Climate, weather, and geography shape seed mass variation and decline across western North America

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Abstract

Seed mass influences the probability of germination, the timing of emergence, and the likelihood of survival and establishment, and can affect restoration and conservation efforts. Here, we investigated the temporal, geographic, and environmental patterns that influence seed mass across 2,800 species of native plants from over 13,000 populations across the western US using two decades of collections from a national program, Seeds of Success. The majority of species exhibited low variation in seed mass, though there were exceptions, with some species varying in seed mass by up to 220% over their occupied area. Species with the most variation in seed mass were collected across sites with a wide range of minimum temperatures, from more northern latitudes, and collected across a wide range of dates, and seeds were generally larger in areas where it was wetter and warmer. We observed an overall decrease in seed mass by an average of 0.012 mg each year, though there were many species-specific differences. Fifty-five percent of species decreased in seed mass, 20% strongly so, and 17% of species increased appreciably in mass. Relationships between seed mass and environmental variables varied widely in strength, identity, and direction among species, including those that often co-occur. Measures of climate change (30 year changes in seasonal temperatures and precipitation) were associated with changes in seed mass in nearly 20% of species. In sum, these results support the need to continue native seed collections for conservation and restoration, as plant reproductive strategies may be shifting with changing climates.

Significance

Seeds are an essential reproductive strategy for most plants, and seed mass is predicted to respond to environmental factors, but we do not know if climate-related size changes observed in other organisms will also be reflected in seed mass. We assessed how weather, climate, and geography affect seed mass in thousands of native plants of the western US. Minimum temperatures and precipitation had strong impacts on seed mass for many species, though there were many species-specific responses. Overall, seed mass declined for more than half of observed species. Measures of climate change influenced seed mass in nearly one in five species, which could be evidence of adaptation to new optimal values, or be a signal of challenges ahead.

Keywords: Seed mass; Intraspecific variation; Climate Change; Interannual variation

Introduction

Seed production is an essential component of fitness for the majority of plants. Because adult plants are immobile, barring long distance dispersal, their reproductive strategies must adapt to local environments in order to persist (Clausen et al. 1940; Leimu and Fischer 2008; Baughman et al. 2019). Seed mass can strongly influence plant fitness during the seed-to-seedling transition, a crucial life history stage (Moles and Westoby 2004; Norden et al. 2009; Larson et al. 2015; Leger et al. 2019). Natural selection should favor an optimal seed mass, balancing seed mass with seed number, with local optimums determined by interacting selection pressures including competition, dispersal, and herbivores (Venable 1992; Muller-Landau 2010; Seale and

Nakayama 2020; Tuthill et al. 2023). Yet, seed mass varies greatly within and among individuals (Völler et al. 2012; Liu et al. 2013) possibly due to fitness benefits of variation in seed mass such as reducing competition among siblings, or bet-hedging in unpredictable landscapes (McGinley et al. 1987; Westoby et al. 1996). Variation in environmental sensitivity of seed mass could lead to the loss of some species in response to climate change if there is a mis-match between local optima and expressed traits, or increasing dominance of highly variable or adaptable species. In the era of climate change, understanding how environmental factors influence seed mass as a reproductive strategy is critical for predicting species persistence (Cochrane et al. 2015; Tangney et al. 2020).

Seed traits vary across geographic, temporal, and phylogenetic scales (Westoby et al. 1992; Moles et al. 2007; Gorden et al. 2016). Larger seeds are typically more common in resource-poor environments where maternal provisioning is necessary for survival, and the opposite in resource-rich environments, where many small seeds may increase fitness (Smith and Fretwell 1974; Adler et al. 2013). At the largest spatial scale, environment affects seed mass across latitudinal gradients (Moles et al. 2007), with larger seeded species found closer to the equator. Hypotheses for this pattern include correlations with plant growth form (greater dominance of trees in the tropics), differences in seed dispersal strategies (e.g. wind vs. animal dispersal), and net primary productivity (greater towards the equator) (Murray et al. 2004). Latitudinal gradients in seed mass are present but weaker in North America (Liu et al. 2013; Gorden et al. 2016), possibly due to topographic variability (Malanson et al. 2007; Albrecht and McCarthy 2009). Further, these broad gradients may result from taxonomic turnover

across latitudes but may not explain intraspecific, among-population variation in seed mass (Hulshof et al. 2013). It is also possible that within a community, species may produce different seed sizes in response to the same environmental conditions, which would be predicted if seed size plays a role in niche partitioning and community assembly (Turnbull et al. 1999; Leishman 2001; Muller-Landau 2010). Understanding the geographic, temporal, and taxonomic patterns of seed mass will provide valuable insight into evolutionary pressures experienced by native plants, including ongoing climate change (Frenne et al. 2013; Cochrane et al. 2015).

Biologists have characterized variation in seed characteristics for centuries, yet only recently do we have the fine-scaled resolution and longitudinal data to closely link seed traits with maternal environmental conditions (Kattge et al. 2011; Liu et al. 2019). In North America, we have an opportunity to examine the effects of geography and environment on seed mass through Seeds of Success (hereafter “SOS” see: blm.gov/sos), which is the national native seed collection effort in the United States led by the Bureau of Land Management. Through collaborative efforts and labor of thousands of field interns and seed processing technicians, SOS has made over 27,000 native seed collections across the United States since 2001 (Barga et al. 2020) (Fig. 1*A*). The mission of SOS is to collect wildland native seed for development, conservation, and restoration, and target species include restoration priorities as well as taxa not previously collected. Therefore, the dataset includes multiple accessions of the same species over multiple years from many locations, from a broad range of taxa, collected using a consistent protocol. The scale and scope of this effort has resulted in an invaluable source of seed for conservation and restoration across the US, and has

generated an unparalleled wealth of information about the properties of seed in wild plant populations that can be used to inform ecological theory, global change biology, and restoration practices (Siefert et al. 2015; Moran et al. 2016).

To assess patterns of seed mass variation within and among species, we first took a broad approach, maximizing the inclusion of data to identify patterns of seed mass variation at the largest possible scale, asking 1) where do plants produce bigger seeds, and is there evidence of widespread changes in seed mass over time. Then, we investigated environmental influence on seed mass for more well-sampled species, both as a group and individually, asking 2) if there are environmental, climate variables, or life history traits that have a consistent influence on seed mass across and within species. Finally, we asked 3) if environment and geography predict not only seed mass but also seed mass variation across the range of collections, including a phylogenetic perspective.

Results

Seed mass ranged from 0.0046 mg (the average across-population mass of *Epipactis gigantea*) to 827.7 mg (for *Pinus sabiniana*) with a mean across species of 4.4 mg and median of 1.2 mg (Fig. 1D). Certain plant families, including Fabaceae and Ericaceae, consistently had larger seeds whereas others (e.g. Juncaceae and Onagraceae) exhibited smaller seeds (Fig. 2). Seed mass ranged from highly conserved across populations (e.g. CV of 0.0005 for *Wyethia magna*) to highly variable (CV of 2.2 for *Juncus occidentalis*), with a mean CV of 0.32 and median of 0.27 (Fig. 2).

Most areas across the western US were dominated by smaller seeds with no obvious spatial segregation (Fig. 1*A*; *SI Appendix* 1, Fig. S1). Latitude had a small,

positive effect on seed mass in models that included latitude, longitude, and elevation as predictors (GLM: $\beta = 0.027$, $p < 0.001$) as well as models that included plant family as a random factor, which had a better model fit than geography alone (GLMM: $\beta = 0.031$, $p < 0.001$; Fig. 1*B*, *SI Appendix* Q1, Table S2). Seeds were, on average, 1.03 mg larger for every 1 degree north, in contrast to global patterns, though in models that considered seed mass by growth form, shrubs had a contrasting response to other plant growth forms, with smaller seeds in more northern latitudes (*SI Appendix Table* S2). Longitude had a small negative effect on seed mass (GLM: $\beta = -0.005$, $p = 0.089$, GLMM: $\beta = -0.01$, $p < 0.001$), with smaller seeds (0.989 mg smaller for every 1 degree) in more eastern areas.

