**Temporal responses of mammal body size to increasing temperature**

Kristina Riemer, Ethan P White

**Abstract**

**Introduction**

Changes in climate can influence the traits of organisms, resulting in downstream effects on the functioning of natural systems. In particular, the potential for organisms to become smaller in response to increasing global temperatures has received growing attention as a potential universal response to climate change (Gardner et al., 2011; Sheridan and Bickford, 2011; Riemer et al., 2018a). The idea of warmer temperatures possibly resulting in decreased body size is based on Bergmann’s rule, a negative spatial relationship between the size of individuals of endotherm species and the temperature of the location at which they occur (Bergmann, 1847; Brown and Lee, 1969; Ashton, 2002; Freckleton et al., 2003; Meiri & Dayan, 2003). This rule has been extrapolated to predict that increasing temperatures from climate change should cause individuals of endotherm species to decrease in size as temperatures increase. This has been supported by syntheses of published studies, which suggest that endotherms have generally been decreasing in size over the last several decades (Gardner et al., 2011; Sheridan and Bickford, 2011; Yom-Tov and Geffen, 2011). Because organismal size is an important ecological characteristic that affects many aspects of ecosystems, including metabolic rates (Brown et al., 2004), food web structure (Woodward et al., 2005), and energy flux (Dickie et al., 2018), changes in size due to climate change are likely to influence ecosystem structure and function (Riemer et al., 2018a; Ohlberger et al., 2011; Yvon-Durocher and Allen, 2012).

In ectotherms, the mechanism that underlies the relationship between temperature and organismal size is well supported by empirical and theoretical work (van der Have and de Jong, 1996; Walters and Hassall, 2006; Forster et al., 2011). In contrast, most proposed mechanisms for endotherms have been called into question (Watt et al., 2010) and the generality of the empirical relationship has been cast in doubt by data-intensive analysis that evaluate Bergmann’s rule for man species simultaneously (McNab, 1971; Meiri et al., 2004; Riemer et al., 2018b). For example, when this relationship was recently examined for nearly 1,000 bird and mammal species using a century of global data, only 14% of species showed significant negative relationships (Riemer et al., 2018b). This calls into question how likely it is that endotherms will decrease in size in response to temperature shifts from climate change.

These data-intensive studies generally use museum collections and therefore usually have mixed spatial and temporal data as specimens are sampled across both space and time (McNab, 1971; Meiri et al., 2004; Riemer et al., 2018b). Therefore, while these analyses question Bergmann’s rule in general, they do not directly address whether organisms will tend to get small through time because responses of ecosystems across time do not necessarily match their responses across space (Fukami and Wardle, 2005). Recent studies that have suggested that species are getting smaller through time are limited by small numbers of species (Teplitsky et al., 2008; Husby et al., 2011; Canale et al., 2016), small numbers of sites (Van Buskirk et al., 2010; Salewski et al., 2010), and data that is collected over short time periods (Smith et al., 1998). Syntheses of these results (e.g., Millien et al., 2006) are potentially affected by both limitations of individual studies and potential publication bias due to negative results being less frequently published (Koricheva et al., 2013; Riemer et al., 2018b). Therefore, in order to determine how the size of species will respond to climate change, shifts in size and their relationship to increasing temperature needs to be examined in a data-intensive manner.

We directly assessed temporal shifts in body size and how these shifts related to changing temperature in a data-intensive manner by compiling long-term time series data on mammal communities and their associated temperatures from three geographic locations. This consisted of size measurements for 128,710 individuals, which were used to determine the average annual mass of 32 unique species-site combinations with observations for at least five individual years spread across a minimum timespan of a decade. This data-intensive approach addresses limitations of previous work on the temperature-mass relationship, which consisted of studies on single species and meta-analyses derived from those studies.

**Methods**

*Datasets*

Organismal size data was compiled from three long-term studies of small mammals, which all had individual-level body mass measurements. We only included datasets that had at least ten years of continuous data. Two of the sites, Portal and Fray Jorge, are long-term experimental studies of community dynamics in mammal communities. Portal is located in the United States in southeastern Arizona (Ernest et al., 2018). Fray Jorge is in the national park of the same name in Chile (Kelt et al., 2013). These two datasets were downloaded using the Data Retriever (Morris and White, 2013; Senyondo et al., 2017), with additional metadata taken from Ecological Archives. The Sevilleta dataset is from a Long Term Ecological Research project in the southwestern United States, which is collected because it is at the intersection of several major biomes. Data are collected at eight subsites that are in close proximity, which we chose to integrate due to similar patterns across the sites (Supplement 1). This time series dataset was downloaded, along with metadata, from the University of New Mexico digital repository (Newsome, 2016). The locations of the three sites are shown in Figure 1.

