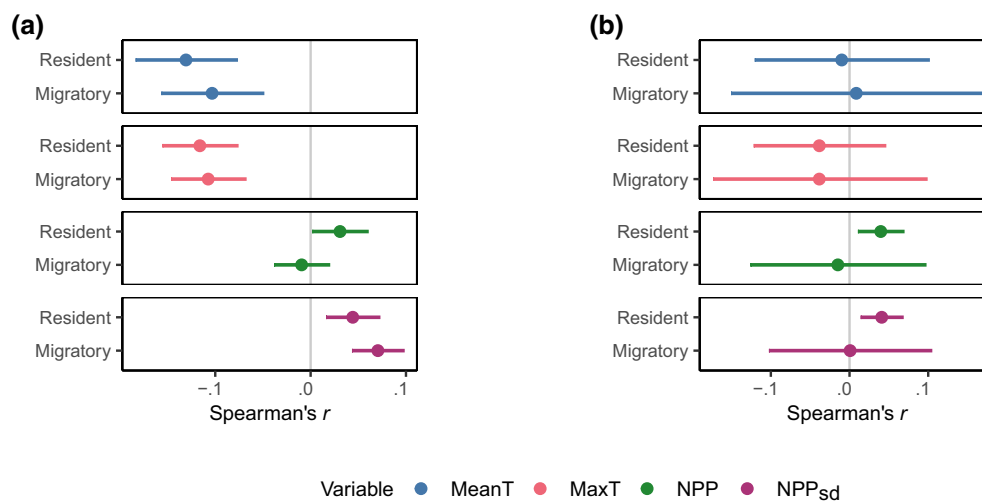
FIGURE 3 Results of meta-regression models testing the validity of the main hypotheses in migratory and resident species of (a) birds and (b) mammals. Points indicate the summary effect size of intraspecific correlations between body size and environmental predictors for resident ($n = 957$ birds, $n = 531$ mammals) and migratory ($n = 579$ birds, $n = 36$ mammals) species. Horizontal bars indicate the 95% confidence intervals. Environmental variables include mean annual temperature (MeanT), maximum annual temperature (MaxT), mean annual net primary productivity (NPP) and the annual standard deviation of NPP (NPP_{sd})

to our results, another multi-species study found little evidence of Bergmann's rule or the converse in amphibians at the intraspecific level (Adams & Church, 2008). This and our study strongly suggest that, although thermal body size clines may be observed in individual species (e.g., mock viper, *Psammodynastes pulverulentus*, r = −.53; foothill yellow-legged frog, *Rana boylii*, r = −.63), the heat balance hypothesis does not generally explain intraspecific body size variation in ectothermic species.

We also found that other environmental factors (precipitation, productivity and seasonality) did not generally explain within-species body size variation in amphibians. Similarly in reptiles, there were no clear patterns observed between body size and resource availability and seasonality. This concurs with previous studies that only detected intraspecific relationships with resource availability for a small proportion of species (18%, Pincheira-Donoso & Meiri, 2013). Interspecific studies have mirrored these results. A large-scale study at the interspecific level found that climatic variables poorly predict body size in amphibians (Slavenko & Meiri, 2015). However, another study carried out at the interspecific level found evidence of the water conservation hypothesis in three clades of amphibians, but these relationships were weak (Gouveia & Correia, 2016). Others have argued that interspecific body size variation in reptiles cannot be explained by a single mechanism (Olalla-Tárraga et al., 2006). Together with our results, this suggests a lack of general patterns in ectotherms at both intra- and interspecific levels. It is however possible that this lack of support reflects methodological constraints related to spatial resolution and extent, and to geographic coverage. First, body size variation in ectotherms may be governed by factors acting at a finer resolution, such as microclimatic conditions or small-scale variation in prey availability. The heterogeneity of environmental conditions may also vary between locations; thus some cells may more accurately represent the actual conditions the organisms experience than others. Hence, environmental gradients measured at 10-km resolution may not be fully representative of the different conditions that ectothermic populations experience. However, increasing the resolution of our analyses would have made our results sensitive to coordinate uncertainty, leading to inaccurate matching between size records and environmental factors. Second, body size records for ectotherm species were collected in relatively smaller areas than for endotherms. In fact, data for mammals and birds covered about twice the latitudinal range of ectotherms (Supporting Information Appendix S3). This could reflect the fact that many ectotherms have narrow geographic ranges (Pie et al., 2021), and are thus exposed to a limited range of environmental conditions. Substantial environmental variation within a range is needed for size clines to become evident (Gaston et al., 2008; Meiri et al., 2007). Indeed, our results corroborate that intraspecific body size clines along precipitation gradients (i.e., the water conservation hypothesis, where organisms become smaller in mesic versus arid environments) become apparent for amphibian species exposed to more variation in precipitation across their distribution. Third, the records included in the VertNet database are biased to certain locations (see Figure 1)

and, although we collected additional records, the coverage for ectotherms is considerably poorer than that for endotherms.