We examined relationships between seed mass, environment, and time for well collected species (10,958 collections from 859 species collected from at least 3 populations) and found that, overall, seed mass decreased by 0.012 mg each year (Fig. 1C, $\beta = -0.010$, SE = 0.004, $p = 0.007$). When considering species independently, 38% changed appreciably in seed mass, representing a distribution of change with greater density in the tails of the distribution (species getting larger or smaller) than would be expected from a normal distribution (kurtosis = 11.153, $z = 10.596$, $p < 0.001$). Of the 631 species that were collected from 3 unique populations and years, 55% were declining in seed mass over time, with 132 declining significantly and 107 increasing significantly (at $p < 0.05$) in seed mass. Multiple environmental variables had consistent positive effects on seed mass across species (Fig. 3A). The strongest positive relationships were between seed mass and cumulative precipitation over the previous 6 months leading up to collection ($\beta = 0.051$, SE = 0.012, $p < 0.0001$), as well as annual

minimum temperature ($\beta = 0.044$, SE = 0.011, $p < 0.001$), with generally greater seed mass in the relatively wetter and warmer collection sites (Fig. 3A, SI Appendix Table S4). Clay content and slope also had positive relationships with seed mass ($\beta = 0.045$, SE = 0.011, $p < 0.001$, and $\beta = 0.045$, SE = 0.011, $p < 0.001$ respectively), with generally larger seeds in areas with higher clay content and steeper slopes. Heat load also had a positive relationship with seed mass ($\beta = 0.024$, SE = 0.012, $p = 0.038$), with larger seeds in relatively warm collection sites. Neither growth form (shrub, grass, forb, etc.) nor duration (annual, perennial, etc.) were retained as important effects in the model selection process.

In the results described thus far, we maximized statistical power for the detection of environmental effects by including all species with at least 3 collections. Now we turn to results using fewer species, with 20 collections each (111 species, 5196 total collections); these models allow us to examine variation among species in environment-seed mass effects. We found several common predictors of seed mass among species, confirming previous results (Fig. 4, *SI Appendix* Table S6). Specifically, annual minimum temperature, clay content, heat load, cumulative precipitation six months prior to collection, soil pH, and day of year were statistically significant in at least 10 species models. However, the strength and direction of relationships varied widely among species (Fig. 3*C*-*N*; Fig. 4). For example, soil pH had a strong positive influence on seed mass of *Balsamorhiza hookeri*, increasing seed mass 1.095 mg as soil pH increased by 1 (Fig. 3*C*, Fig. 4), while *Elymus elymoides* had the opposite response, decreasing seed mass by 0.889 mg as soil pH increased by 1 (Fig 3*D*, Fig 4). We used a resampling approach to investigate the influence of variation in sample size (the

number of populations) on species-specific results; results were robust to systematic reductions in the number of populations included in models (*SI Appendix*).

Multiple measures of climate change across a species collection range (including change in spring and fall maximum temperatures, change in precipitation, and change in fall minimum temperatures) were included as important predictors in 47 species models (out of a possible 111 species) and were significant 23 times in 22 models (Fig. 4). Of those, 11 had a statistically significant negative correlation between measures of climate change and seed mass and 12 climate change coefficients were positive, again illustrating heterogeneity of responses (Fig. 4, *SI Appendix* Table S5). *Atriplex polycarpa* and *Artemisia tridentata* were particularly responsive to climate change, including three measures of climate change in each species model, with change in precipitation significantly affecting seed mass (*SI Appendix* Table S6).

Our models thus far have assessed mean seed mass, but because natural selection acts on variation, we also quantified seed mass variation among populations of a single species to understand the potential for evolutionary change. Here, we aggregated our data at the species level to ask how environment and geography predict seed mass coefficient of variation while considering phylogenetic relationships among species. Species differed in the amount of variation (CV) in seed mass across collection locations and collection years (Fig. 2). Most species exhibited low variation in seed mass, but some, including *Artemisia frigida, Phacelia hastata, Chaenactis stevioides,* and *Sphaeralcea munroana*, exhibited CV values above 1 indicating higher variation. Considering the 235 species that had been collected at least 10 times and for which phylogenetic information was available, the strongest predictors of seed mass variation

were the maximum latitude from which a species was collected ($\beta = 0.091$, SE = 0.037, $p = <0.001$), the range of annual minimum temperatures experienced across the collection area ($\beta = 0.068$, SE = 0.041, $p = 0.101$), and the range of collecting days (difference between first and last day of collection) ($\beta = 0.055$, SE = 0.041, $p = 0.180$; Fig. 3*B, SI Appendix* Table S7). Neither growth form nor duration were selected as important, and, when included in models with environmental covariates or alone in a simple model, neither predicted seed mass variation (results not shown).

Discussion

Climate change continues to affect the morphology of individual species of plants and animals, but due to challenges of amassing quality datasets, effects across entire assemblages of species are rarely investigated (Sheridan and Bickford 2011; Violle et al. 2012). Further, there is increasing consensus about the importance of intraspecific variation for understanding ecological and evolutionary processes that affect species and community responses to climate change (Siefert et al. 2015). Yet, we often lack consistent population-level replication for specific fitness related traits, leading to uncertainties in identifying these intraspecific patterns (Moran et al. 2016). By assessing seed mass variation within and among species simultaneously, our results offer a unique perspective on plant reproductive biology and species coexistence, illuminating how environment affects propagule size in land plants.

We found spatial patterns and environmental predictors of seed mass across all species and common environmental predictors of seed mass within multiple species, including precipitation, heat load, and soil characteristics like pH. Seeds were generally larger in warmer and wetter areas, consistent with tree seed sizes observed in Boreal

forests (Liu et al. 2013). However, we observed even stronger signals within species, though often in heterogeneous directions and magnitudes, confirming that intraspecific seed trait-environment relationships can be idiosyncratic, and differ from broad interspecific patterns (Gorden et al. 2016). Heterogeneity in response among species may be an important form of resilience, which can only be seen when analyzing traits at the scale of communities and entire floras. Conservation and restoration practices could benefit from considering intraspecific variation in addition to interspecific variation (Sgrò et al. 2011). While conservationists may prioritize protecting species that are more sensitive to climate and climate change, practitioners may benefit from planting species with seed traits that are less sensitive to climate change or selecting a mix of species that are sensitive to different factors, thereby incorporating natural resilience into restoration.

While seed mass was highly conserved for most species, others varied more across space and time, including species collected across broader minimum temperature gradients, higher latitudes, and those with longer collecting seasons. Given that warming minimum temperatures are an early consequence of anthropogenic climate change (Parry et al. 2007), with northern latitudes showing particular acute change (Bunn et al. 2007), these sensitivities suggest that climate change will be exerting selection pressure on seed mass in plants. Indeed, we observed overall declines in seed mass across the western US over the past 20 years, though some species increased in seed mass, consistent with heterogeneous changes observed in seed mass in alpine plants (Zhang et al. 2019). Given the importance of seed mass for plant regeneration (Moles and Westoby 2004) and the role of seeds as a food source

for granivores especially in arid lands (Solbreck and Knape 2017; Dylewski et al. 2020), these small changes in seed mass could have cascading effects on ecosystems (Sheridan and Bickford 2011).

