No general relationship between mass and temperature in endothermic species

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Bergmann's rule is a widely-accepted biogeographic rule stating that individuals within a species are smaller in warmer environments. While there are many single-species studies and integrative reviews documenting this pattern, a data-intensive approach has not been used yet to determine the generality of this pattern. We assessed the strength and direction of the intraspecific relationship between temperature and individual mass for 952 bird and mammal species. For eighty-seven percent of species, temperature explained less than 10% of variation in mass, and for 79% of species the correlation was not statistically significant. These results suggest that Bergmann's rule is not general and temperature is not a dominant driver of biogeographic variation in mass. Further understanding of size variation will require integrating multiple processes that influence size. The lack of dominant temperature forcing weakens the justification for the hypothesis that global warming could result in widespread decreases in body size.

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INTRODUCTION

Bergmann's rule describes a negative relationship between body mass and temperature across space that is believed to be common in endothermic species (Bergmann, 1847; Brown and Lee, 1969; Kendeigh, 1969; Freckleton et al., 2003; Carotenuto et al., 2015). Many hypotheses have been proposed to explain this pattern (Blackburn et al., 1999; Ashton, 2002; Watt et al., 2010) including the heat loss hypothesis, which argues that the higher surface area to volume ratio of smaller individuals results in improved heat dissipation in hot environments (Bergmann, 1847). Though originally described for closely-related species (i.e., interspecific; Blackburn et al., 1999), the majority of studies have focused on the intraspecific form of Bergmann's rule (Rensch, 1938; Meiri, 2011) by assessing trends in individual size within a species (Langvatn and Albon, 1986; Gardner et al., 2009; Yom-Tov and Geffen, 2006). Bergmann's rule has been questioned both empirically and mechanistically (McNab, 1971; Geist, 1987; Huston and Wolverton, 2011; Teplitsky & Millien, 2014) but the common consensus from recent reviews is that the pattern is general (Ashton, 2002; Watt et al., 2011; Ashton et al., 2000; Meiri and Dayan, 2003).

It has recently been suggested that this negative relationship between mass and temperature could result in decreasing individual size across species in response to climate change (Sheridan and Bickford, 2011) and that this may be a “third universal response to warming” (Gardner et al., 2011). The resulting shifts in size distributions could significantly alter ecological communities (Brose et al., 2012), especially if the rate of size decrease varies among species (Sheridan and Bickford, 2011). While there is limited empirical research on body size responses to changes in temperature through time (but see Teplitsky and Millien, 2014; Smith et al., 1995; Caruso et al., 2014), the apparent generality of Bergmann's rule across space indicates the likelihood of a similar relationship in response to temperature change across time.

The generality of Bergmann's rule is based on many individual studies that analyze empirical data on body size across an environmental gradient (e.g., Langvatn and Albon, 1986; Barnett, 1977; Fuentes and Jaksic, 1979; Dayan et al., 1989; Sand et al., 1995) and reviews that compile and evaluate the results from these studies (Ashton, 2002; Watt et al., 2010; Meiri and Dayan 2003). Most individual studies of Bergmann's rule are limited by: 1) analyzing only one or a few species (e.g., Langvatn and Albon, 1986); 2) using small numbers of observations (e.g., Fuentes and Jaksic, 1979); 3) only including data at the small scales typical of ecological studies (e.g., Sand et al., 1995); 4) using latitude instead of directly assessing temperature (e.g., Barnett, 1977); and 5) focusing on statistical significance instead of the strength of the relationship (e.g., Dayan et al., 1989). The reviews tabulate the results of these individual studies and assess patterns in the direction and significance of relationships across species. Such aggregation of published results allows for a more general understanding of the pattern but, in addition to limitations of the underlying studies, the conclusions may be influenced by publication bias and selective reporting where studies or individual analyses that do not support Bergmann's rule are published less frequently (Koricheva et al., 2013).

Previous analyses of publication bias in the context of Bergmann’s rule have found no evidence for selective publication, which supports the idea that it is a general rule (Ashton, 2002; Meiri et al., 2004). However, two of the most extensive studies of Bergmann’s rule, which both used museum records to assess dozens of intraspecific Bergmann’s rule relationships simultaneously, found that the majority of species did not exhibit significant negative relationships between latitude and size (McNab, 1971; Meiri et al., 2004). As a result, understanding the generality of this ecophysiological rule and its potential implications for global change requires more extensive analysis.

A data-intensive approach to analyzing Bergmann's rule, evaluating the pattern using

large amounts of broad scale data, has the potential to overcome existing limitations in the literature and provides a new perspective on the generality of the intraspecific form of Bergmann's rule. Understanding the generality of the temperature-mass relationship has important implications for how size will respond to climate change. We use data from Vertnet (Constable et al., 2010), a large compilation of digitized museum records that contains over 700,000 globally distributed individual-level size measures, to evaluate the intraspecific relationship between temperature and mass for 952 mammal and bird species. The usable data consist of 273,901 individuals with an average of 288 individuals per species, with individuals of each species spanning an average of 75 years and 34 latitudinal degrees. This approach reduces or removes many of the limitations to previous approaches and the results suggest that Bergmann's rule is not a strong or general pattern.

RESULTS

Most of the species in this study showed weak non-significant relationships between temperature and mass (Figures 1 and 2). The distribution of correlation coefficients was centered near zero with a mean correlation coefficient of -0.05 across species (Figure 2A). Relationships for 79% of species were not significantly different from zero, while 14% of species' relationships were significant and negative and 7% were significant and positive (Figure 2A). Temperature explained less than 10% of variation in mass (i.e., $-0.316 < r < 0.316$) for 87% of species, indicating that temperature explained very little of the observed variation in mass for these species (Figure 2A).

