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

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**Abstract**

**Introduction**

Current and future changes in the climate will affect the traits of organisms, which will have downstream effects on how natural systems function. In particular, the potential for organisms to become smaller in response to increasing global temperatures has received growing attention as one of the possible universal response to climate change (Gardner et al., 2011; Sheridan and Bickford, 2011). Warmer temperatures resulting in decreased body size comes from Bergmann’s rule, which states that there is 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 at many locations 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 could result in drastic changes in ecosystem structure and function.

The general relationship between endotherm size and temperature on which predictions for decreasing size have been based on has, however, been questioned due to data-intensive analyses that evaluate this relationship for many species simultaneously (McNab, 1971; Meiri et al., 2004; Riemer et al., 2018). For example, when this relationship was recently examined for nearly 1,000 bird and mammal species using a century of global data, most species had weak relationships (Riemer et al., 2018). While this suggests that Bergmann’s rule is not as generally applicable as previously believed, the analysis included data for spatial and temporal variation in size. Because responses of ecosystems across time do not necessarily match their responses across space (Fukami and Wardle, 2005), the predicted general decline in size could still occur. In order to understand how species will generally respond to climate change, this relationship needs to be examined in a similar data-intensive fashion with an explicit focus on changes through time. Recent studies that have suggested that species are getting smaller 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., 2018).

We directly assessed temporal shifts in body size due to temperature in a data-intensive manner by compiling long-term time series data on mammal communities 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 years spread across at least ten years. This was combined with a global temperature dataset to determine how both temperature and species mass changed through time for each species at each site, and to assess the strength and direction of the relationship between mass and temperature. 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. We were able to show how mammal size is impacted by temperature over time.

**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 (Supplement 4).

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 all of each species mean annual masses 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 that temperature had. 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 5. To determine the effect of temperature on mass, we calculated the p-value for each species, which were adjusted to take into account the impact of multiple comparisons (Benajmini & Hochberg, 1995), and chose an alpha cut-off of 0.05. All cleaning and analysis was completed using R (R Core Team, 2017), with code and data downloads provided reproducibly on GitHub (https://github.com/KristinaRiemer/temporal\_MRT) and archived on Zenodo (citation).

**Results**

Most species had a positive relationship between mean annual mass and mean annual temperature, instead of the expected negative relationship. Temperatures increased at all sites (Fig. 2A, B, C) in accordance with climate change trends. Some species had a decrease in mass or no change in mass, though the majority (69%) of species had an increase (Fig. 2D, E, F, G, H, I; Supplement 6). Of 11 species with a significant temperature-mass relationship, ten of them had a positive relationship (Fig. 3; Supplement 7). The prevalence of positive relationships is also shown in the comparison of absolute change in temperature with percent change in each species mass (Fig. 4). Most values are in the upper right quadrant, instead of the lower right or upper left which would indicate negative temperature-mass relationships.

While more species had positive temperature-mass relationships, all species exhibited weak relationships. Temperature explained less than 10% of the variance in mean annual mass for most species (66%; Fig. 3D, E, F), and explained only 54% of the variance for the species with the strongest relationship. According to the dynamic regression models, temperature had a statistically significant effect on the mass time series for 11 of the 32 species (Fig. 4; Supplement 8).

**Discussion**

In accordance with Bergmann’s rule, we would expect most species in this study to get smaller because temperatures warmed at all sites. Instead, there were species at each site that increased in size and others that decreased in size. Additionally, most species had very weak relationships between temperature and mass. That these relationships were weak and variable in direction indicates that directional change in temperature is likely not a strong driver of shifts in mammal body size, as has been proposed as a response to climate change (Gardner et al., 2011; Sheridan and Bickford, 2011).

Body size is affected by a wide variety of biotic and abiotic factors in addition to temperature, including resource availability (McNab, 2010), anthropogenic fragmentation (Lomolino & Perault, 2007), and island size (Lomolino, 2005). 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). Even if temperature has a strong impact on size variation across time, other factors have substantial and possibly overwhelming impacts.