Further highlighting the impact of climate change on terrestrial plant seeds, we detected sensitivity to direct measures of temperature and precipitation changes for approximately one fifth of well-collected species, though directionality was not consistent. For example, showy milkweed, *Asclepias speciosa*, an important host plant for the Monarch butterfly, makes larger seeds in warmer areas, while *Plantago ovata* shows the opposite pattern. Another very important species in the region, big sagebrush (*Artemisia tridentata),* was particularly responsive to climate change, with three of our four measures of climate change affecting seed mass. It is possible that seed mass sensitivity to climate change represents an adaptive response, or if changes are a result of resource limitation, it could indicate that these species are particularly vulnerable to climate change. Field studies of the relationship between seed mass and fitness in highly sensitive species identified here would be important to understand if these plants should be prioritized in conservation efforts.

We are particularly fascinated by the many cases where species had strong responses to the same variables, but in contrasting ways (Fig. 4). For example, soil pH had a strong positive relationship with seed mass in the widespread forb *Balsamorhiza hookeri*, while *Elymus elymoides*, a widely distributed perennial grass commonly used in ecological restoration had the opposite response. Other species did not change seed mass in response to any of the variables we considered, maintaining nearly constant seed mass across collection locations and years (e.g. *Chimaphila umbellata*). Some

species varied in seed mass across space and time but not in response to any environmental variables we included here (e.g. *Chaenactis douglasii*). It may be that other ecological influences such as herbivory, competition, success of insect pollination, or polyploidy may have an effect on seed size in these species (Paige and Whitham 1987; Vaughton and Ramsey 1997; Chan et al. 2022). In the future, close monitoring of native plant communities may uncover these ecological effects on seed mass, and our results could inform comparative studies across species with contrasting levels of seed mass variation.

Overall, few species exhibited high (>1) coefficient of variation, supporting our understanding that seed mass is a highly conserved trait with some exceptions (Zhang et al. 2020), and it is possible that species that are more variable in seed mass may be poised to adapt to changing climates (Frei et al. 2014; Cochrane et al. 2015). However, species demonstrating changes in seed mass in response to climate change may be adjusting seed mass in maladaptive ways. For example, if smaller seeds confer greater dispersal capability, but a longer, warmer growing season results in larger seeds, this may reduce dispersal distances and lead to greater competition with siblings (Harper et al. 1970; Greene and Johnson 1993). In contrast, species that are demonstrating decreasing seed mass in response to warming temperatures may be experiencing resource limitation, and changes in seed mass may reduce progeny resources and stress tolerance (Westoby et al. 1996).

Understanding where and how species vary in seed mass can help elucidate the reproductive strategies of land plants, and understanding the consequences of these changes will be essential for informing applied science. This work provides a foundation

for multifaceted future investigations into these issues, and highlights the need to increase our population level monitoring and consider intraspecific variation in key traits. Our findings also support the need for continued collection of locally adapted native seeds from many sites for restoration through Seeds of Success (National Academies of Sciences, Engineering, and Medicine 2023), and the species-specific nature of seed mass responses to climate support targeting a wide range of collection sites to collect and preserve high quality seed for multiple species. Additionally, because the reproductive output of many native plant species in the western US is sensitive to climate change, the urgency to continue native seed collections for conservation is greater than ever.

Methods

Seed mass from Seeds of Success

SOS collecting teams follow a consistent seed collection protocol (*SI Appendix* 1), collecting from at least 50 plants of all sizes per location, aiming for a representative population sample. The majority of the SOS seed collections are made in the western continental US, and the vast majority of those are processed at the USDA Forest Service Seed Extractory in Bend, Oregon (BSE, *SI Appendix* 1). Seed mass is assessed at BSE by weighing 5 subsamples of 100 seeds from each collection. After merging BSE and national SOS datasets, we retained 13,004 unique accessions with seed mass, collection date, and location information (Fig. 1*A*).

Environmental Data

We explored a variety of potential environmental factors that may affect seed characteristics, and selected 14 environmental variables to move forward into analysis:

four measures of local change in temperature and precipitation, three annual weather variables (annual minimum temperature, cumulative precipitation over the 6 months prior to collection, and a composite of temperature and precipitation of the month prior to collection), slope, aspect, an estimate of heat load (Dilts et al. 2015), and four soil variables (clay content, an estimate of water content, soil pH, and organic content (Beaudette et al. 2022) (*SI Appendix* 2, Table S1).

Statistical Analyses

We first investigated spatial patterns of seed mass by using the full SOS dataset in generalized linear (GLM) and mixed (GLMM) models with log-transformed seed mass. Then, we subset the data to species collected from at least 3 populations to ask whether there were environmental influences on seed mass that could be estimated across a large species pool, with seed mass scaled within each species. Next, we reduced the data to species collected from at least 20 populations, and ran individual species models, with log-transformed seed mass, asking how the local environment influences seed mass for that subset of well-sampled species. Finally, we aggregated our data at the species level to ask if environment and geography predict seed mass variation for species that had been collected at least 10 times, including a phylogenetic perspective. Models were assessed with visual inspection of QQ plots and VIF scores.

We mapped seed mass to visually assess spatial patterns separately for grasses, forbs, and shrubs, using the full dataset of 13,004 accessions. To predict seed mass across the western United States, we used inverse Distance Weighting (IDW) interpolation of the full dataset using the idw function in the gstat package in R (Pebesma and Graeler 2023). To test if there is a spatial gradient in seed mass among

all species and populations in the western United States, we ran a GLM with log-transformed seed mass as the response variable using the full dataset with latitude, longitude and elevation as predictors; we also ran a second model that was identical but added growth form and duration as fixed effects. We next ran a GLMM with the same three spatial variables and response variable but also included plant family as a random factor to account for taxonomic variation. Not all species were collected from multiple populations, therefore we used family, rather than species, as a random intercept effect using the lmer function from the lme4 package in R (Bates et al. 2024). Similar to the GLM, we also ran a version of this model that included growth form and duration as fixed effects. After observing an effect of growth form in this model, we ran individual GLM and GLMM models for three highly collected growth forms to understand how seed-environment relationships varied among shrubs, grasses, and forbs.

To investigate whether there were consistent influences on seed mass across species, we analyzed relationships between seed mass and a series of predictors for all species that had a minimum of 3 collections in a spatial simultaneous autoregressive error model (SAR) using the errorsarlm function from the R package spatialreg (Bivand et al. 2024). This dataset contained 10,958 collections from 859 species from 73 plant families, and we scaled seed mass within each species. Prior to running the SAR, covariate selection was done using a random forest variable selection pipeline across all species, which implemented the Boruta function from the Boruta package in R (max runs = 100, $p < 0.0001$, *SI Appendix* Q2) (Kursa and Rudnicki 2010), considering the suite of 14 environmental variables discussed above (*SI Appendix* 2, Table S1), along with day of year, year, plant growth form and duration. We also assessed how seed

mass has changed each year for species collected in at least 3 years (631) with individual models containing year as a predictor, and tabulated the standardized coefficients (*SI Appendix* Q2).

To understand how local environmental variables affect seed mass for each of the most well-sampled species separately, we ran individual SAR models for each species that was collected a minimum of 20 times (N = 111 species, N = 5196 total collections, *SI Appendix*). We initiated covariate selection using the random forest feature selection pipeline (described above and *SI Appendix* Q3) separately for each species. For seven species, no variables were confirmed, and thus they were not analyzed but are included in our presentation of results. To determine whether sampling effort affected our ability to estimate environment-seed mass relationships, we ran additional linear models on subsets of data (*SI Appendix* Q3).