On the contrary, in endotherms the results were largely concordant with our hypotheses (Table 1). In birds we found support for the temperature-related hypotheses and the starvation resistance hypothesis, with the resource availability hypothesis being supported in non-migratory birds only. In mammals only the resource availability and the starvation resistance hypotheses were clearly supported, particularly in sedentary species, suggesting that the most plausible mechanisms underlying within-species body size variation in this taxon are phenotypic adaptations to resource availability and resource pulses in seasonal environments. Matching the findings of several other single- and multi-species studies of Bergmann's rule (intraspecific level: Ashton, 2002; James, 1970; Meiri & Dayan, 2003; Romano et al., 2021; Sun et al., 2017; interspecific level: Olson et al., 2009), we found that the majority of bird species formed negative body size clines with mean and maximum temperatures, particularly in species exposed to a wider range of temperature variation. For mammals, our findings revealed no relationship between body size and maximum temperature, thus shedding doubt about the validity of heat dissipation as the causal mechanism of intraspecific mammalian body size clines (Ashton et al., 2000). Conversely, Riemer et al. (2018) found no general relationship between body size and temperature for either mammals or birds using the same dataset as this study but with a different analytical approach based on tallying the number of statistically significant correlation coefficients. Our meta-analytical approach is expected to be more robust than previous studies that used vote-counting approaches (Ashton, 2002; Meiri & Dayan, 2003; Meiri et al., 2004), as vote-counting tends to overweight the effect of species (or studies) with small sample sizes, ignoring statistical uncertainty (Gurevitch et al., 2018).

Body size variation in mammals was also explained by the resource availability hypothesis, in line with a single-species study reporting a positive relationship between body size and resource availability in Molina's hog-nosed skunk, *Conepatus chinga* (Schiaffini, 2016). Overall, increased access to food can allow for more energy to be allocated to growth (McNab, 2010). Yet, one difficulty with the interpretation of this relationship is that the effect of productivity may be indirect for higher trophic levels. Higher primary productivity represents greater food availability for herbivores, but this effect becomes less clear with predator species. For instance, the body size of carnivores may instead be related to prey size, as observed in wolves in North America (*Canis lupus*; Geist, 1987). Furthermore, brown bear skull size (a proxy for body size) is better explained by the distance to the nearest salmon spawning area (*Ursus arctos*; Meiri et al., 2007). Thus, although our results suggest that endotherms follow the resource availability hypothesis, future investigations could further clarify the mechanisms behind this pattern.

We provide further evidence for the positive relationship between body size and seasonality in resources for both birds and mammals. Positive intraspecific relationships between body size (based on skeletal measurements) and seasonality have been

previously reported in birds (e.g., house sparrow, *Passer domesticus*, Murphy, 1985) and mammals (e.g., muskrat, *Ondatra zibethicus*, Boyce, 1978), but this is the first time that we provide this evidence among hundreds of species. In environments with intense seasonal resource shortages, large-bodied endotherms may benefit from increased fat storage to avoid starvation during periods of limited resources (Lindstedt & Boyce, 1985). For instance, the body size of the Sika deer was found to increase with the normalized difference vegetation index (NDVI) and winter coldness index (Kubo & Takatsuki, 2015). Additionally, due to high mortality during resource shortages, surviving individuals may experience less competition, allowing better access to resources during the seasonal productivity pulse (Lindstedt & Boyce, 1985). Although fasting endurance has been hypothesized to be a more important factor in birds at the intraspecific level than the traditional hypothesis of heat conservation (Ashton, 2002), our findings reveal that temperature remains the main factor underlying within-species size variation in avian faunas.

For birds, the support for the resource availability hypothesis depended on migratory behaviour, but we did not find consistent evidence for a difference in the strength of Bergmann's rule and other hypotheses (Table 1) between migratory and sedentary species. Whether migratory birds adhere to Bergmann's rule less than resident species remains contentious, with some studies supporting this at both intraspecific (Meiri & Dayan, 2003; Zink & Remsen, 1986) and interspecific levels (Mainwaring & Street, 2021), and another study lacking consistent evidence of this pattern at the intraspecific level (Ashton, 2002). Our study, based on a larger number of species, suggests that both non-migratory and migratory birds follow Bergmann's rule, and also comply with the heat dissipation and starvation resistance hypotheses. Resident species do not avoid harsher winter conditions (e.g., lower temperatures and NPP in highly seasonal environments), and therefore may exhibit stronger relationships between body size and the environment. However, although migratory birds can escape extreme environmental conditions in non-breeding areas, they also tend to be larger-bodied and inhabit higher latitudes, where seasonality is greater (Blackburn & Gaston, 1996). Additionally, a greater number of breeding migratory species have been found in highly seasonal environments, possibly because they benefit from a surplus in resources (Somveille et al., 2015), or because they can thrive in these uncertain conditions by relocating in space, often over long distances (Sheard et al., 2020). The lack of consistent evidence for the effect of bird migratory behaviour on adherence to these ecogeographic rules may also depend on the classification of migration. Some studies, including ours, classify species as migratory or resident (Ashton, 2002; Meiri & Dayan, 2003), while others further differentiate between long- and short-distance migrants (Mainwaring & Street, 2021), which may be a more accurate measure that could be further explored in future intraspecific assessments of Bergmann's rule and other hypotheses underlying body size variation. In contrast, in mammals our results reveal that the evidence for species adhering to the resource availability and starvation resistance hypotheses is clearer in sedentary species than

in migratory species, which display more variable size–environment relationships.