Though empirical evidence of a negative temperature-mass relationship has been documented for over a century, a mechanistic explanation has not been confirmed. Many hypotheses for this pattern have been proposed, including starvation resistance and dispersal (Blackburn et al., 1999). The initial and most commonly referenced hypothesis is that it is beneficial for individuals to be bigger in warmer environments because they have an increasing surface area to volume ratio and therefore lose heat relatively more quickly (Bergmann, 1847), though there is no evidence for this (McNab, 2010). It has been shown that morphological changes in fur characteristics are more effective than heat regulation for some mammals (Steudel et al., 1994).

Our results suggest that the response of mammal body size to changes in temperature is likely to be highly variable, with some species increasing in size while others decrease or show no size response. However, while our data include over 100,000 individual size measurements, it is still too limited in scope to draw general conclusions about endotherm size response to climate change. Three of the seven species that occurred at multiple sites had contradictory size responses (Supplement 4). Having more data for the same species in more geographic locations could confirm the variability of temperature-mass relationships. This analysis should be expanded to include larger and non-nocturnal mammals, and to bird species as there are recent studies suggesting decreasing size in birds (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 be included to determine the generality of the temporal size response.

Based on the variable size response to temperature across time for the mammal species in this study, it seems unlikely 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 additional factors, and the difficulty of determining which factors are most important and how they impact size means that predicting size response to climate change in general will be difficult. This should be a priority due to the importance of size in ecological systems.

**References**

Aguilera, L.E., Armas, C., Cea, A.P., Gutiérrez, J.R., Meserve, P.L. & Kelt, D.A. (2016) Rainfall, microhabitat, and small mammals influence the abundance and distribution of soil microorganisms in a Chilean semi-arid shrubland. *Journal of Arid Environments*, **126**, 37–46.

Ashton, K. (2002) Patterns of within‐species body size variation of birds: strong evidence for Bergmann’s rule. *Global Ecology and Biogeography*, **11**, 505–523.

Benajmini, Y. & Hochberg, Y. (1995) Controlling the False Discovery Rate : A Practical and Powerful Approach to Multiple Testing Author ( s ): Yoav Benjamini and Yosef Hochberg Source : Journal of the Royal Statistical Society . Series B ( Methodological ), Vol . 57 , No . 1 Published by : *J R Statist Soc B*, **57**, 289–300.

Bergmann, C. (1847) Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien*, **1**, 595–708.

Blackburn, T., Gaston, K. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann’s rule. *Diversity and distributions*, 165–174.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Brown, J.H. & Lee, A.K. (1969) Bergmann ’ s Rule and Climatic Adaptation in Woodrats ( Neotoma ). *Evolution*, **23**, 329–338.

Canale, C.I., Ozgul, A., Allain??, D. & Cohas, A. (2016) Differential plasticity of size and mass to environmental change in a hibernating mammal. *Global Change Biology*, **22**, 3286–3303.

Dickie, L.M., Kerr, S.R. & P.R., B. (2018) Size-Dependent Processes Underlying Regularities in Ecosystem Structure. **57**, 233–250.

Ernest, S.K.M., Yenni, G.M., Erica, M., Meiners, J.M., Munger, J., Restrepo, C., Samson, D.A. & Michele, R. (2018) The Portal Project : a long-term study of a Chihuahuan desert ecosystem.

Freckleton, R., Harvey, P. & Pagel, M. (2003) Bergmann’s rule and body size in mammals. *The American Naturalist*, **161**, 821–825.

Fukami, T. & Wardle, D.A. (2005) Long-term ecological dynamics : reciprocal insights from natural and anthropogenic gradients. 2105–2115.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011) Declining body size: a third universal response to warming? *Trends in ecology & evolution*, **26**, 285–91.

Husby, A., Hille, S.M. & Visser, M.E. (2011) Testing Mechanisms of Bergmann’s Rule: Phenotypic Decline but No Genetic Change in Body Size in Three Passerine Bird Populations. *The American Naturalist*, **178**, 202–213.

Kelt, D.A., Meserve, P.L., Gutiérrez, J.R., Milstead, W.B. & Previtali, M.A. (2013) Long-term monitoring of mammals in the face of biotic and abiotic influences at a semiarid site in north-central Chile. *Ecology*, **94**, 977.