Finally, to understand the factors that affect the degree of variation in seed mass among species, we calculated the coefficient of variation (CV) of seed mass for each species that had been collected at least 10 times by dividing the standard deviation by the mean seed mass per species, corrected for sampling effort (*SI Appendix* Q4). We incorporated phylogenetic relatedness in these models using relationships described in Mishler et al. (2020). Seventy-nine species were not present in the phylogenetic tree even after correction and cross checking taxonomy, thus, our final model for assessing variation in seed mass included 235 species from 6865 populations.

We aggregated environmental and climate variables across all collections for each species for a total of 33 environmental, spatial, temporal, and life history variables in addition to growth form and duration describing each of 235 species (*SI Appendix* Q4,

Table S1). Next, we ran all 33 variables through the random forest feature selection pipeline (described above and *SI Appendix*). Confirmed important attributes were then moved into a GLM with log-transformed unbiased CV as response to check VIF (all were below 5) and model diagnostics. Then, attributes were moved into a phylogenetic generalized least squares regression (PGLS) using Pagel's correlation of trait evolution and the phylogeny from Mishler et al. (2020).

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Data Availability

The dataset will be available on Dryad.

Literature Cited

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJB. 2013. Trait-based tests of coexistence mechanisms. Ecol Lett. 16(10):1294–1306. doi:10.1111/ele.12157.

Albrecht MA, McCarthy BC. 2009. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. J Ecol. 97(5):1037–1049. doi:10.1111/j.1365-2745.2009.01527.x.

Barga SC, Olwell P, Edwards F, Prescott L, Leger EA. 2020. Seeds of Success: A conservation and restoration investment in the future of U.S. lands. Conserv Sci Pract. 2(7):e209. doi:10.1111/csp2.209.

Baughman OW, Agneray AC, Forister ML, Kilkenny FF, Espeland EK, Fiegener R, Horning ME, Johnson RC, Kaye TN, Ott J, et al. 2019. Strong patterns of intraspecific variation and local adaptation in Great Basin plants revealed through a review of 75 years of experiments. Ecol Evol. 9(11):6259–6275. doi:https://doi.org/10.1002/ece3.5200.

Beaudette D, Skovlin J, Roecker S, Brown A. 2022. soilDB: Soil Database Interface. [accessed 2022 Oct 5]. https://CRAN.R-project.org/package=soilDB.

Bivand R, Piras G, Anselin L, Bernat A, Blankmeyer E, Chun Y, Gómez-Rubio V, Griffith D, Gubri M, Halbersma R, et al. 2024. spatialreg: Spatial Regression Analysis. [accessed 2024 Mar 11]. https://cran.r-project.org/web/packages/spatialreg/index.html.

Bunn AG, Goetz SJ, Kimball JS, Zhang K. 2007. Northern high-latitude ecosystems respond to climate change. Eos Trans Am Geophys Union. 88(34):333–335. doi:10.1029/2007EO340001.

Chan JCS, Ooi MKJ, Guja LK. 2022. Polyploidy but not range size is associated with seed and seedling traits that affect performance of pomaderris species. Front Plant Sci. 12. doi:10.3389/fpls.2021.779651. [accessed 2024 May 13]. https://www.frontiersin.org/journals/plant-science/articles/10.3389/fpls.2021.779651/full.

Clausen J, Keck DD, Hiesey WM. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Exp Stud Nat Species Eff Varied Environ West North Am Plants.(520). [accessed 2023 Jan 25]. https://www.cabdirect.org/cabdirect/abstract/19421601306.

Cochrane A, Yates CJ, Hoyle GL, Nicotra AB. 2015. Will among-population variation in seed traits improve the chance of species persistence under climate change? Glob Ecol Biogeogr. 24(1):12–24. doi:10.1111/geb.12234.

Dilts TE, Weisberg PJ, Dencker CM, Chambers JC. 2015. Functionally relevant climate variables for arid lands: a climatic water deficit approach for modelling desert shrub distributions. J Biogeogr. 42(10):1986–1997. doi:10.1111/jbi.12561.

Dylewski Ł, Ortega YK, Bogdziewicz M, Pearson DE. 2020. Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecol Lett. 23(6):1024–1033. doi:https://doi.org/10.1111/ele.13499.

Frei ER, Ghazoul J, Matter P, Heggli M, Pluess AR. 2014. Plant population differentiation and climate change: responses of grassland species along an elevational gradient. Glob Change Biol. 20(2):441–455. doi:10.1111/gcb.12403.

Frenne PD, Graae BJ, Rodríguez-Sánchez F, Kolb A, Chabrerie O, Decocq G, Kort HD, Schrijver AD, Diekmann M, Eriksson O, et al. 2013. Latitudinal gradients as

natural laboratories to infer species' responses to temperature. J Ecol. 101(3):784–795. doi:https://doi.org/10.1111/1365-2745.12074.

Gorden NLS, Winkler KJ, Jahnke MR, Marshall E, Horky J, Hudelson C, Etterson JR. 2016. Geographic patterns of seed mass are associated with climate factors, but relationships vary between species. Am J Bot. 103(1):60–72. doi:https://doi.org/10.3732/ajb.1500295.

Greene DF, Johnson EA. 1993. Seed Mass and Dispersal Capacity in Wind-Dispersed Diaspores. Oikos. 67(1):69–74. doi:10.2307/3545096.

Harper JL, Lovell PH, Moore KG. 1970. The Shapes and Sizes of Seeds. Annu Rev Ecol Syst. 1(1):327–356. doi:10.1146/annurev.es.01.110170.001551.

Hulshof CM, Violle C, Spasojevic MJ, McGill B, Damschen E, Harrison S, Enquist BJ. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. J Veg Sci. 24(5):921–931. doi:10.1111/jvs.12041.

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, et al. 2011. TRY – a global database of plant traits. Glob Change Biol. 17(9):2905–2935. doi:https://doi.org/10.1111/j.1365-2486.2011.02451.x.

Kursa MB, Rudnicki WR. 2010. Feature Selection with the Boruta Package. J Stat Softw. 36(11). doi:10.18637/jss.v036.i11. [accessed 2023 May 8]. http://www.jstatsoft.org/v36/i11/.

Larson JE, Sheley RL, Hardegree SP, Doescher PS, James JJ. 2015. Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. J Appl Ecol. 52(1):199–209. doi:10.1111/1365-2664.12350.

Leger EA, Atwater DZ, James JJ. 2019. Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. J Appl Ecol. 56(6):1343–1354. doi:10.1111/1365-2664.13367.

Leimu R, Fischer M. 2008. A Meta-Analysis of Local Adaptation in Plants. PLOS ONE. 3(12):e4010. doi:10.1371/journal.pone.0004010.

Leishman MR. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. Oikos. 93(2):294–302. doi:https://doi.org/10.1034/j.1600-0706.2001.930212.x.

Liu J, Bai Y, Lamb EG, Simpson D, Liu G, Wei Y, Wang D, McKenney DW, Papadopol P. 2013. Patterns of Cross-Continental Variation in Tree Seed Mass in the Canadian Boreal Forest. PLOS ONE. 8(4):e61060. doi:10.1371/journal.pone.0061060.

Liu U, Cossu TA, Dickie J. 2019 Jun 13. Royal Botanic Gardens, Kew's Seed Information Database (SID): A compilation of taxon-based biological seed characteristics or traits. Biodivers Inf Sci Stand. doi:10.3897/biss.3.37030. [accessed 2023 May 1]. https://www.proquest.com/docview/2282401665/abstract/5E5AFC61B9AA47F5PQ/1.

Malanson GP, Butler DR, Fagre DB, Walsh SJ, Tomback DF, Daniels LD, Resler LM, Smith WK, Weiss DJ, Peterson DL, et al. 2007. Alpine treeline of Western North America: linking organism-to-landscape dynamics. Phys Geogr. 28(5):378–396. doi:10.2747/0272-3646.28.5.378.