From each dataset, we retained only individual records that were identified as a rodent species, had an associated mass measurement, and were indicated as adults. For the two experimental sites, Portal and Fray Jorge, only individuals collected from control treatments were included. We kept all instances of the same individual being recaptured, which is common at these sites. We only included individuals of each species from years in which at least 15 individuals were collected, as it has been shown that a signal of temporal size change is noticeable with a minimum of 14 specimens per year for mammals (Yom-Tov & Geffen, 2011). After restricting each species data to include only those years that had data for at least 15 individuals, we kept only those species that had at least five years of data. Doubling these two thresholds did not change trends in temporal mass change or the relationship between temperature and mass (Supplement 2). The resulting dataset had 32 mass time series (i.e., unique combinations of species and sites; Supplement 3) from 128,710 individual records and 25 species (Table 1). Trends in mass for species common to more than one site were compared.

For temperature data, we used a global dataset with monthly average temperature values from 1900 to 2014 on a 0.5 degrees latitude by 0.5 degrees longitude grid, which is created and maintained by the University of Delaware and National Oceanic and Atmospheric Administration (Willmott and Matsuura, 2001). The coordinates for each of the three sites were determined from metadata or related citations (Aguilera et al., 2016), and were used to extract all of the monthly temperatures for each site from the temperature dataset. Mean annual temperatures were calculated from the monthly temperatures, and then were combined with the mass dataset to provide a temperature for each species at each site in each year.

*Analysis*

We visually examined how temperature and mass varied through time at each site, and compared each species mean annual mass with corresponding average annual temperatures using linear regression. We calculated and compiled the r values from all regressions to evaluate the strength and direction of the temperature-mass relationship among all species at each site. To examine how mass and temperature concurrently changed over time, we compared the percent change in each species mass to the absolute change in temperature over the years with sufficient data.

We additionally used a dynamic regression model of the mass time series for each species to determine the effect of temperature while controlling for temporal autocorrelation. We used an ARIMA model with an automatically chosen order, after confirming that this order was appropriate. Mean annual temperature was included as an external variable and the resulting model residuals were reviewed. All model diagnostics are in Supplement 4. To determine the effect of temperature on mass, we calculated the p-value for each species, which were adjusted to take into account for multiple comparisons (Benajmini & Hochberg, 1995), and chose an alpha cut-off of 0.05. We additionally determined the trend in each species mass time series using a dynamic regression model including drift. All cleaning and analysis was completed using R (R Core Team, 2016), with code and data downloads provided reproducibly on GitHub (https://github.com/KristinaRiemer/temporal\_MRT) and archived on Zenodo (citation).

**Results**

Temperatures increased at all sites (Fig. 2A, B, C) in accordance with broader scale climate change. Most species time series (one time series per species per site) had positive slopes (66%; Fig. 2D, E, F), indicating that increases in size were most common, in opposition to the expected trend. Most of these trends were weak, with only 6% being statistically significant (Fig. 2G, H, I; Supplement 5). Most time series also showed no significant relationship between temperature and mass over time (66%; Fig. 3D, E, F; Supplement 6). Of the relationships that were significant, almost all of them (10 out of 11) had positive relationships between mean annual mass and mean annual temperature, instead of the expected negative relationship (1 out of 11: Fig. 3; Supplement 7). There was no relationship between the absolute change in temperature over the time series and the percent change in species mass (Fig. 4). Most relationships are in the upper right quadrant (increase in temperature and increase in size), instead of the lower right or upper left which would indicate the expected negative temperature-mass relationships (Fig. 4). There were seven species that occurred at both the Portal and Sevilleta sites, of which four had opposite relationships between temperature and mass at the two sites (Supplement 8).