Kironde, H., D. Morris, B., Goel, A., Zhang, A., Narasimha, A., Negi, S., J. Harris, D., Gertrude Digges, D., Kumar, K., Jain, A., Pal, K., Amipara, K., Simran Singh Baweja, P. & P. White, E. (2017) Retriever: Data Retrieval Tool. *The Journal of Open Source Software*, **2**, 451.

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013) *Handbook of meta-analysis in ecology and evolution*,.

Lomolino, M. V. (2005) Body size evolution in insular vertebrates: Generality of the island rule. *Journal of Biogeography*, **32**, 1683–1699.

Lomolino, M. V. & Perault, D.R. (2007) Body size variation of mammals in a fragmented, temperate rainforest. *Conservation Biology*, **21**, 1059–1069.

McNab, B.K. (1971) On the ecological significance of Bergmann’s rule.

McNab, B.K. (2010) Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia*, **164**, 13–23.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann’s rule. *Journal of Biogeography*, 331–351.

Meiri, S., Dayan, T. & Simberloff, D. (2004) Carnivores, biases and Bergmann’ s rule. *Biological Journal of the Linnean Society*, **81**, 579–588.

Millien, V., Kathleen Lyons, S., Olson, L., Smith, F. a, Wilson, A.B. & Yom-Tov, Y. (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology letters*, **9**, 853–69.

Morris, B.D. & White, E.P. (2013) The EcoData Retriever: Improving Access to Existing Ecological Data. *PLoS ONE*, **8**, 1–7.

Newsome, S. (2016) Small Mammal Mark-Recapture Population Dynamics at Core Research Sites at the Sevilleta National Wildlife Refuge, New Mexico (1989 - present).

Riemer, K., Guralnick, R.P. & White, E.P. (2018) No general relationship between mass and temperature in endothermic species. *eLife*, **7**, 1–16.

Salewski, V., Hochachka, W.M. & Fiedler, W. (2010) Global warming and Bergmann’s rule: do central European passerines adjust their body size to rising temperatures? *Oecologia*, **162**, 247–260.

Sheridan, J.A. & Bickford, D. (2011) Shrinking body size as an ecological response to climate change. *Nature Climate Change*, **1**, 401–406.

Smith, F., Browning, H. & Shepherd, U. (1998) The influence of climate change on the body mass of woodrats Neotoma in an arid region of New Mexico, USA. *Ecography*.

Steudel, K., Porter, W.P. & Sher, D. (1994) The biophysics of Bergmann’s rule: a comparison of the effects of pelage and body size variation on metabolic rate. *Canadian Journal of Zoology*, **72**, 70–77.

Stirling, I. & Derocher, A.E. (2012) Effects of climate warming on polar bears: A review of the evidence. *Global Change Biology*, **18**, 2694–2706.

Team, R.C. (2016) R: A Language and Environment for Statistical Computing.

Teplitsky, C., Mills, J. a, Alho, J.S., Yarrall, J.W. & Merilä, J. (2008) Bergmann’s rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 13492–6.

Van Buskirk, J., Mulvihill, R.S. & Leberman, R.C. (2010) Declining body sizes in North American birds associated with climate change. *Oikos*, **119**, 1047–1055.