McGinley MA, Temme DH, Geber MA. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. Am Nat. 130(3):370–398. doi:10.1086/284716.

Mishler BD, Guralnick R, Soltis PS, Smith SA, Soltis DE, Barve N, Allen JM, Laffan SW. 2020. Spatial phylogenetics of the North American flora. J Syst Evol. 58(4):393–405. doi:10.1111/jse.12590.

Moles AT, Ackerly DD, Tweddle JC, Dickie JB, Smith R, Leishman MR, Mayfield MM, Pitman A, Wood JT, Westoby M. 2007. Global patterns in seed size. Glob Ecol Biogeogr. 16(1):109–116. doi:https://doi.org/10.1111/j.1466-8238.2006.00259.x.

Moles AT, Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature. J Ecol. 92(3):372–383. doi:10.1111/j.0022-0477.2004.00884.x.

Moran EV, Hartig F, Bell DM. 2016. Intraspecific trait variation across scales: implications for understanding global change responses. Glob Change Biol. 22(1):137–150. doi:10.1111/gcb.13000.

Muller-Landau HC. 2010. The tolerance–fecundity trade-off and the maintenance of diversity in seed size. Proc Natl Acad Sci. 107(9):4242–4247. doi:10.1073/pnas.0911637107.

Murray BR, Brown AHD, Dickman CR, Crowther MS. 2004. Geographical gradients in seed mass in relation to climate. J Biogeogr. 31(3):379–388. doi:10.1046/j.0305-0270.2003.00993.x.

National Academies of Sciences, Engineering, and Medicine. 2023. An assessment of native seed needs and the capacity for their supply: final report. Washington, D.C.: National Academies Press. [accessed 2024 Sep 26]. https://www.nap.edu/catalog/26618.

Norden N, Daws MI, Antoine C, Gonzalez MA, Garwood NC, Chave J. 2009. The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. Funct Ecol. 23(1):203–210. doi:https://doi.org/10.1111/j.1365-2435.2008.01477.x.

Paige KN, Whitham TG. 1987. Overcompensation in Response to Mammalian Herbivory: The Advantage of Being Eaten. Am Nat. 129(3):407–416.

Parry M, Canziani O, Palutikof J, van der Linden P, Hanson C. 2007. Climate change 2007: impacts, adaptation and vulnerability. In: contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change.

Pebesma E, Graeler B. 2023. gstat: Spatial and Spatio-Temporal Geostatistical Modelling, Prediction and Simulation. [accessed 2024 Mar 11]. https://cran.r-project.org/web/packages/gstat/index.html.

Seale M, Nakayama N. 2020. From passive to informed: mechanical mechanisms of seed dispersal. New Phytol. 225(2):653–658. doi:10.1111/nph.16110.

Sgrò CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evol Appl. 4(2):326–337. doi:10.1111/j.1752-4571.2010.00157.x.

Sheridan JA, Bickford D. 2011. Shrinking body size as an ecological response to climate change. Nat Clim Change. 1(8):401–406. doi:10.1038/nclimate1259.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV, et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett. 18(12):1406–1419. doi:10.1111/ele.12508.

Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring. Am Nat. 108(962):499–506.

Solbreck C, Knape J. 2017. Seed production and predation in a changing climate: new roles for resource and seed predator feedback? Ecology. 98(9):2301–2311. doi:10.1002/ecy.1941.

Tangney R, Merritt DJ, Callow JN, Fontaine JB, Miller BP. 2020. Seed traits determine species' responses to fire under varying soil heating scenarios. Funct Ecol. 34(9):1967–1978. doi:10.1111/1365-2435.13623.

Turnbull LA, Rees M, Crawley MJ. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. J Ecol. 87(5):899–912.

Tuthill JE, Ortega YK, Pearson DE. 2023. Seed size, seed dispersal traits, and plant dispersion patterns for native and introduced grassland plants. Plants. 12(5):1032. doi:10.3390/plants12051032.

Vaughton G, Ramsey M. 1997. Seed mass variation in the shrub banksia spinulosa (proteaceae): resource constraints and pollen source effects. Int J Plant Sci. 158(4):424–431. doi:10.1086/297452.

Venable DL. 1992. Size-number trade-offs and the variation of seed size with plant resource status. Am Nat. 140(2):287–304.

Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. Trends Ecol Evol. 27(4):244–252. doi:10.1016/j.tree.2011.11.014.

Völler E, Auge H, Prati D, Fischer M, Hemp A, Bossdorf O. 2012. Geographical and land-use effects on seed-mass variation in common grassland plants. Basic Appl Ecol. 13(5):395–404. doi:10.1016/j.baae.2012.06.006.

Westoby M, Jurado E, Leishman M. 1992. Comparative evolutionary ecology of seed size. Trends Ecol Evol. 7(11):368–372. doi:10.1016/0169-5347(92)90006-W.

Westoby M, Leishman M, Lord J, Poorter H, Schoen DJ. 1996. Comparative ecology of seed size and dispersal [and discussion]. Philos Trans Biol Sci. 351(1345):1309–1318.

Zhang C, Li J, Willis CG, Ma Z. 2020. Among-population variation in seed mass for 190 Tibetan plant species: Phylogenetic pattern and ecological correlates. Glob Ecol Conserv. 23:e01163. doi:10.1016/j.gecco.2020.e01163.

Zhang C, Ma Z, Zhou H, Zhao X. 2019. Long-term warming results in species-specific shifts in seed mass in alpine communities. PeerJ. 7:e7416. doi:10.7717/peerj.7416.