The weak, non-directional intraspecific relationships indicated by the distribution of correlation coefficients are consistent across taxonomic groups and temporal lags. Mean

correlation coefficients for both endothermic classes are -0.006 and -0.065, for mammals and birds respectively (Figure 2B). Similarly, correlation coefficient distributions were approximately centered on zero for all of the 30 orders analyzed ($-0.2 < \bar{r} < 0.003$ for orders with more than 10 species; Figure 3 and Figure 3—figure supplement 1), or for migrant or nonmigrant bird species (Figure 2-figure supplement 1). Correlation coefficient distributions for temperature-mass relationships using lagged temperatures were centered around zero like those using temperature from the collection year (Figure 4 and Figure 4–figure supplement 1), indicating that there was not a temporal lag effect on the response of species' masses to temperature. Correlation coefficients did not vary systematically by sample size (Figure 5A), extent of variation in temperature or mass (Figure 5B,C), species' average mass (Figure 5D), or species' average latitude (Figure 5E). While temperature is considered the actual driver, some studies use latitude as a proxy when evaluating variation in size (Bergmann, 1847; Stillwell, 2010) Using latitude, the mean correlation coefficient was -0.05 with no statistically significant latitude-mass relationship for 71% of species (Figure 2–figure supplement 2), while the respective values for temperature were -0.05 and 79% (Figure 2A). Results were robust to a variety of decisions and stringencies about how to filter the size (Figure 2–figure supplement 3 and 4) and species data (Figure 2—figure supplement 5 and 6).

DISCUSSION

In contrast to conventional wisdom and several recent review papers, our analysis of 952 species shows little to no support for a negative intraspecific temperature-mass relationship that is sufficiently strong or common to be considered a biogeographic rule. Three quarters of bird and mammal species show no significant change in mass across a temperature gradient and temperature explained less than 10% of intraspecific variation in mass for 87% of species (Figure

2A). This was true regardless of taxonomic group (Figure 2 and 3), temporal lag in temperature (Figure 4), species' size, location, or sampling intensity or extent (Figure 5). These results are consistent with two previous studies that examined museum specimen size measurements across latitude. The first study showed that 22 out of 47 North American mammal species studied had no relationship between latitude and length, and 10 of the 25 significant relationships were opposite the expected direction (McNab, 1971). The second found a similar proportion of non-significant results (42/87), but a lower proportion of significant relationships that opposed the rule (9/45) for carnivorous mammals (Meiri et al., 2004). While more species had significant negative relationships than positive in both our study and these two museum-based studies, in all cases less than half of species had significant negative correlations (14 – 41%). In combination with these two smaller studies, our results suggest that there is little evidence for a strong or general Bergmann's rule when analyzing raw data instead of summarizing published results.

Our results are inconsistent with recent reviews, which have reported that the majority of species conform to Bergmann's rule (Ashton, 2002; Watt et al., 2010; Meiri and Dayan, 2003). While these reviews included results that were either non-significant or opposite of Bergmann's rule, the proportion of significant results in support of Bergmann's rule was higher and therefore resulted in conclusions that supported the generality of the temperature-mass relationship. Generalizing from results in the published literature involves the common challenges of publication bias and selective reporting (Koricheva et al., 2013). In addition, because the underlying Bergmann's rule studies typically report minimal statistical information, often providing only relationship significance or direction instead of p-values or correlation coefficients (Meiri and Dayan, 2003), proper meta-analyses and associated assessments of biological significance are not possible. While several reviews found no evidence for publication bias using limited analyses (Ashton, 2002; Meiri et al., 2004), the notable differences between

168 the conclusions of our data-intensive approach and those from reviews suggests that publication
169 bias in papers about Bergmann's rule warrants further investigation. These differences also
170 demonstrate the value of data-intensive approaches in ecology for overcoming potential
171 weaknesses and biases in the published literature. Directly analyzing large quantities of data
172 from hundreds of species allows us to assess the generality of patterns originally reported in
173 smaller studies while avoiding the risk of publication bias. This approach also makes it easier to
174 integrate other factors that potentially influence size into future analyses. The new insight gained
175 from this data-intensive approach demonstrates the value of investing in large compilations of
176 ecologically-relevant data (Hampton et al., 2013) and the proper training required to work with
177 these datasets (Hampton et al., 2017).

178 Our analyses and conclusions are limited to the intraspecific form of Bergmann's rule.
179 This is the most commonly studied and well-defined form of the relationship and the one most
180 amenable to analyses using large compilations of museum data. Difficulty in interpreting
181 Bergmann's original formulation has resulted in an array of different ideas and implementations
182 of interspecific analyses (Blackburn et al., 1999; Meiri and Thomas, 2007; Watt et al., 2010;
183 Meiri, 2011). The most common forms of these interspecific analyses involve correlations
184 between various species-level size metrics and environmental measures and are conducted at
185 various taxonomic levels from genus to class (e.g., Clauss et al., 2013; Diniz-Filho, 2007; Boyer
186 et al., 2010; Blackburn and Gaston, 1996). Efforts to apply data-intensive approaches to the
187 interspecific form of this relationship will need to address the fact that occurrence records are not
188 evenly distributed across the geographic range of species and determine how the many
189 interpretations of interspecific Bergmann's rule are related to one another and the biological
190 expectations for interspecific responses to temperature.