**Discussion**

Our results do not support a general decrease in size through time for endotherm species or a general negative relationship between body size and temperature at a single site time series. Instead, species, showed idiosyncratic changes through time and relationships with temperature at each site, with some species increasing in size, some remaining unchanged, and others decreasing in size. This variability occurred even within a single species, as three of the seven species that occurred at more than one site had different size responses at different sites (Supplement 8). Additionally, most species had weak or non-significant relationships between temperature and mass. That these relationships were weak and variable in direction indicates that changes in temperature are unlikely to be a dominant driver of shifts in mammal body size, which further suggests that declining body size is not likely to be a third universal response to climate change in endotherms (Gardner et al., 2011; Sheridan and Bickford, 2011).

While temperature does not seem to dominate dynamic changes in size, this does not mean that it has no influence on size. Body size is affected by a wide variety of biotic and abiotic factors, including resource availability (McNab, 2010), anthropogenic fragmentation (Lomolino & Perault, 2007), island size (Lomolino, 2005), and competition from other species (Menge, 1972). Variation in the response of body size across time has been previously documented and ascribed to other environmental changes (Gardner et al., 2011; Yom-Tov & Geffen, 2011; Sheridan & Bickford, 2011). For example, one mammal species was shown to have increased in size due to plants developing later in the year (Canale et al., 2016) and declining polar bear size was linked to the availability of sea ice (Stirling and Derocher, 2012). Therefore, even if temperature directly influences size across time, this influence may be overpowered by the other factors influencing size, resulting in there not being general trends in size.

While temperature could influence size in endotherms, the mechanism underlying this remains unclear. While empirical evidence of a negative temperature-mass relationship in endotherms has been documented for over a century, there is no agreed upon mechanistic explanation though many have been proposed. The initial and most commonly referenced hypothesis is that it is beneficial for individuals to be smaller in warmer environments because they have an increasing surface area to volume ratio and therefore lose heat relatively more quickly (Bergmann, 1847). However, there is no direct evidence for this mechanism (McNab, 2010) and it has been shown that morphological changes in fur characteristics are more effective than heat regulation for some mammals (Steudel et al., 1994). Other proposed mechanisms include starvation resistance, dispersal, predator-prey interactions, and productivity pulses but none of these mechanisms have been directly supported (Blackburn et al., 1999; Watt et al., 2010).

Our results suggest that the response of mammal body size to changes in climate are likely to be highly variable. However, while our data include over 100,000 individual size measurements, it is still too limited in scope to draw general conclusions about how endotherm size will change in the future. Doing so will require increasing the number of locations and species sampled. Having more data for the same species in multiple geographic locations will also be important for assessing the observed variability of temperature-mass relationships within species observed in this study. The taxonomic breadth of this analysis should also be expanded to include larger and non-nocturnal mammals, and to bird species. An analysis of birds in this context is particularly important because there are some smaller recent studies suggesting decreasing size in bird size (Van Buskirk et al., 2010; Husby et al., 2011; Teplitsky et al., 2008). Sites with more diverse environments, including constant or decreasing temperatures and greater precipitation, should also be included to determine the generality of the temporal size response and how it is influenced by climate factors besides temperature. Finally, mean annual temperature may not be the most important aspect of temperature to measure. Minimum or maximum temperatures may have more directly influences on species sizes (e.g., Smith et al., 1995).

The variable size response to temperature across time for the mammal species in this study calls into question the idea that decreases in size will represent a third universal response to global warming as has been proposed (Gardner et al., 2011; Sheridan and Bickford, 2011). Body sizes are likely responding to many factors that interact in potentially complex and non-linear ways. Understanding the key factors influencing size and how they will interact to determine size response to climate change should be a priority due to the importance of size in ecological systems.