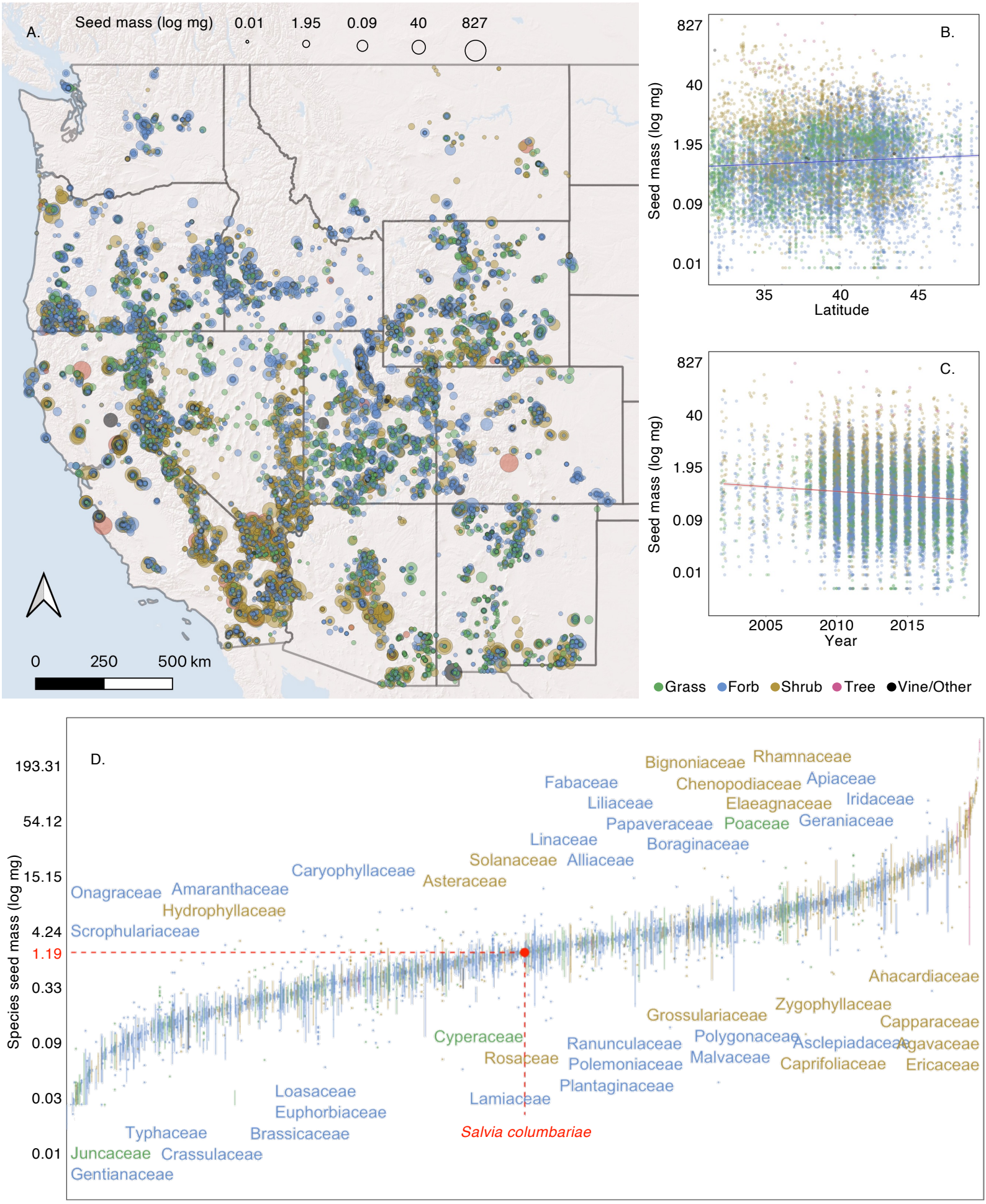
Figure Legends

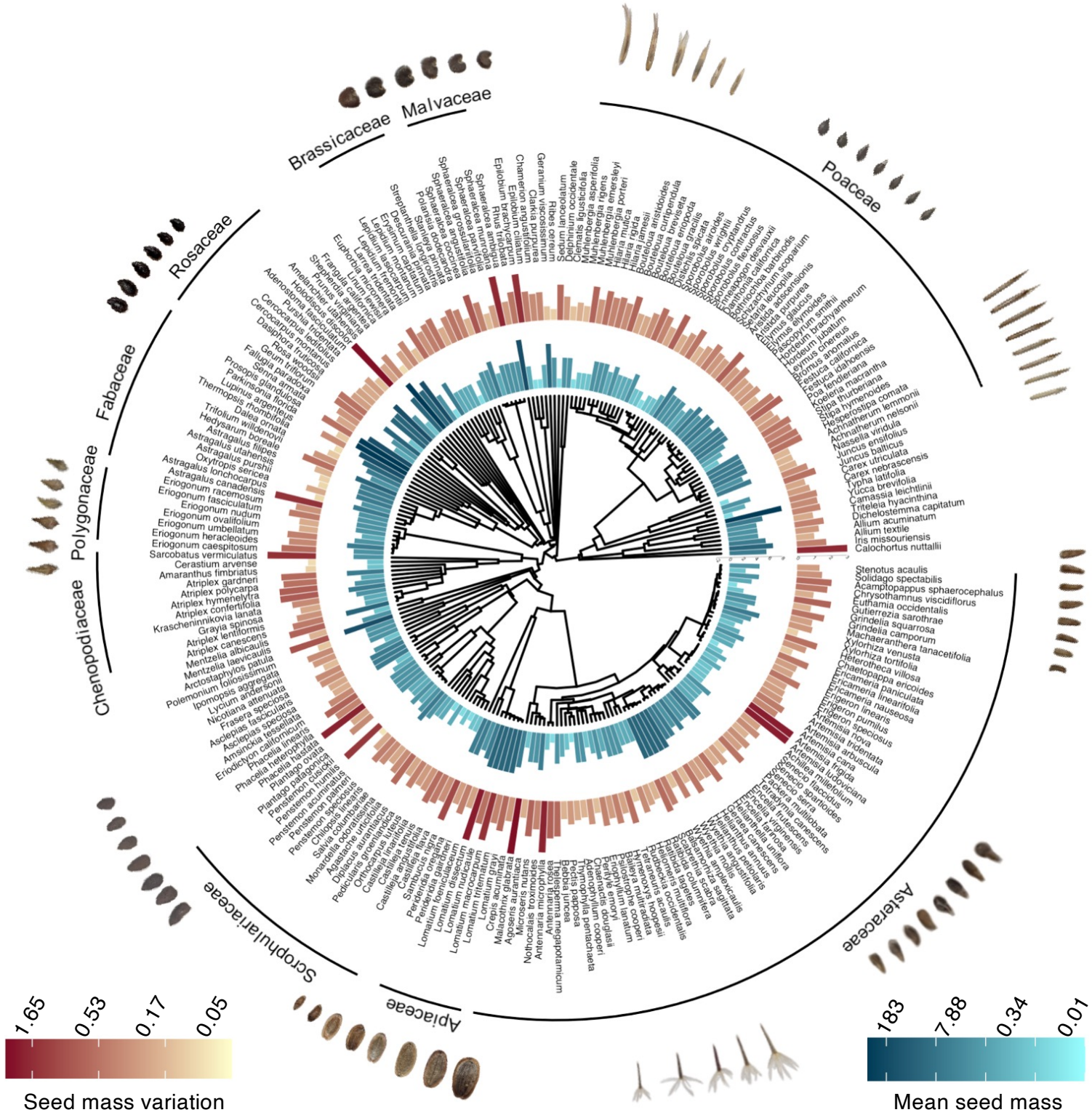
Figure 1. Seed mass of over 2,000 native plant species colored by growth form. A) Collection locations of 13,004 filled seed lots from Seeds of Success. Each point is a site sampled by a field crew after scouting and careful phenology tracking, representing a collection of at least 10,000 seeds from at least 50 plants. Seed mass was log-transformed for analysis, and sized by 20 quantile groups (5 examples shown at top). Log transformed seed mass of 13,004 populations plotted along B) latitude and C) year with 5 log breaks indicated on the y axis, lines represent simple linear regression of seed mass and latitude or year on the 3 collection dataset (see Q2, Q3 and *SI Appendix* Table S2, S4 for full generalized linear model and full spatial simultaneous autoregressive error model results, partial effects est = 0.0266, $p < 0.0001$; est = -0.010, $p = 0.007$ respectively). D) Log-transformed seed mass for 2093 species from 108 plant families from a dataset of seed collections across 11 western US states. For each species, the interquartile range of seed mass is shown by the lines and outliers are indicated as points and are colored by growth form. The y axis is on a log 10 scale in seed mass and species are ordered along the x axis by mean seed mass; the subset of families represented in the 10 sample dataset are listed near the first time the largest species appears in the distribution. *Salvia columbariae* is labeled as the median species, for reference. Seed mass was generated from the US Forest Service's Bend Seed Extractory (BSE) processing of the Bureau of Land Management's collections (BSE weighs a subset of 500 seeds per collection) and as part of the Seeds of Success program, which has been collecting native seeds since 2000.