191 The original formulation of Bergmann's rule, and the scope of our conclusions, apply

192 only to endotherms. However, negative temperature-mass relationships have also been
193 documented in ectotherms, with the pattern referred to as the size-temperature rule (Ray, 1960;
194 Angilletta and Dunham, 2003). In contrast to the hypotheses for Bergmann's rule, which are
195 based primarily on homeostasis (Gardner et al., 2011), the size-temperature rule in ectotherms is
196 thought to result from differences between growth and development rates (Forster et al., 2011).
197 The current version of Vertnet contained ectotherm size data for only seven species, which is not
198 sufficient to complete a comprehensive analysis of the ectotherm size-temperature rule. Future
199 work exploring the ectotherm size-temperature rule in natural systems using data-intensive
200 approaches is necessary for understanding the generality of this rule in ectotherms, and data may
201 be sought for this effort in the literature or via a coordinated effort by museums to continue
202 digitizing size measurements for specimens.

203 A number of mechanisms have been suggested to explain why higher temperatures
204 should result in lower body sizes, including heat loss, starvation, resource availability, migratory
205 ability, and phylogenetic constraints (Blackburn et al., 1999). Most of the proposed hypotheses
206 have not been tested sufficiently to allow for strong conclusions to be drawn about their potential
207 to produce Bergmann's rule (Blackburn et al., 1999; Watt et al., 2010; Teplitsky and Millien,
208 2014) and the widely studied heat loss hypothesis has been questioned for a variety of reasons
209 (Blackburn et al., 1999; Watt et al., 2010; McNab, 1971; James, 1970; McNamara et al., 2016).
210 While no existing hypotheses have been confirmed, it is possible that some processes are
211 producing negative relationships between size and temperature. The lack of a strong relationship
212 does not preclude processes that result in a negative temperature-mass relationship, but it does
213 suggest that these processes are have less influence relative to other factors that influence
214 intraspecific size.

215 The relative importance of the many factors besides temperature that can influence size

216 within a species is as yet unknown. Size is affected by abiotic factors such as humidity and
217 resource availability (Teplitsky and Millien, 2014), characteristics of individuals like clutch size
218 (Boyer et al., 2009), and community context, including if and what kinds of gaps there are in
219 size-related niches (Smith et al., 2010) and the trophic effects of primary productivity on
220 consumer size (Sheridan and Bickford, 2011). Temperature itself can have indirect effects on
221 size, such as via habitat changes in water flow or food availability, that result in size responses
222 opposite of Bergmann's rule (Gardner et al., 2011). Anthropogenic influences have been shown
223 to influence the effect of temperature on size (Faurby and Araùjo, 2016), and similar impacts of
224 dispersal, extinctions, and the varying scales of climate change have been proposed (Clauss et
225 al., 2013). Because our data primarily came from North America, further analyses focused on
226 species native to other continents could reveal differing temperature-mass relationships due to
227 varying temperature regimes. While our work shows that more species have negative significant
228 relationships between temperature and mass than positive, only 21% of species have statistically
229 significant relationships and it consequently appears that some combination of other factors more
230 strongly drives intraspecific size variation for most taxa.

231 The lack of evidence for temperature as a primary determinant of size variation in
232 endothermic species calls into question the hypothesis that decreases in organism size may
233 represent a third universal response to global warming. The potentially general decline in size
234 with warming was addressed by assessments that evaluated dynamic body size responses to
235 temperature using similar approaches to the Bergmann's rule reviews discussed above (Teplitsky
236 and Millien, 2014; Sheridan and Bickford, 2011; Gardner et al., 2011). These temporal reviews
237 had similar results to those for spatial relationships, but the conclusions of these studies clearly
238 noted the variability in body size responses and the need for future data-intensive work (Sheridan
239 and Bickford, 2011; Gardner et al., 2011) using broader temperature ranges (Teplitsky and

240 Millien, 2014) to fully assess the temperature-size relationship.

241 Our results in combination with those from other studies suggest that much of the
242 observed variation in size is not explained simply by temperature. While there is still potential
243 for the size of endotherms, and other aspects of organismal physiology and morphology, to
244 respond to both geographic gradients in temperature and climate change, these responses may
245 not be as easily explained solely by temperature as has been suggested (Sheridan & Bickford,
246 2011; Gardner et al., 2011). This requires that future attempts to explain variation in the size of
247 individuals across space or time use an integrative approach to include the influence of multiple
248 factors, and their potential interactions, on organism size. This will be facilitated by analyzing
249 spatiotemporal data similar to that used in this study, which includes wide ranges of time, space,
250 and environmental conditions for large numbers of species and individuals. This data-intensive
251 approach provides a unique perspective on the general responses of bird and mammal species to
252 temperature, and has potential to assist in further investigation of the complex combinations of
253 factors that determine biogeographic patterns of endotherm size and how species respond to
254 changes in climate.

255

256 **METHODS**

257 **Data**

258 Organismal data were obtained from Vertnet, a publicly available data platform for
259 digitized specimen records from museum collections primarily in North America, but also
260 includes global data (Constable et al., 2013). Body mass is routinely measured when organisms
261 are collected, with relatively high precision and consistent methods, by most field biologists,
262 whose intent is to use those organisms for research and preservation in natural history collections
263 (Winker, 2000; Hoffmann, 2010). These measurements are included on written labels and

ledgers associated with specimens, which are digitized and provided in standard formats, e.g., Darwin Core (Wieczorek, 2012). In addition to other trait information, mass has recently been extracted from Darwin Core formatted records published in Vertnet and converted to a more usable form (Guralnick et al., 2016). This crucial step reduces variation in how these measurements are reported by standardizing the naming conventions and harmonizing all measurement values to the same units (Guralnick et al., 2016). We downloaded the entire datasets for Mammalia, Aves, Amphibia, and Reptilia available in September 2016 (Bloom et al., 2016a; Bloom et al., 2016b; Bloom et al., 2016c; Bloom et al., 2016d) using the Data Retriever (Morris and White, 2013) and filtered for those records that had mass measurements available. Fossil specimen records with mass measurements were removed.