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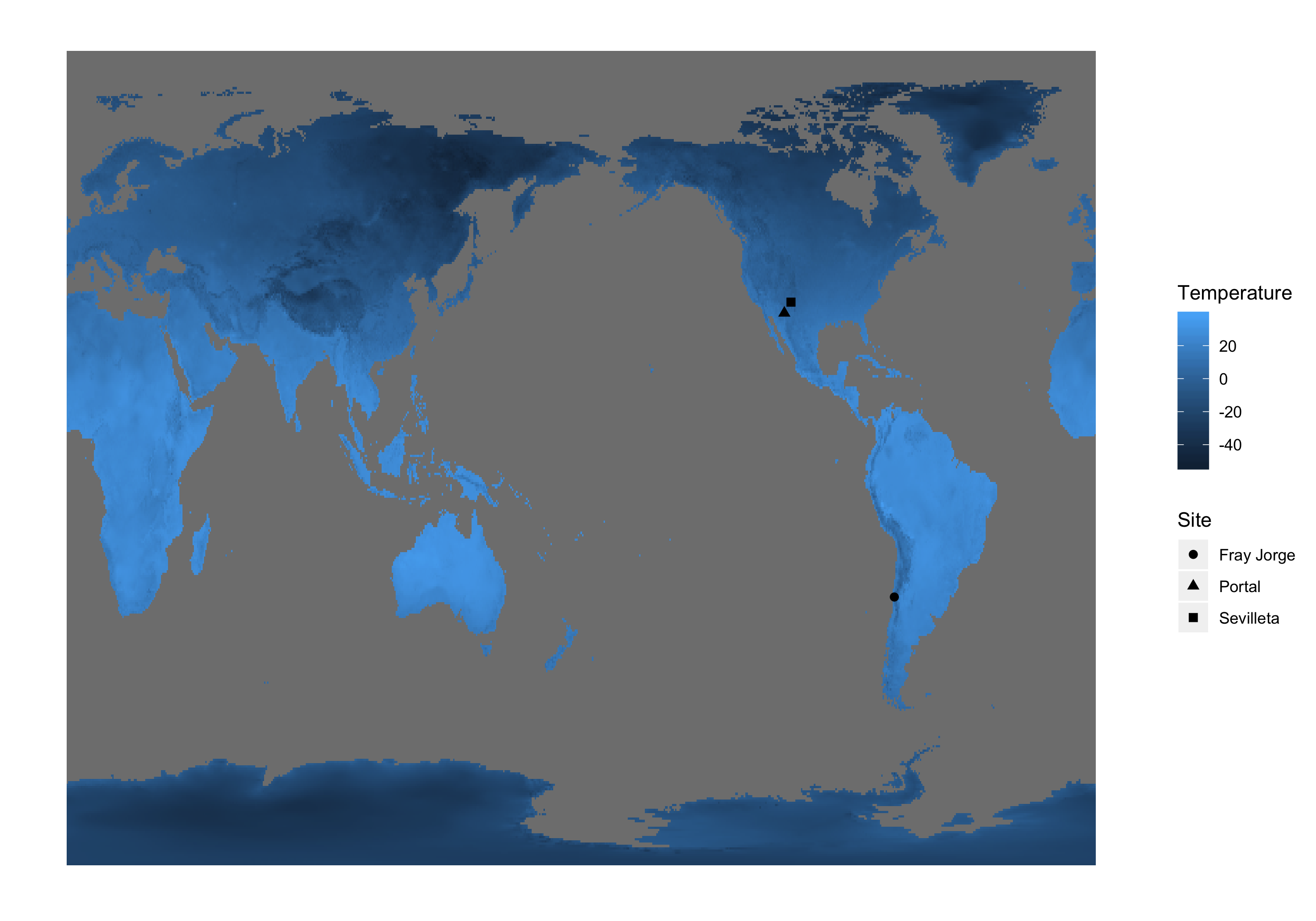
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