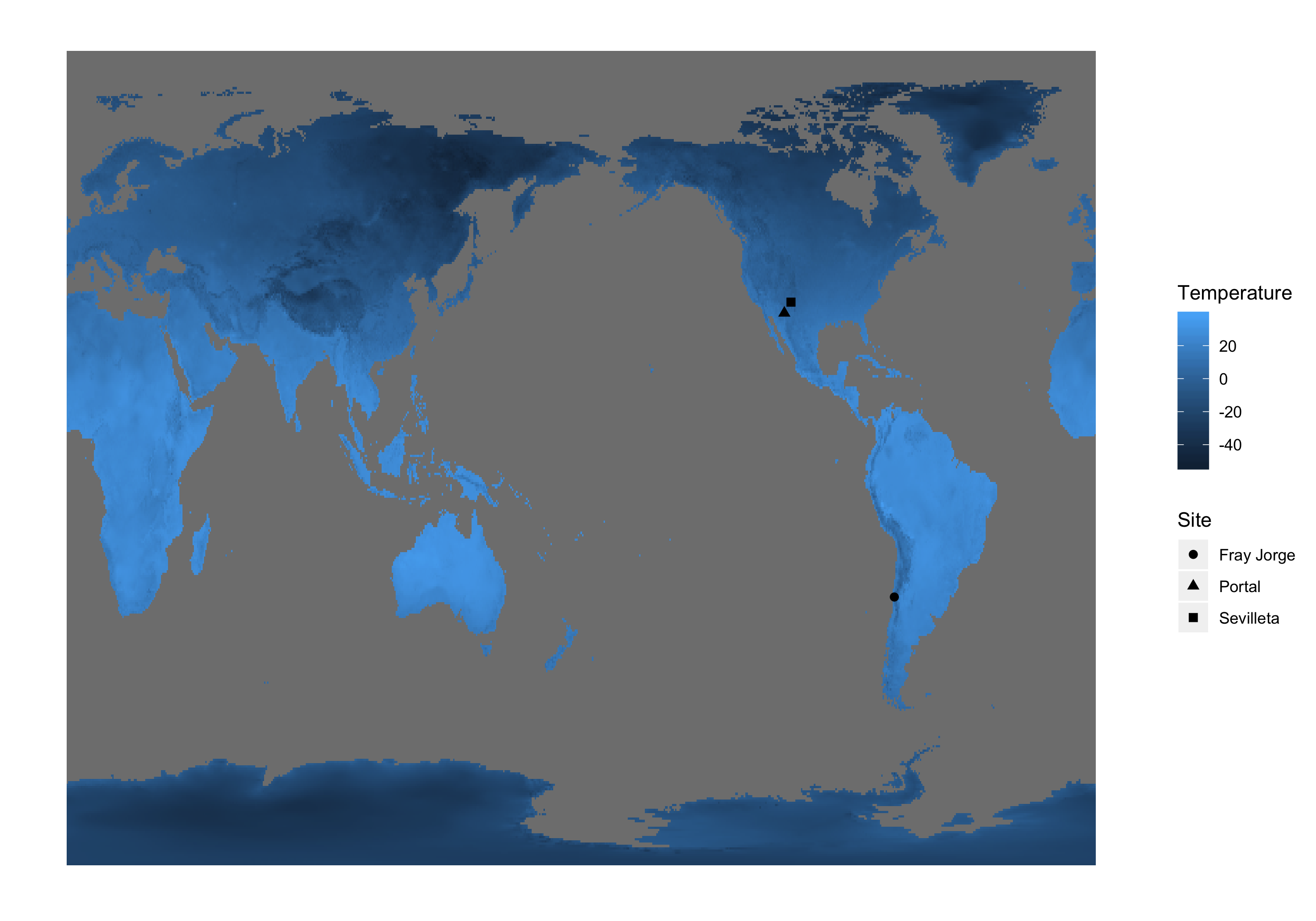
Willmott, C.J. & Matsuura, K. (2001) Terrestrial Air Temperature and Precipitation: Monthly and Annual Time Series (1950-1999).

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology and Evolution*, **20**, 402–9.

Yom-Tov, Y. & Geffen, E. (2011) Recent spatial and temporal changes in body size of terrestrial vertebrates: Probable causes and pitfalls. *Biological Reviews*, **86**, 531–541.