We only analyzed species with at least 30 georeferenced individuals whose collection dates spanned at least 20 years and collection locations at least five degrees latitude, in order to ensure sufficient sample size and spatiotemporal extent to accurately represent each species' temperature-mass relationship. To determine if these thresholds were appropriate, we additionally explored the impact of increasing and decreasing them (Figure 2–figure supplement 5 and 6). We selected individual records with geographic coordinates for collection location, collection dates between 1900 and 2010, and species-level taxonomic identification, which were evaluated to assure no issues with synonymy or clear taxon concept issues. To minimize inclusion of records of non-adult specimens, we identified the smallest mass associated with an identified adult life stage category for each species and removed all records with mass values below this minimum adult size. Results were not qualitatively different due to either additional filtering based on specimen lifestage (Figure 2–figure supplement 3) or removal of outliers (Figure 2–figure supplement 4). Temperatures were obtained from the Udel_AirT_Precip global terrestrial raster provided by NOAA from their website at http://www.esrl.noaa.gov/psd/, a 0.5

288 by 0.5 decimal degree grid of monthly mean temperatures from 1900 to 2010 (Willmott and
289 Matsuura, 2001). For each specimen, the mean annual temperature at its collection location was
290 extracted for the year of collection.

291 This resulted in a final dataset containing records for 273,901 individuals from 952 bird
292 and mammal species (MSB Mammal Collection (Arctos), 2015; Ornithology Collection
293 Passeriformes - Royal Ontario Museum, 2015; MVZ Mammal Collection (Arctos), 2015; MVZ
294 Bird Collection (Arctos), 2015; KUBI Mammalogy Collection, 2016; CAS Ornithology (ORN),
295 2015; DMNS Bird Collection (Arctos), 2015; UCLA Donald R, 2015; DMNS Mammal
296 Collection (Arctos), 2015; UAM Mammal Collection (Arctos), 2015; UWBM Mammalogy
297 Collection, 2015; UAM Bird Collection (Arctos), 2015; UMMZ Birds Collection, 2015; CUMV
298 Bird Collection (Arctos), 2015; CUMV Mammal Collection (Arctos), 2015; MLZ Bird
299 Collection (Arctos), 2015; LACM Vertebrate Collection, 2015; CHAS Mammalogy Collection
300 (Arctos), 2016; Ornithology Collection Non Passeriformes - Royal Ontario Museum, 2015;
301 KUBI Ornithology Collection, 2014; MSB Bird Collection (Arctos), 2015; Biodiversity
302 Research and Teaching Collections - TCWC Vertebrates, 2015; TTU Mammals Collection,
303 2015; CAS Mammalogy (MAM), 2015; Vertebrate Zoology Division - Ornithology, Yale
304 Peabody Museum, 2015; University of Alberta Mammalogy Collection (UAMZ), 2015; UAZ
305 Mammal Collection, 2016; Conner Museum, 2015; SBMNH Vertebrate Zoology, 2015; Cowan
306 Tetrapod Collection - Birds, 2015; Cowan Tetrapod Collection - Mammals, 2015; NMMNH
307 Mammal, 2015; Schmidt Museum of Natural History_Mammals, 2015; USAC Mammals
308 Collection, 2013; MLZ Mammal Collection (Arctos), 2015; Ohio State University Tetrapod
309 Division - Bird Collection (OSUM), 2015; AMNH Mammal Collections, 2015; DMNH Birds,
310 2015; CM Birds Collection, 2015; WNMU Mammal Collection (Arctos), 2015; UCM Mammals
311 Collection, 2015; UWYMV Bird Collection (Arctos), 2015; NCSM Mammals Collection, 2015;

Vertebrate Zoology Division - Mammalogy, Yale Peabody Museum, 2015; HSU Wildlife Mammals, 2016; WNMU Bird Collection (Arctos), 2015; UWBM Ornithology Collection, 2015; UCM Birds, 2015; University of Alberta Ornithology Collection (UAMZ), 2015; SDNHM Birds Collection, 2015). The average number of individuals per species was 288, ranging from 30 to 15,415 individuals. The species in the dataset were diverse, including volant, non-volant, placental, and marsupial mammals, and both migratory and non-migratory birds. There were species from all continents except Antarctica, though the majority of the data were concentrated in North America (Figure 1A). The distribution of the species' mean masses was strongly right-skewed, as expected for broad scale size distributions (Brown and Nicoletto, 1991), with 74% of species having average masses less than 100 g. Size ranged from very small (3.7 g desert shrew *Notiosorex crawfordi* and 2.6 g calliope hummingbird *Stellula calliope*) to very large (63 kg harbor seal *Phoca vitulina* and 5.8 kg wild turkey *Meleagris gallopavo*). These specimen data and code have been deposited online in the Dryad Data Repository (http://datadryad.org/).

Analysis

We fit the intraspecific relationship between mean annual temperature and mass for each species with ordinary least squares linear regression (e.g., Figure 1B,C,D and Figure 1–figure supplement 1-12) using the statsmodels.formula.api module in Python (Seabold and Perktold, 2010). The strength of each species' relationship was characterized by the correlation coefficient and its significant at alpha of 0.05. When assessing statistical significance with large numbers of correlations it is important to consider the expected distribution of these correlations under the null model that no correlation exists for any species.