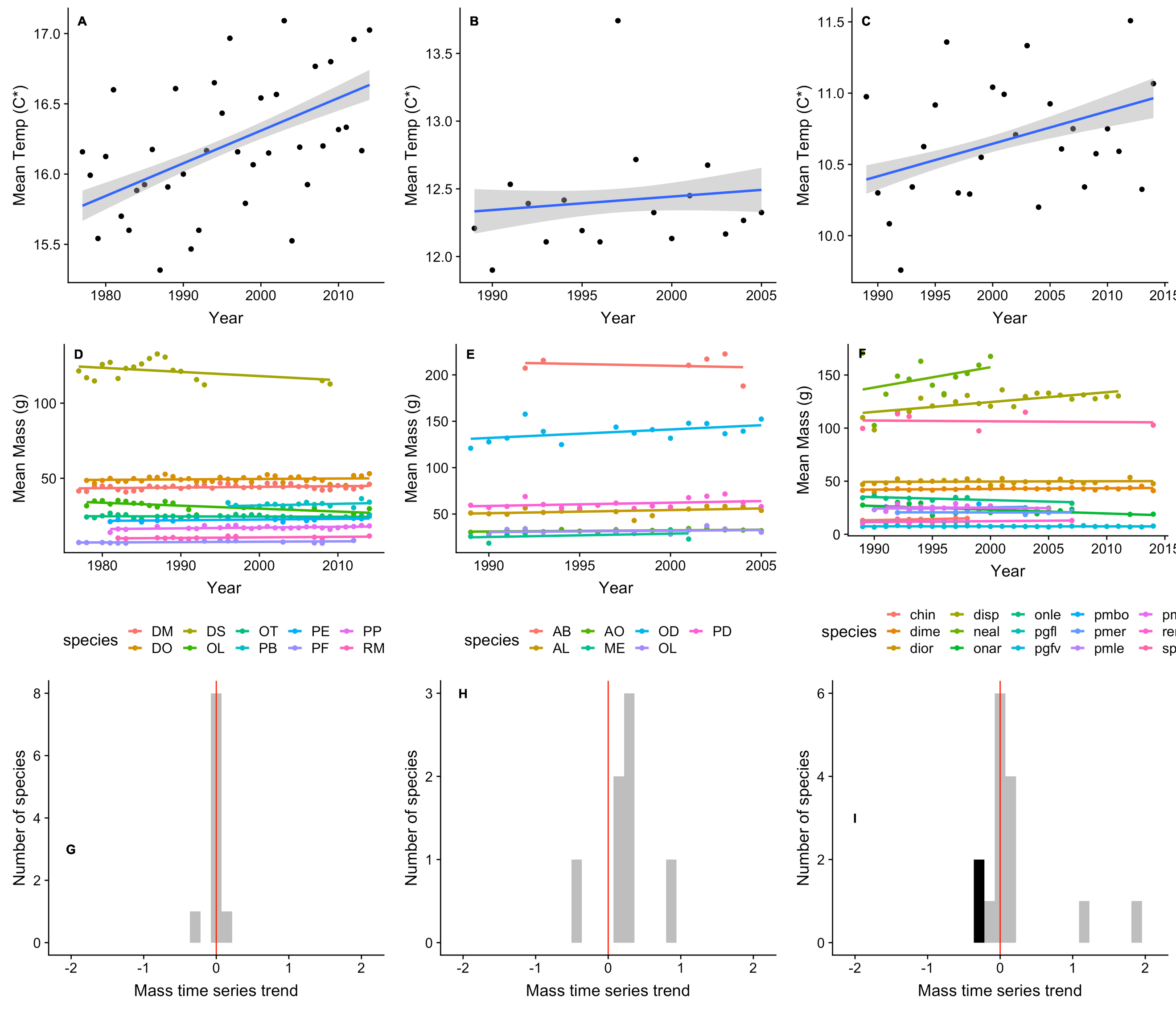
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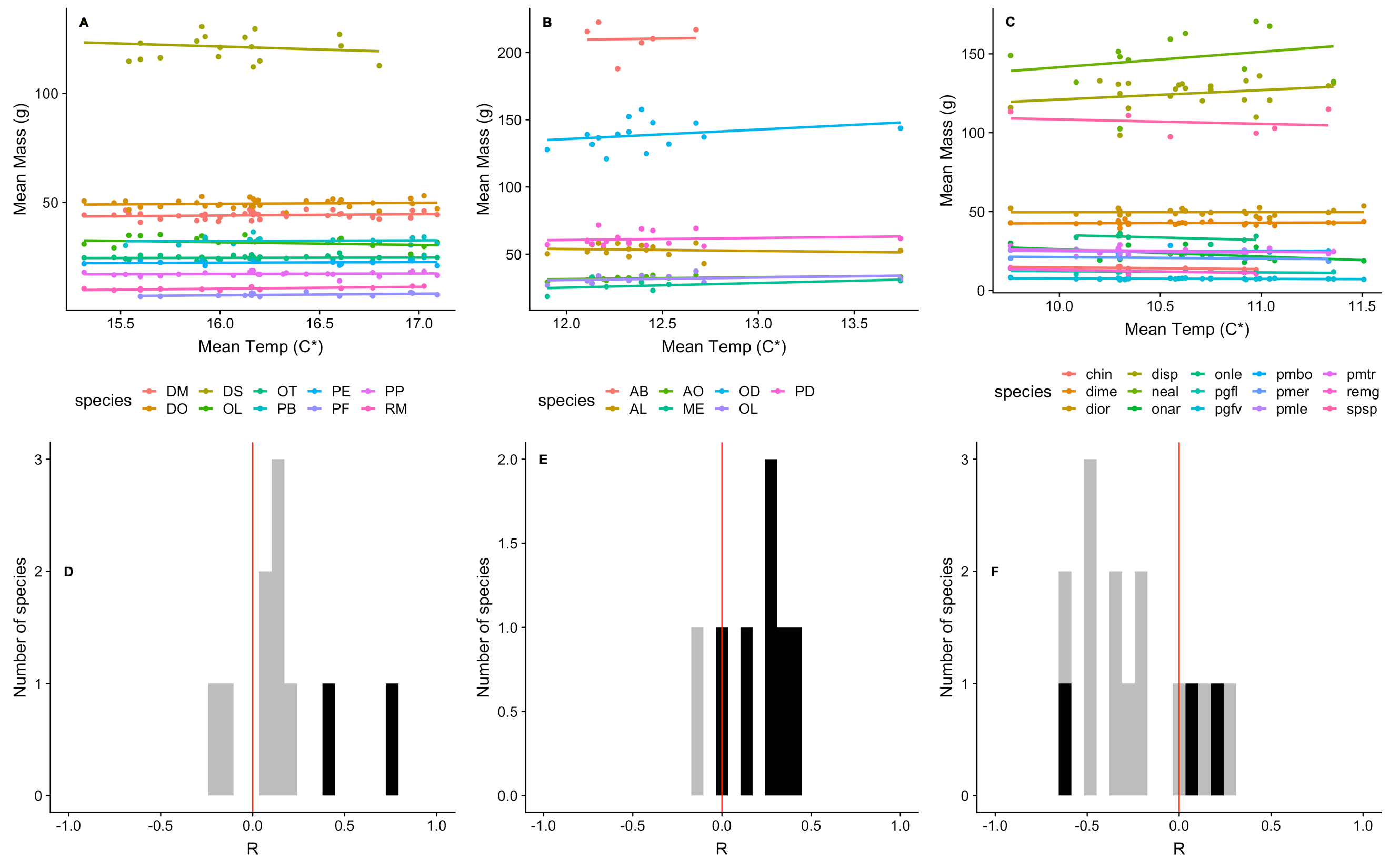
**Main figures**