Although we explored body size clines using a vast dataset of body size records, the data used in our analyses are geographically biased towards North America, and have a very limited coverage in the case of ectotherms. As more body size records from disparate areas across the globe become available, it would be possible to test whether the patterns reported in this study become stronger or disappear, and if these patterns vary based on geographic region. In this sense, the recent mobilization of large quantities of ecological data, with many natural history museums digitizing their collections, plus the development of open science and data sharing policies (Gallagher et al., 2019; Michener, 2015), will allow researchers to not only further investigate the full array of hypotheses and mechanisms underlying geographic body size variation, but also to expand the focus towards the factors explaining phenotypic variability in body size at the population level across latitudinal and environmental gradients.

While we restricted our analyses to size–environment relationships, anthropogenic influences may complicate the interpretation of our results. For example, biodiversity threats like hunting, urbanization and deforestation have altered interspecific body size patterns in tetrapods globally (Rapacciuolo et al., 2017; Santini et al., 2017), and correlations between such anthropogenic pressures and the environmental variables hypothesized to drive such patterns may hinder our ability to support one or another hypothesis (Santini et al., 2017). Anthropogenic pressures also have the potential to alter intraspecific patterns of body size. For example, harvesting of mammals is usually non-randomly targeted towards large-bodied animals, and directional selection can cause rapid evolution towards small-sized individuals (Coltman et al., 2003). Body size variation patterns are also observed at a temporal scale. Anthropogenic climate change has been associated with widespread reductions in body size over time across many taxa (Gardner et al., 2011). Decreasing body size over time in birds has been linked to climate warming over the past several decades, which concurs with our finding that bird body size decreases with increasing temperature (Gardner et al., 2009; Van Buskirk et al., 2010; Weeks et al., 2020). Such decreases in body size with climate warming have also been detected for ectotherms, for example in the tree wasp (*Dolichovespula sylvestris*, Polidori et al., 2020), and in woodland salamanders (genus *Plethodon*, Caruso et al., 2015), although we did not find strong evidence of these patterns at a geographic scale.

In addition, while we focused on many potential predictors of body size variation, there are other factors that we did not consider, like sexual dimorphism and competition, which may be especially relevant at the intraspecific level. Because body size is significantly different between sexes in dimorphic species, this may have prevented the observation of intraspecific body size clines in some cases, as records were pooled at the population level regardless of sex, which was not always reported in VertNet.

Finally, in our analyses we did not account for the migration distance across migratory species, as well as the fact that some

migratory species are partial migrants. However, this information is only sparsely available, and when available it is rarely linked to specific regions, hence blurring the effect of partial migration on the different hypotheses assessed in this study.

5 | CONCLUSIONS

Here we conducted a large-scale investigation of intraspecific body size patterns in terrestrial vertebrates. We found that body size in birds depends on temperature, therefore supporting the role of the heat conservation and heat dissipation mechanisms. Additionally, bird and mammal body size are related to seasonality in resources and, in mammals, to resource availability. There was little support for the main hypotheses explaining body size clines in ectotherms, and we found no evidence that body size clines differ between thermoregulating and thermoconforming ectotherms. Contrary to the findings of previous studies, we found that body size clines for birds do not depend on migratory behaviour in general, with migratory and sedentary birds adhering similarly to the heat conservation, heat dissipation and starvation resistance hypotheses. However, we found that migratory behaviour may play a role in the strength of body size clines along productivity gradients, as resident birds showed a positive size–NPP relationship while evidence of this relationship for migratory birds was less clear. In turn, sedentary mammals showed a positive relationship with primary productivity and seasonality, whereas migratory mammals did not. Our results for endotherms suggest that the environmental factors driving geographic intraspecific body size variation may differ and vary in intensity across species. Further, the fact that body size clines for ectotherms were not explained by any coarse-grained environmental predictor hints at the possibility that within-species variation in cold-blooded terrestrial vertebrates may be explained by microclimatic and microhabitat conditions, or intraspecific variations may be limited due to the more limited environmental gradients experienced by the species. Finally, our research highlights important differences with previous studies focusing on interspecific patterns (e.g., mammals), suggesting that while mechanisms are potentially the same, the main drivers of inter- and intraspecific trait variation may differ. Insights into the factors affecting body size variation contribute to a better understanding of the primary mechanisms behind species adaptations and geographic distributions, and can be particularly useful in predicting the effect of climate change on community composition and trait adaptations. Further investigation of the mechanisms underlying body size patterns may benefit from applying mechanistic approaches to better disentangle individual processes through simulation experiments.

CONFLICT OF INTEREST

None of the co-authors has any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data used for this study are available at https://doi.org/10.6084/m9.figshare.17042993. This dataset was generated using raw data following the steps outlined in the Methods. The original data are openly available for download from VertNet (Bloom, 2016a, 2016b, 2016c, 2016d). Scripts and data used in the analyses are provided at https://github.com/anabenlop/BergmannRule.

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