We addressed this issue by using false discovery rate control (Benajmini and Hochberg, 1995) implemented with the stats package in R (R Core Team, 2016). This method determines

336 the expected distribution of values for p (or Z) in the case where no relationship exists for
337 individual correlation and adjusts observed values to control for excessive false positives.
338 Specifically, it maintains the Type I error rate (proportion of false positives) across all tests at the
339 chosen value of alpha and therefore gives an accurate estimate of the number of significant
340 relationships (Benajmini and Hochberg, 1995). This allows us to estimate the number of species
341 with true positive and negative correlations (i.e., those that have values that exceed those
342 expected from the null distribution). We then compared the number of species with positive and
343 negative correlation coefficients, and the proportion of those with statistically significant
344 adjusted p-values.

345 We investigated various potential correlates of the strength of Bergmann's rule. Because
346 it has been argued that Bergmann's rule is exhibited more strongly by some groups than others
347 (McNab, 1971), we examined correlation coefficient distributions within each class and order.
348 Additionally, distributions for migrant and nonmigrant bird species were compared due to
349 conflicting evidence about the impact of migration on temperature-mass relationships (Ashton,
350 2002). As a temporal lag in size response to temperature is likely due to individuals of a species
351 responding to temperatures prior to their collection year (e.g., Stacey and Fellowes, 2002), we
352 assessed species' temperature-mass relationships using temperatures from 1 to 110 years prior to
353 collection year. We also examined the relationship between species' correlation coefficients and
354 five variables to understand potential statistical and biological influences on the results. We did
355 so with the number of individuals, temperature range, and mass range to determine if the
356 relationship was stronger when more data points or more widely varying values were available.
357 Because it has been argued that Bergmann's rule is stronger in larger species (Steudel et al.,
358 1994) and at higher latitudes (Freckleton et al., 2003; Faurby and Araùjo, 2016), we examined
359 variability with both mean mass and mean latitude for each species. We also conducted all

analyses using latitude instead of mean annual temperature.

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No competing financial interests