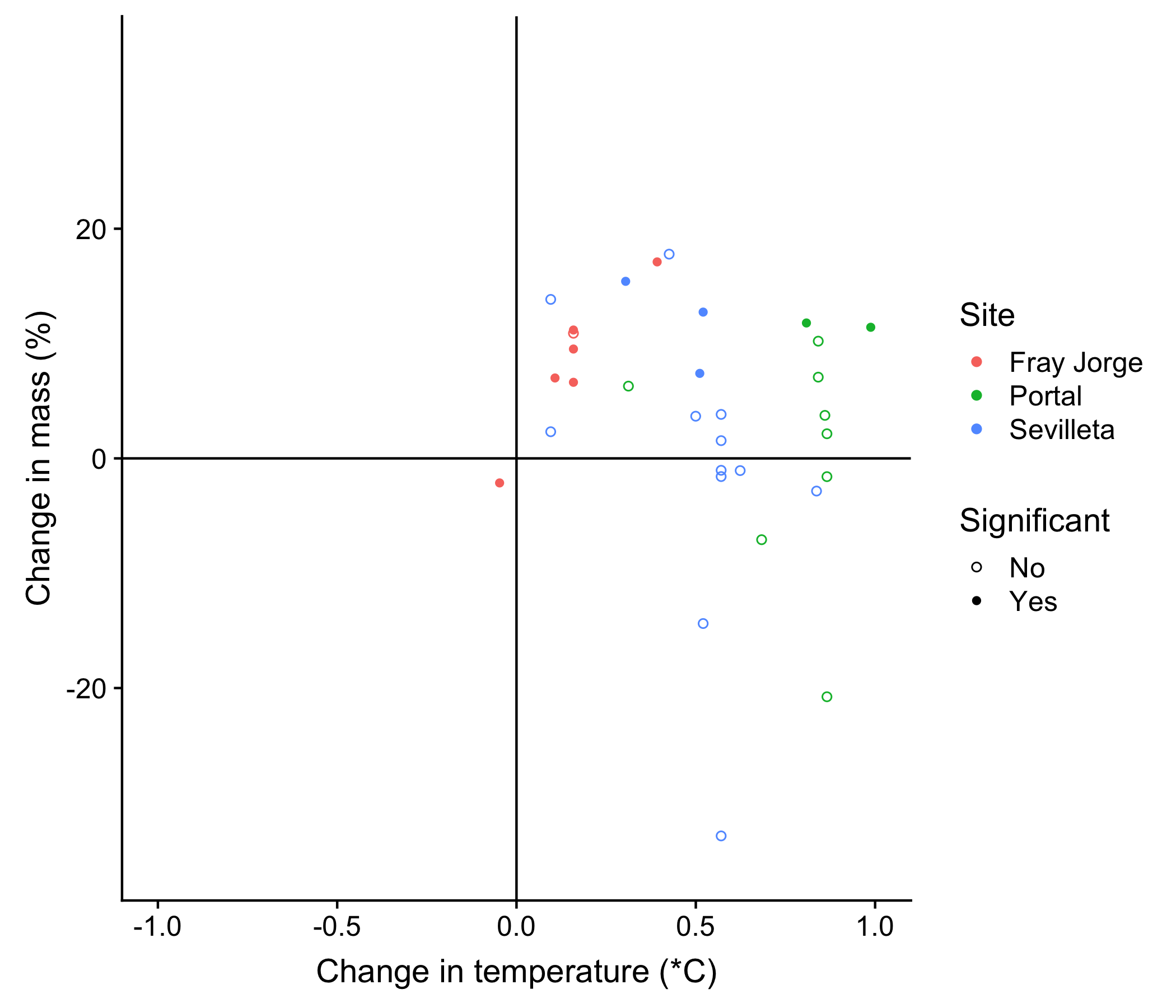
**Figure 1.** Map of global terrestrial temperatures for December 2014 showing spatial locations of three sites.