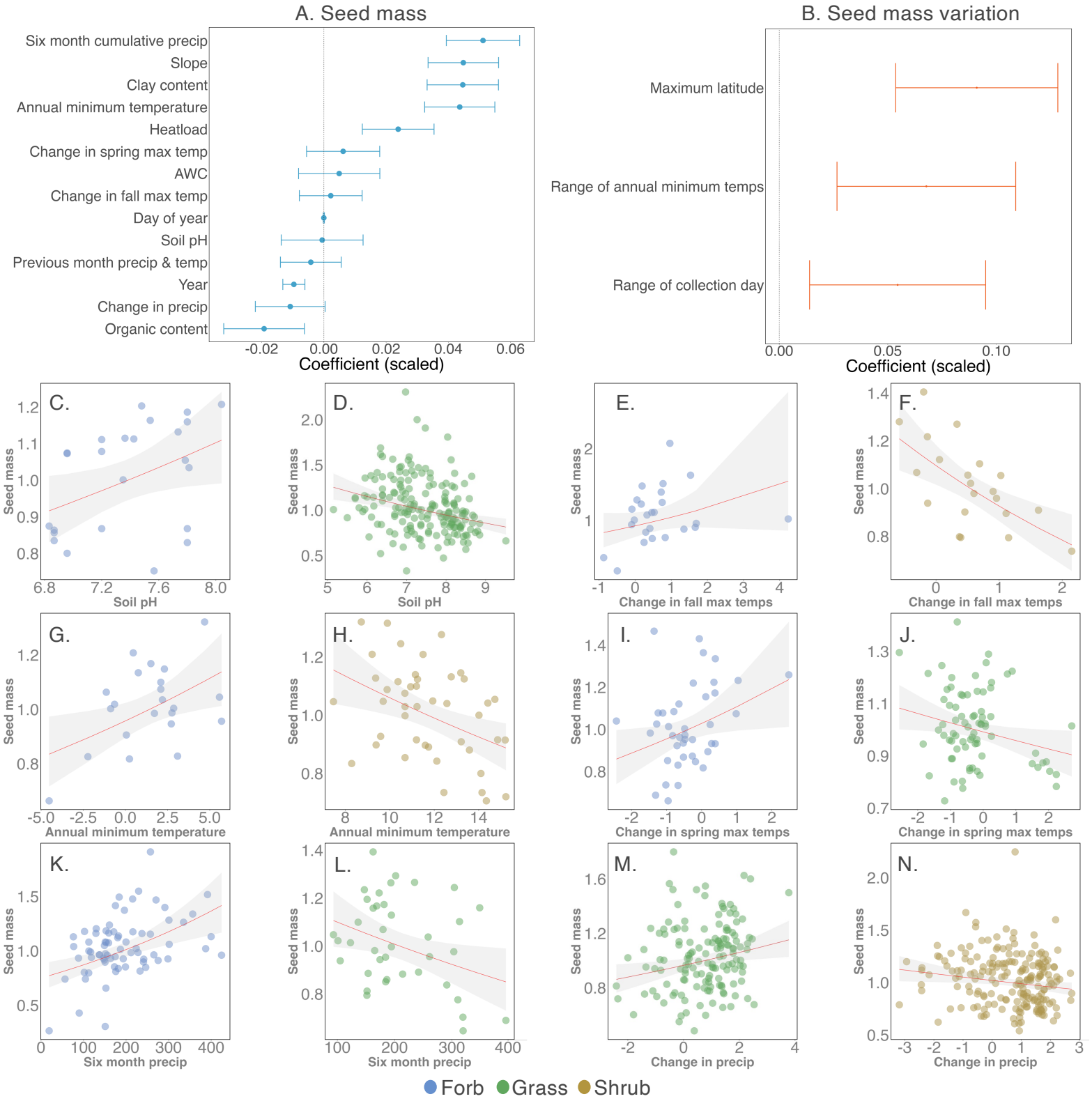
Figure 2. Phylogenetic tree of 235 plant species from 44 families collected from at least 10 populations using phylogenetic tree from Mishler et al. (2020). Inner bar chart represents log-transformed mean seed mass of each species, outer bar chart represents log-transformed coefficient of variation of seed mass for each species. Seed mass is from the US Forest Service's Bend Seed Extractory processing the Bureau of Land Management's Seeds of Success collections. Seed mass coefficient of variation is calculated as $CV_{unbiased}=(1+14\times N)\times CV$. Images of native seeds are included; species names are indicated with a nearby bullet (photos: LL).

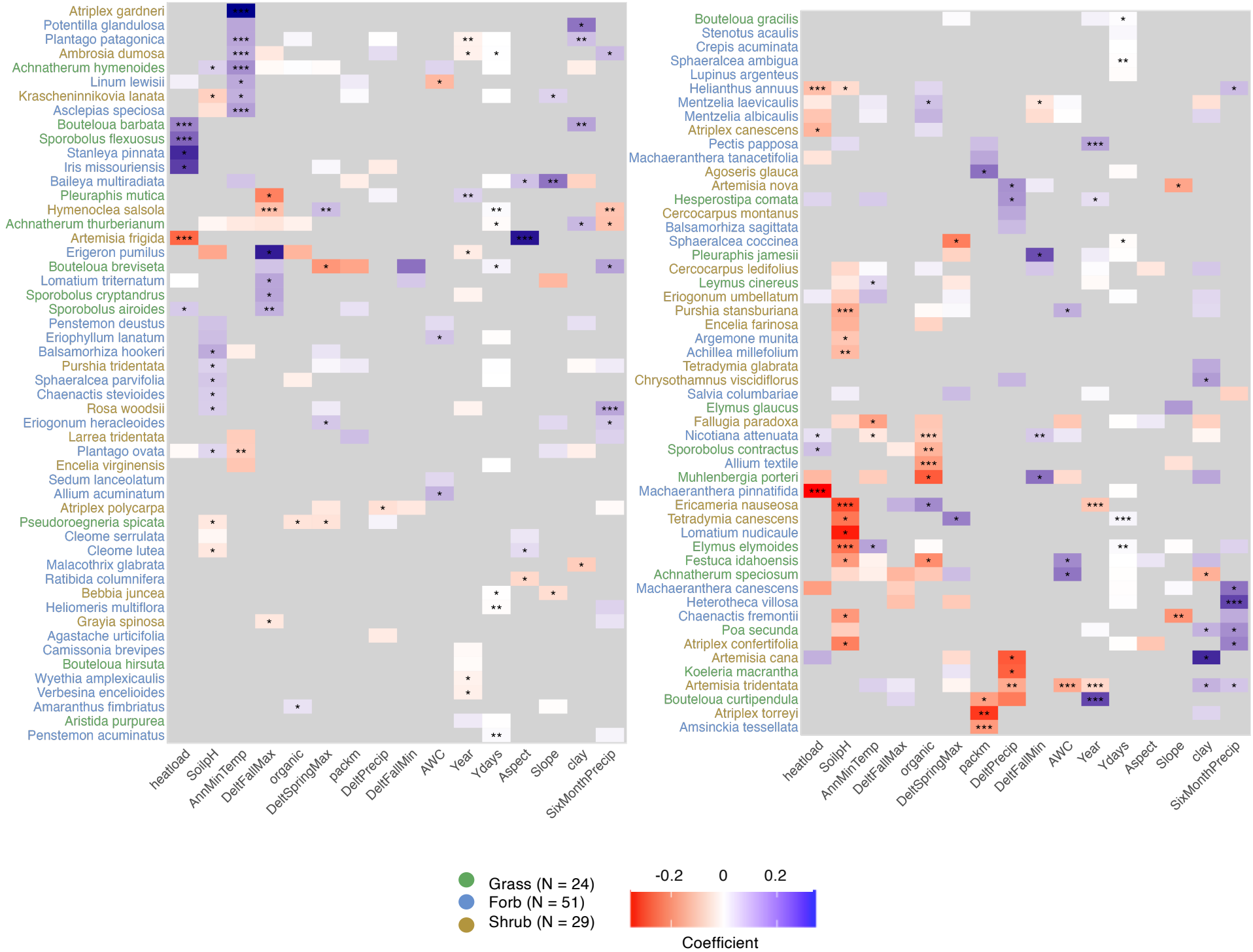
Figure 3. Relationships between seed mass and environment for native plant species from across the western US. Environmental influence on A) seed mass using a spatial simultaneous autoregressive error model (N = 859 species, 10,958 populations, 73 plant families in the 3 collection dataset) and B) the variability of seed mass estimated from a phylogenetic generalized least squares regression (N = of 235 species, 6865 total populations, in the 10 collection dataset). Covariates are centered and scaled, and error bars represent standard error produced by the PGLS. Relationships between soil pH and seed mass for C) *Balsamorhiza hookeri* and D) *Elymus elymoides*; relationships between change in fall maximum temperatures 30 years prior to each collection and seed mass for E) *Erigeron pumilus* and F) *Hymenoclea salsola*; relationships between annual minimum temperature and seed mass for G) *Asclepias speciosa* and H) *Plantago ovata*; relationships between change in spring maximum temperatures 30 years prior to each collection and seed mass for I) *Eriogonum heracleoides* and J) *Pseudoroegneria spicata*; relationships between cumulative precipitation six months leading up to collection and seed mass for K) *Heterotheca villosa* and L) *Achnatherum thurberianum*; relationships between change in annual precipitation 30 years prior to each collection and seed mass for M) *Hesperostipa comata* and N) *Artemisia tridentata*. For C-N, relationships were analyzed with a spatial simultaneous autoregressive error model (SAR) seed mass is log-transformed and predictor variables are centered and scaled; species specific results and full model structures are in *SI Appendix* Table S6. Lines represent the semi-partial regression plots between a single predictor variable and seed mass, points are colored by growth form.