**Main figures**

* Figure 1: Site location map

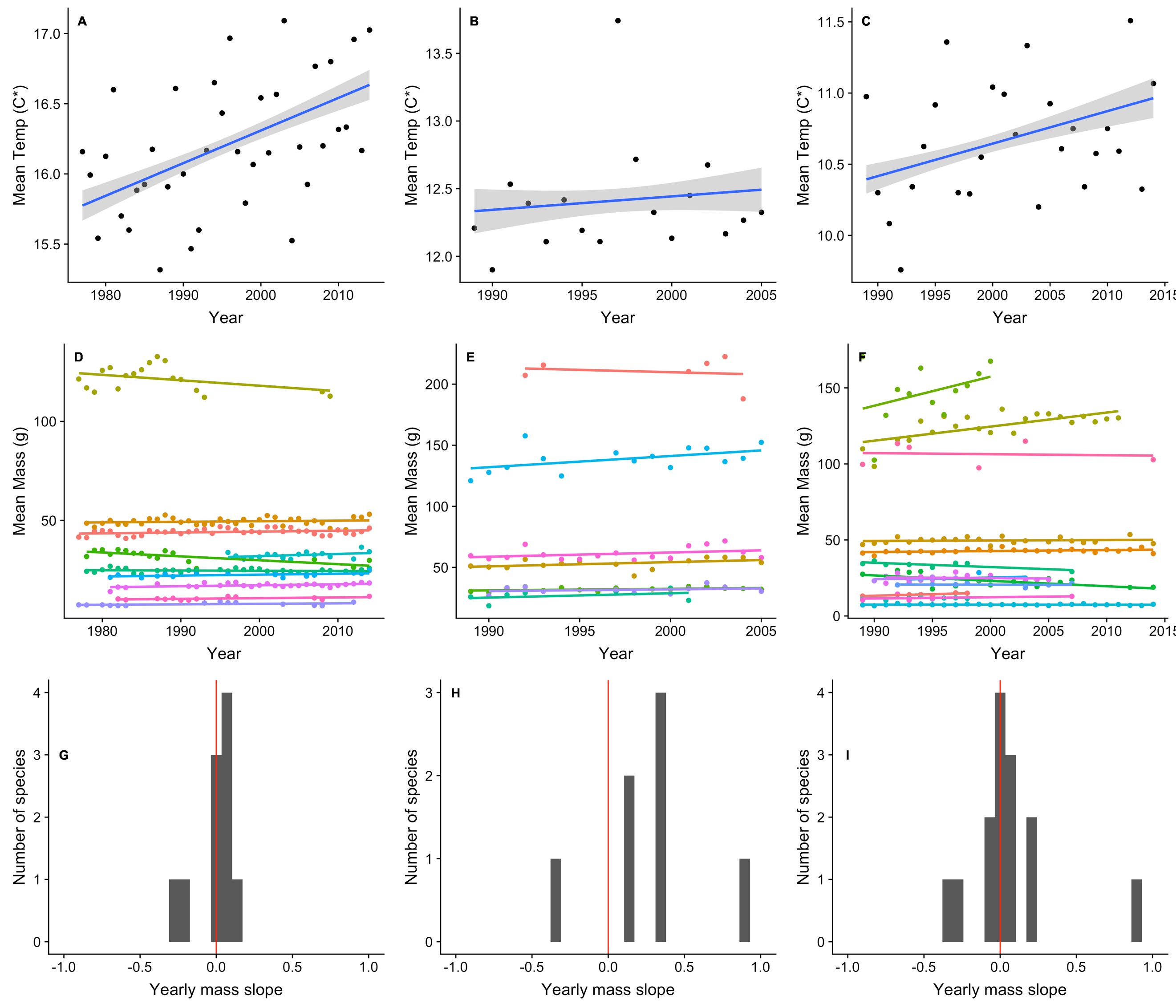


* Table 1: Site dataset metrics

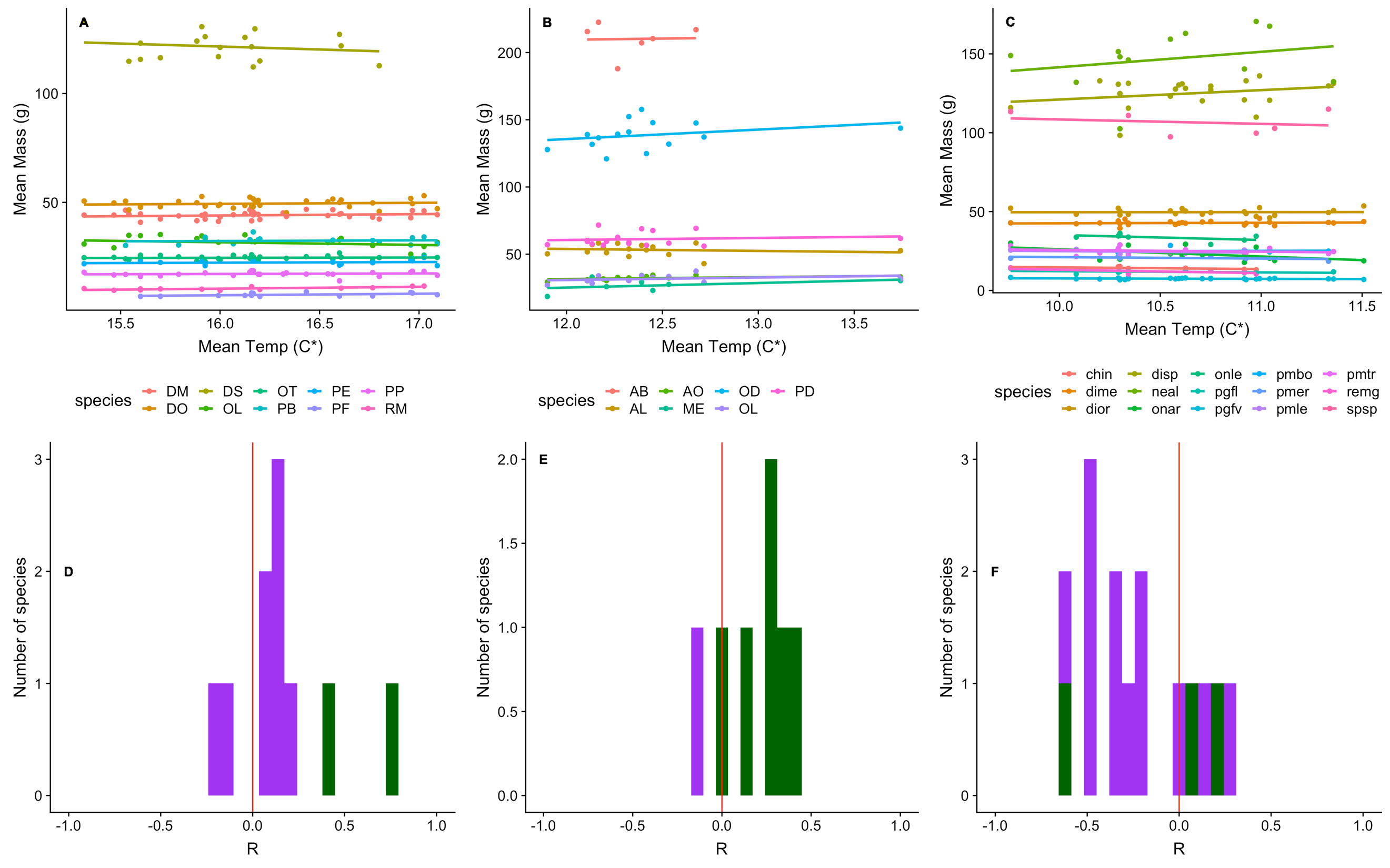
| Individuals | Species |
| --- | --- |
| 128710 | 32 |

| Site | Individuals | Species | Years | Individuals (min) | Individuals (max) | Years (min) | Years (max) |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Fray Jorge | 83670 | 7 | 17 | 15.000 | 9613.000 | 6.000 | 17.000 |
| Portal | 28293 | 10 | 38 | 15.000 | 635.000 | 13.000 | 38.000 |
| Sevilleta | 16747 | 15 | 26 | 15.000 | 706.000 | 5.000 | 26.000 |