**Figure 2.** Trends in temperature and mass at each site. Mean annual temperatures at Portal (A), Fray Jorge (B), and Sevilleta (C) are black points, with linear regression trend for temperature as blue line and confidence intervals as grey shading. (D-F) Species mean annual masses shown as points of different colors, with linear regression line of corresponding color for trend in mass, by site. (G-I) Distribution of mean annual mass slope from mass time series dynamic regression model for all species by site, with statistically significant values shown in black and not statistically significant in grey. Vertical red line at slope of zero.



**Figure 3.** Each species relationship between mean annual temperature and mean annual mass shown as points, with one color per species, for Portal (A), Fray Jorge (B), and Sevilleta (C). Liner regression trend for each species temperature-mass relationship shown in corresponding color. (D-F) Distribution of r values from linear regression for each species temperature-mass relationship by site, with statistically significant values shown in black and not statistically significant in grey. Vertical red line at slope of zero.



**Figure 4.** Absolute change in temperature experienced by each species, from linear regression of mean annual temperatures, compared to the percent change in each species mass, from linear regression of mean annual masses. Points for species with statistically significant temperature-mass relationships are filled, while open points show not statistically significant relationships. Sites are indicated by color of points.

**Table 1.** Summary statistics for all individual records and by site.

| Individuals | Species |
| --- | --- |
| 128710 | 32 |

| Site | Individuals | Species | Years | Individuals (min) | Individuals (max) | Years (min) | Years (max) |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Fray Jorge | 83670 | 7 | 17 | 15 | 9613 | 6 | 17 |
| Portal | 28293 | 10 | 38 | 15 | 635 | 13 | 38 |
| Sevilleta | 16747 | 15 | 26 | 15 | 706 | 5 | 26 |

**Supplement figure legends**

**Supplement 1.** Trends in mean annual temperature, mean annual mass, and temperature-mass relationships for all species by five Sevilleta subsites.

**Supplement 2.** Slope for mass time series and r value for temperature-mass relationship for each species at each site with actual thresholds for individual records datasets (15 individuals per species per year, 5 years per species) compared to using more individuals (30 individuals per species per year) and more years (10 years per species).

**Supplement 3.** Scientific names for all species with corresponding species codes.

**Supplement 4.** Plots of autocorrelation and partial autocorrelation functions for each species mass time series and residuals plots for each species dynamic regression model for mass time series including temperature as an exogenous variable.

**Supplement 5.** Each species mean mass by year, including linear regression trend line.

**Supplement 6.** Comparison of each species mass (black points and lines) with temperature time series (red points and lines), with dynamic regression model p-value shown at top of each plot.

**Supplement 7.** Relationship between temperature and mass for each species, including linear regression trend line.

**Supplement 8.** Comparison of mean annual mass trends and temperature-mass relationship trends for all species that occur at more than one site.