Figure 4. Environmental and climatic influence on seed mass estimated from 105 individual spatial simultaneous autoregressive error models for species collected from at least 20 different populations (5,010 total populations). Axes indicate individual species models as rows and possible covariates as columns; gray boxes indicate variables that did not enter final models. Red boxes indicate negative relationships, grading to blue for positive relationships. Significance is indicated with *** = P <0.0001, ** = P<0.001, and * = P<0.05. Species' names are colored by growth form. Species and variables are organized by a similarity matrix based on model results. Figure is halved at *Penstemon acuminatus* continuing to *Stenotus acaulis* following the similarity matrix.


A.
Seed mass (log mg)
0.01
1.95
0.09
40
827
0
250
500 km
B.
Seed mass (log mg)
827
40
1.95
0.09
0.01
35
40
45
Latitude
C.
Seed mass (log mg)
827
40
1.95
0.09
0.01
2005
2010
2015
Year
Grass
Forb
Shrub
Tree
Vine/Other
D.
Species seed mass (log mg)
193.31
54.12
15.15
4.24
1.19
0.33
0.09
0.03
0.01
Bignoniaceae
Rhamnaceae
Fabaceae
Chenopodiaceae
Apiaceae
Liliaceae
Elaeagnaceae
Iridaceae
Papaveraceae
Poaceae
Geraniaceae
Linaceae
Boraginaceae
Solanaceae
Alliaceae
Caryophyllaceae
Asteraceae
Onagraceae
Amaranthaceae
Hydrophyllaceae
Scrophulariaceae
Anacardiaceae
Zygophyllaceae
Grossulariaceae
Capparaceae
Cyperaceae
Polygonaceae
Asclepiadaceae
Agavaceae
Ranunculaceae
Rosaceae
Polemoniaceae
Malvaceae
Caprifoliaceae
Ericaceae
Plantaginaceae
Loasaceae
Lamiaceae
Euphorbiaceae
Typhaceae
Brassicaceae
Salvia columbariae
Juncaceae
Crassulaceae
Gentianaceae


Brassicaceae
Malvaceae
Rosaceae
Fabaceae
Polygonaceae
Chenopodiaceae
Scrophulariaceae
Apiaceae
Asteraceae
Poaceae
1.65
0.53
0.17
0.05
Seed mass variation
183
7.88
0.34
0.01
Mean seed mass


A. Seed mass
Six month cumulative precip
Slope
Clay content
Annual minimum temperature
Heatload
Change in spring max temp
AWC
Change in fall max temp
Day of year
Soil pH
Previous month precip & temp
Year
Change in precip
Organic content
-0.02
0.00
0.02
0.04
0.06
Coefficient (scaled)
B. Seed mass variation
Maximum latitude
Range of annual minimum temps
Range of collection day
0.00
0.05
0.10
Coefficient (scaled)
C.
D.
E.
F.
G.
H.
I.
J.
K.
L.
M.
N.
Seed mass
Soil pH
Change in fall max temps
Annual minimum temperature
Change in spring max temps
Six month precip
Change in precip
Forb
Grass
Shrub


Atriplex gardneri
Potentilla glandulosa
Plantago patagonica
Ambrosia dumosa
Achnatherum hymenoides
Linum lewisii
Krascheninnikovia lanata
Asclepias speciosa
Bouteloua barbata
Sporobolus flexuosus
Stanleya pinnata
Iris missouriensis
Baileya multiradiata
Pleuraphis mutica
Hymenoclea salsola
Achnatherum thurberianum
Artemisia frigida
Erigeron pumilus
Bouteloua breviseta
Lomatium triternatum
Sporobolus cryptandrus
Sporobolus airoides
Penstemon deustus
Eriophyllum lanatum
Balsamorhiza hookeri
Purshia tridentata
Sphaeralcea parvifolia
Chaenactis stevioides
Rosa woodsii
Eriogonum heracleoides
Larrea tridentata
Plantago ovata
Encelia virginensis
Sedum lanceolatum
Allium acuminatum
Atriplex polycarpa
Pseudoroegneria spicata
Cleome serrulata
Cleome lutea
Malacothrix glabrata
Ratibida columnifera
Bebbia juncea
Heliomeris multiflora
Grayia spinosa
Agastache urticifolia
Camissonia brevipes
Bouteloua hirsuta
Wyethia amplexicaulis
Verbesina encelioides
Amaranthus fimbriatus
Aristida purpurea
Penstemon acuminatus
heatload
SoilpH
AnnMinTemp
DeltFallMax
organic
DeltSpringMax
packm
DeltPrecip
DeltFallMin
AWC
Year
Ydays
Aspect
Slope
clay
SixMonthPrecip
Bouteloua gracilis
Stenotus acaulis
Crepis acuminata
Sphaeralcea ambigua
Lupinus argenteus
Helianthus annuus
Mentzelia laevicaulis
Mentzelia albicaulis
Atriplex canescens
Pectis papposa
Machaeranthera tanacetifolia
Agoseris glauca
Artemisia nova
Hesperostipa comata
Cercocarpus montanus
Balsamorhiza sagittata
Sphaeralcea coccinea
Pleuraphis jamesii
Cercocarpus ledifolius
Leymus cinereus
Eriogonum umbellatum
Purshia stansburiana
Encelia farinosa
Argemone munita
Achillea millefolium
Tetradymia glabrata
Chrysothamnus viscidiflorus
Salvia columbariae
Elymus glaucus
Fallugia paradoxa
Nicotiana attenuata
Sporobolus contractus
Allium textile
Muhlenbergia porteri
Machaeranthera pinnatifida
Ericameria nauseosa
Tetradymia canescens
Lomatium nudicaule
Elymus elymoides
Festuca idahoensis
Achnatherum speciosum
Machaeranthera canescens
Heterotheca villosa
Chaenactis fremontii
Poa secunda
Atriplex confertifolia
Artemisia cana
Koeleria macrantha
Artemisia tridentata
Bouteloua curtipendula
Atriplex torreyi
Amsinckia tessellata
heatload
SoilpH
AnnMinTemp
DeltFallMax
organic
DeltSpringMax
packm
DeltPrecip
DeltFallMin
AWC
Year
Ydays
Aspect
Slope
clay
SixMonthPrecip
Grass (N = 24)
Forb (N = 51)
Shrub (N = 29)
-0.2
0
0.2
Coefficient