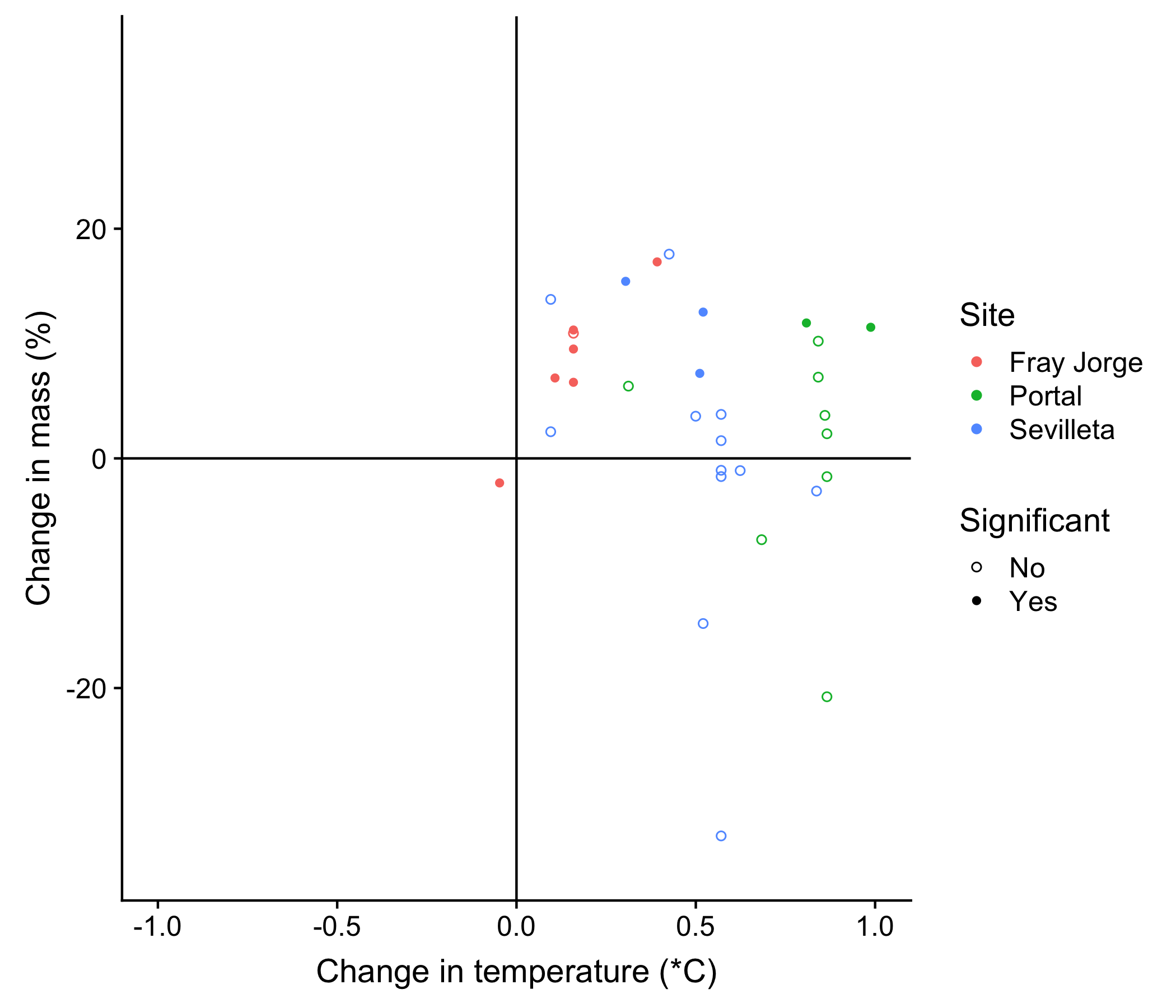
* Figure 2: Yearly temp, yearly mass, and yearly mass slope distribution



* Figure 3: Temp-mass relationship and r distribution (green = statistically significant p-values; purple = not statistically significant p-values)



* Figure 4: Mass change over time compared to temp change over time by species



**Supplemental figures**

* 1: Results broken out for Sevilleta subsites
* 2: Sensitivity analyses for thresholds
* 3: Species codes with scientific names
* 4: Results for species that are in more than one site
* 5: Figures of ARIMA model diagnostics by species
* 6: Yearly mass split out by species
* 7: Mrt split out by species
* 8: Time series of temp and mass together with p-values from model