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FIGURE LEGENDS

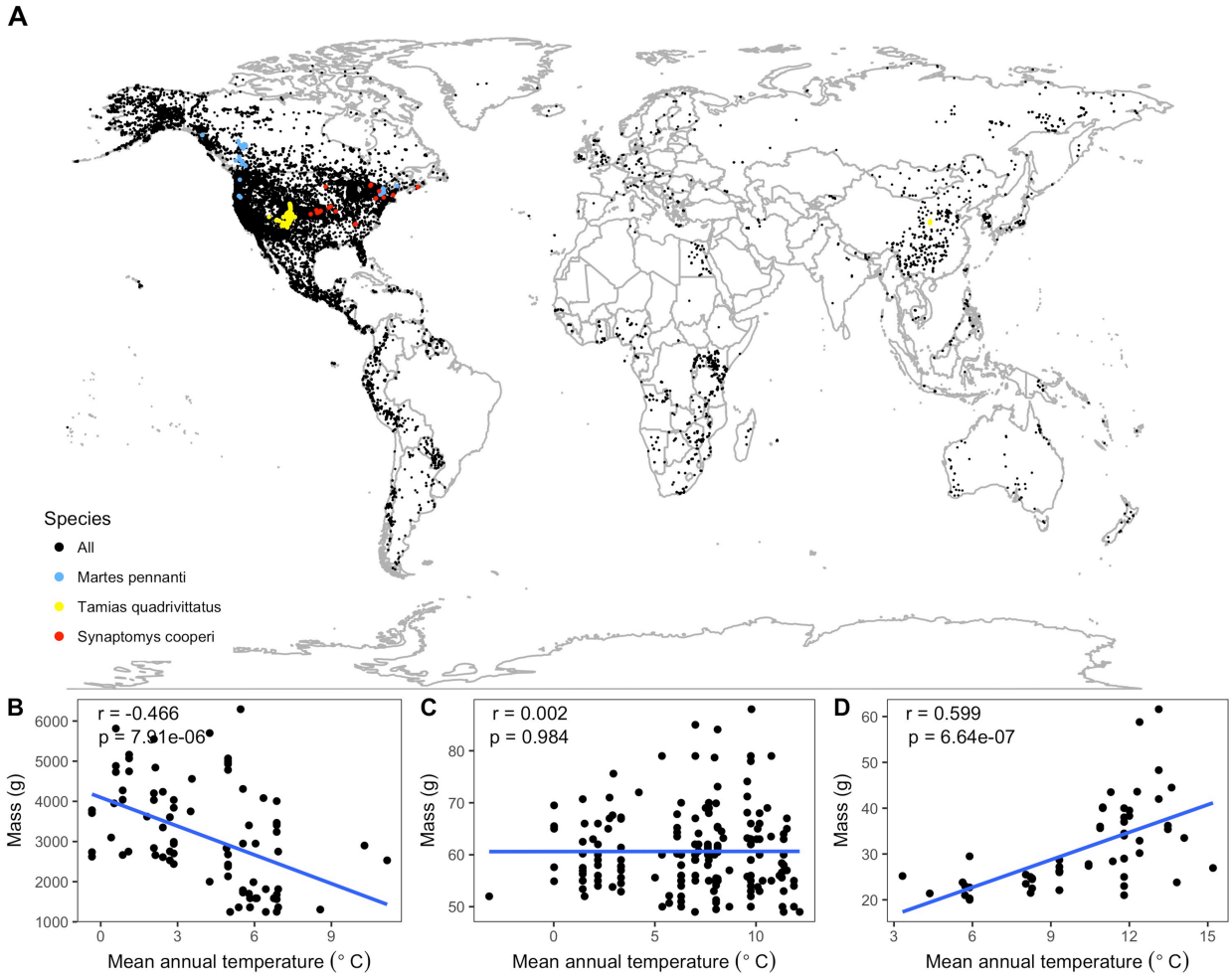


Figure 1. Species spatial distributions and selected temperature-mass relationships. (A) Spatial collection locations of all individual specimens. All species shown with black points except three species, whose relationships between mean annual temperature and mass are shown at bottom (B-D), are marked with colored points. These species were chosen as representative of the variability in relationship strength and direction exhibited by the 952 species from the study: *Martes pennanti* had a negative relationship with temperature explaining a substantial amount of variation in mass (B; blue points); *Tamias quadrivittatus* had no directional relationship between temperature and mass with temperature having little explanatory power (C; yellow points); *Synaptomys cooperi* had a strong positive temperature-mass relationship with a correlation coefficient (r) in the 99th percentile of all species' values (D; red points). Intraspecific temperature-mass relationships are shown with black circles for all individuals and ordinary least squares regression trends as blue lines. Linear regression correlation coefficients and p-values in upper left hand corner of figure for each species. See figure supplement 1.

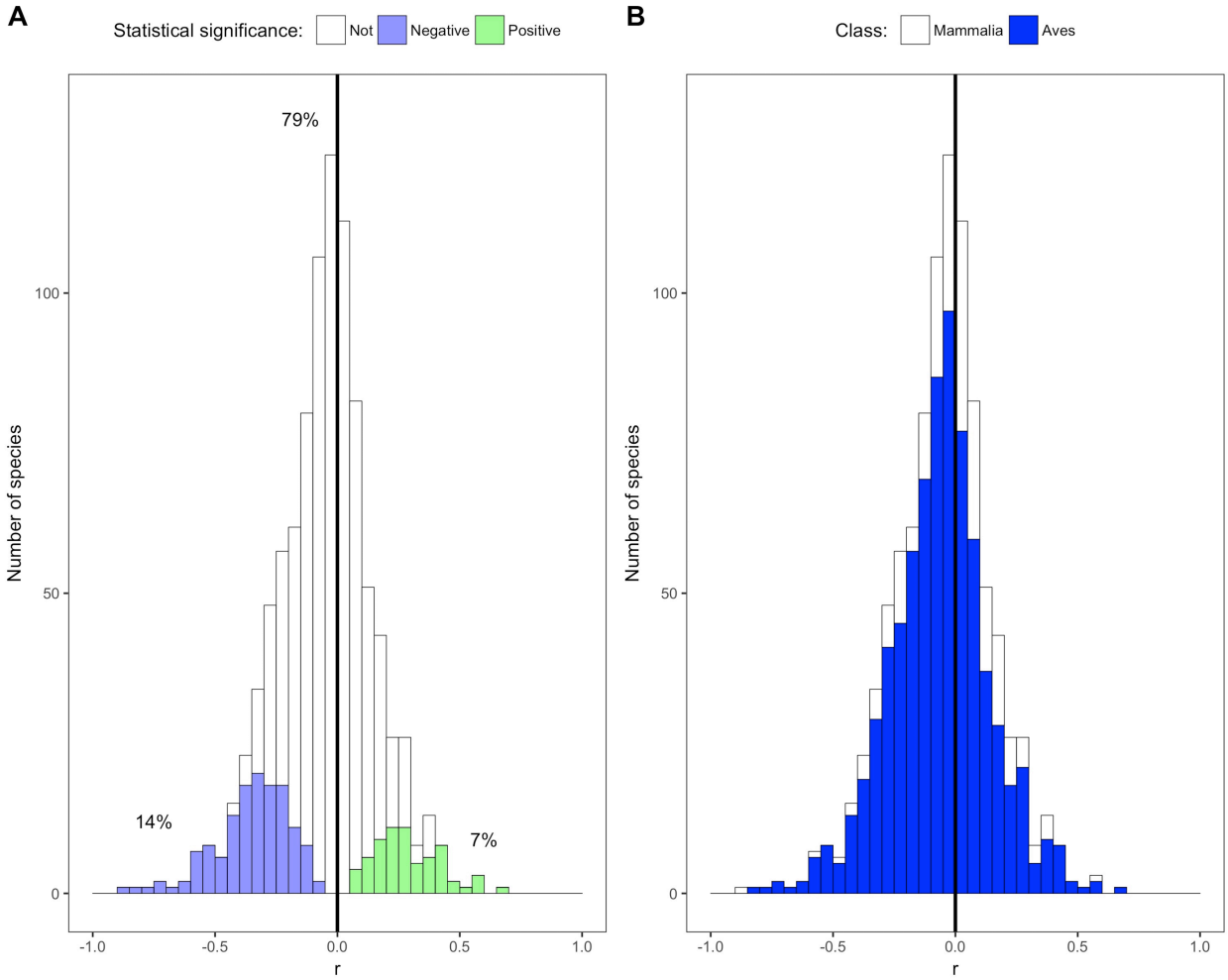


Figure 2. Species correlation coefficients by statistical significance and taxonomic class. (A) Stacked histogram of correlation coefficients (r) for all species' intraspecific temperature-mass relationships. Colored bars show species with statistically significant relationships, both negative (purple) and positive (green), while white bars indicate species with relationship slopes that are not significantly different from zero. Percentages shown are percentages of species in each group. (B) Stacked histogram of all species' correlation coefficients with bar color corresponding to taxonomic class. Dark vertical lines are correlation coefficients of zero. See figure supplements 1-6.

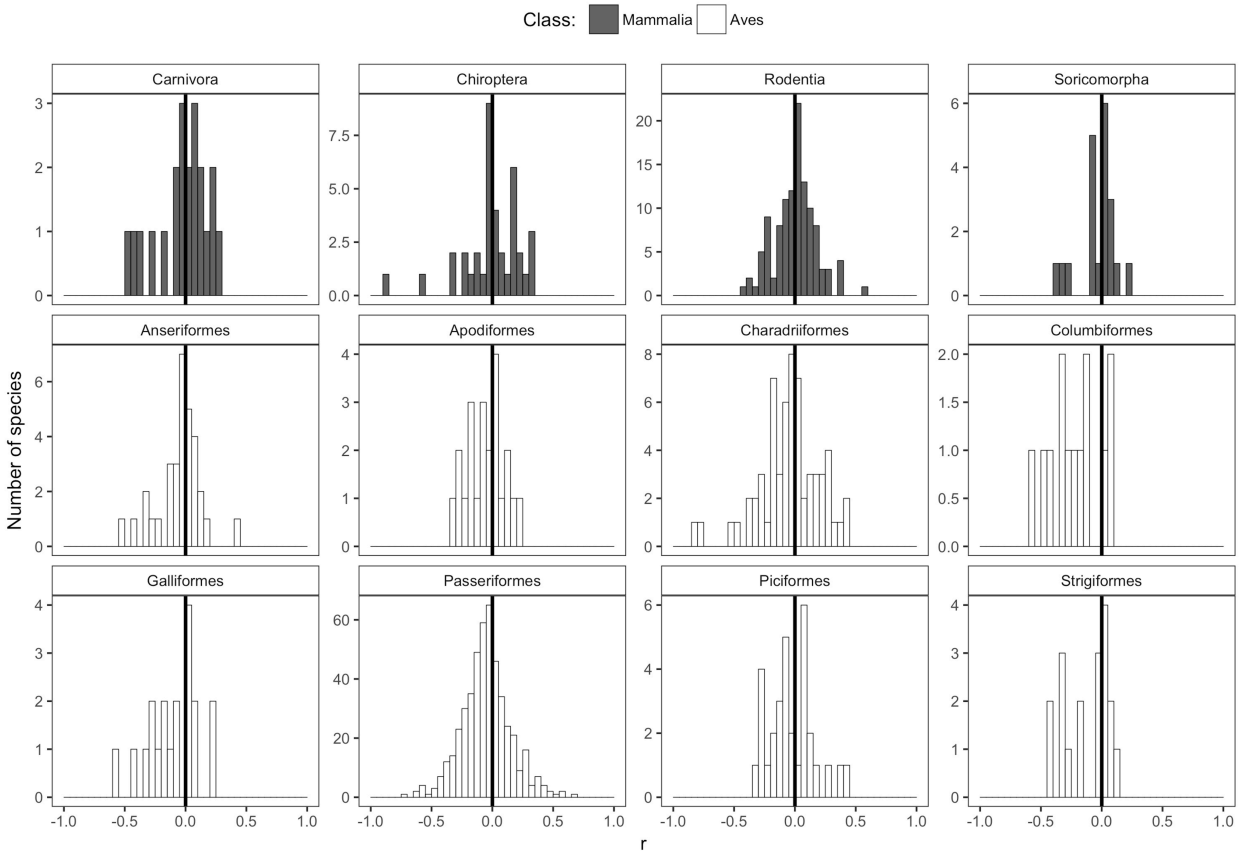
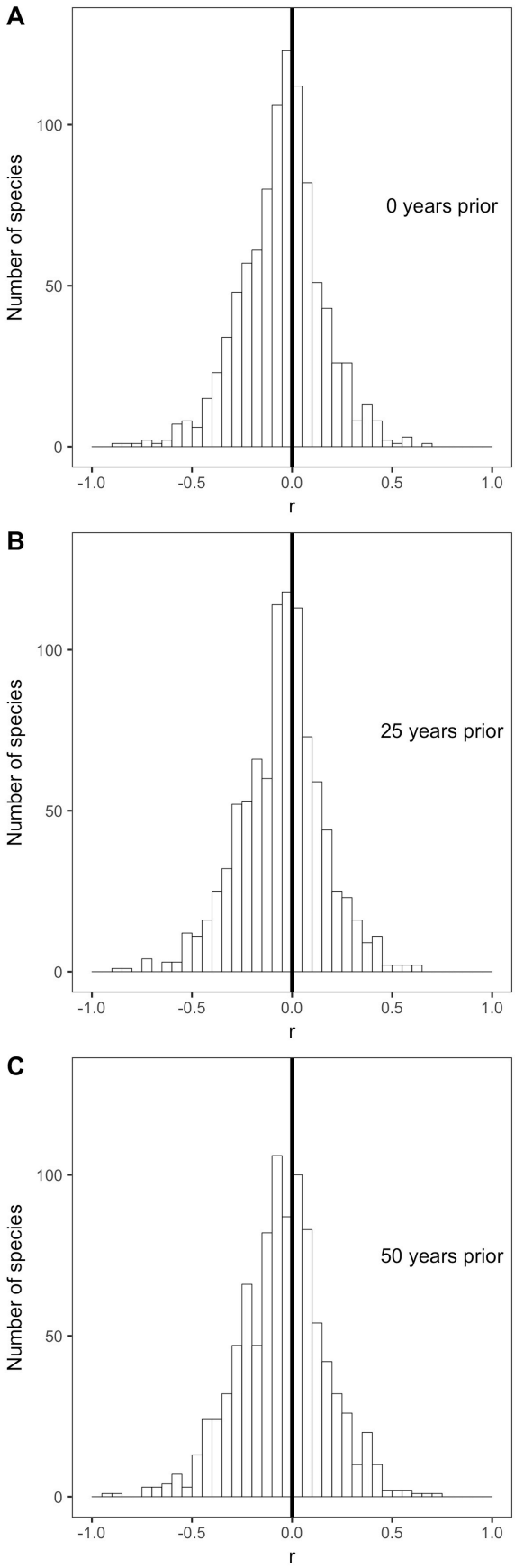


Figure 3. Species correlation coefficients for selected taxonomic orders. Histograms of correlation coefficients (r) from intraspecific temperature-mass relationships for each taxonomic order represented by more than ten species, with order shown above histogram. Height of y-axis varies depending on number of species. Bar color indicates taxonomic class. Dark vertical lines are correlation coefficients of zero. For remaining orders, see figure supplement 1.


A
Number of species
100
50
0
0 years prior
-1.0
-0.5
0.0
0.5
1.0
r
B
Number of species
100
50
0
25 years prior
-1.0
-0.5
0.0
0.5
1.0
r
C
Number of species
100
50
0
50 years prior
-1.0
-0.5
0.0
0.5
1.0
r

740

Figure 4. Species correlation coefficients with selected past year temperatures. Histograms of correlation coefficients (r) for all species' intraspecific temperature-mass relationships with mean annual temperature from (A) the year in which individuals were collected, (B) 25 years prior to collection year, and (C) 50 years prior to collection year. Dark vertical lines are correlation coefficients of zero. For all past year temperatures, see figure supplement 1.

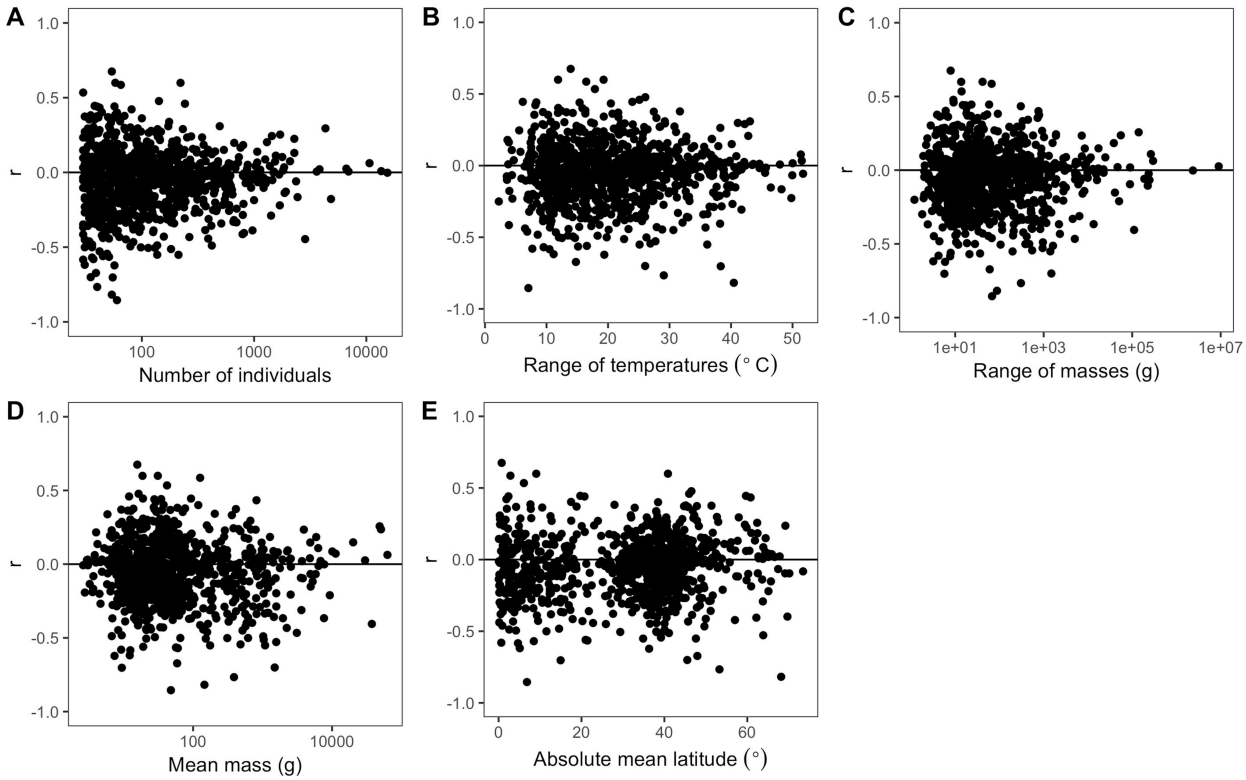


Figure 5. Variability of species correlation coefficients across several variables. Variation in all species' correlation coefficients (r) across the following variables for each species: (A) number of individuals, (B) difference between hottest and coldest collection year temperatures, (C) mass range, (D) mean mass, and (E) absolute mean latitude. Horizontal lines are correlation coefficients of zero. The x-axes of some plots (A, C, D) are on a log scale to better show spread of values.