Mating system and historical climate conditions affect population mean seed mass: Evidence for adaptation and a new component of the selfing syndrome in *Clarkia*

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Abstract

1. The evolution of seed size may be influenced by intrinsic attributes of populations, such as mating system and extrinsic factors, such as climate. Several hypotheses propose that the evolution of self-fertilization from an outcrossing progenitor will be accompanied by a reduction in seed size, but this prediction has not been rigorously tested. Many studies report that the mean seed size of populations or taxa is associated with long-term climate conditions. Here, we examined the effects on seed size of both mating system and climate within a single genus.

2. In the California wildflower genus, *Clarkia* (Onagraceae), we sampled seeds from 58 populations representing three pairs of sister taxa; each pair included a predominantly outcrossing and a facultatively selfing taxon. We then examined the independent effects on population mean seed size of mating system, elevation, long-term (30-year) climate conditions, and climate anomalies (the deviation between conditions in the year of collection and the long-term mean), focusing on maximum monthly temperature (T_{max}), cumulative moisture deficit and cumulative precipitation (PPT) during *Clarkia's* growing season (fall, winter and spring).

3. In each taxon pair, the selfing taxon had smaller seeds than the outcrosser. Local, long-term (1921–1980 and 1981–2000) mean T_{max}, PPT and elevation were independently and negatively associated with seed size. Long-term means for T_{max} and PPT explain geographical variation in seed size better than climate anomalies in the year of collection.

4. *Synthesis*. We corroborated two key hypotheses concerning the drivers of geographical variation in mean seed size. Small seeds in *Clarkia* co-evolve with selfing (although the mechanism remains elusive) and in response to chronically warm and wet conditions. The effect of long-term mean precipitation on seed size differs qualitatively from the effect of precipitation anomalies; relatively large seeds are produced in populations experiencing wetter-than-normal years. Ongoing climate change may therefore generate conflicting selection on seed size in *Clarkia*: intensifying drought is likely to lead to an evolutionary increase in seed size due to its effects on seedling survivorship, while climate-driven declines in pollinators

or selection favouring more rapid reproduction may promote the evolution of self-pollination, facilitating the evolution of smaller seeds.

1 | INTRODUCTION

The study of geographical variation in traits that affect individual fitness can inform our understanding of whether and how natural selection has affected their evolution. Within species, individual seed mass (hereafter referred to as seed size) is among the most well-studied fitness-related traits, affecting viability (Caron et al., 2014), the probability of emergence (Andersson, 1996; Benard & Toft, 2007; Larios, Burquez, Becerra, & Venable, 2014; Stanton, 1984; Winn, 1988), germination time (Arellano & Peco, 2012; Benard & Toft, 2007; Eriksson, 1999; Gomaa & Pico, 2011; Kalisz, 1989; Mazer, 1987), recruitment (Chacon & Bustamante, 2001), seedling growth (Gomaa & Pico, 2011; Gross, 1984; Stanton, 1984), seedling size (Caron et al., 2014; Sage, Koenig, & McLaughlin, 2011; Vaughton & Ramsey, 1998), tolerance of damage (Kahn, 2004), the probability of survival (Arellano & Peco, 2012; Benard & Toft, 2007; Chávez-Pesqueira & Núñez-Farfán, 2016; Hallet, Standish, & Hobbs, 2011; Larios et al., 2014; Vaughton & Ramsey, 1998) and the probability of flowering (Halpern, 2005). Relatively large seed size often improves seed and seedling performance (Agrawal, 2001; Bonfil, 1998; Carón et al., 2014; Chávez-Pesqueira & Núñez-Farfán, 2016; Gross, 1984; Khan, 2004; Simons & Johnston, 2000; Wu, Meng, Wang, Wei, & Jiang, 2018), particularly when seeds are exposed to low light, to intra or interspecific competition (Houssard & Escarré, 1991) or to simulated herbivory (Armstrong & Westoby, 1993; Bartlow, Agosta, Curtis, Yi, & Steele, 2018; Bonfil, 1998). However, negative, conflicting and non-significant relationships between seed size and performance have also been reported (Lázaro & Traveset, 2009).

Investigations at a variety of scales have demonstrated that geographical variation in environmental conditions appears to generate variation in seed size among communities and taxa due to natural selection or species-sorting. In the temperate zone, relatively large-seeded species tend to occupy drier and/or more heavily shaded environments than small-seeded species (Baker, 1972; Mazer, 1989, 1990; Salisbury, 1942, 1975; Tardella, Piermarteri, Malatesta, & Catorci, 2016). Among communities, mean annual temperature has been found to be positively associated with mean seed size (Azcarte, Manzano, & Peco, 2010; Murray, Brown, Dickman, & Crowther, 2004; Simpson, Richardson, & Laughlin, 2016). Climatic variation may also contribute to population differentiation in seed size within species. In some species, larger seeds are associated with warmer or drier climates (Konarzewski, Murray, & Godfree, 2012; Lemke et al., 2015; Liu et al., 2013; Llanderal-Mendoza, Gugger, Oyama, Uribe-Salas, & González-Rodríguez, 2017), whereas in others, smaller seeds are associated with warmer (Carón et al., 2014; Soper Gordon et al., 2016) or drier (Cochrane, Hoyle, Yates, Neeman, & Nictra, 2016; Llanderal-Mendoza et al., 2017; Murray et al., 2004; Volis, Mendlinger, & Ward, 2002) conditions.

Variation among conspecific populations in seed size has also been found to be associated with elevation (Pleuss, Schütz, & Stöcklin, 2005; Qi et al., 2014), but the direction of the change in seed size with elevation differs among regions and taxa, potentially because the effects of elevation on climate, soil quality, percent cover and the degree of competition are region-specific. For example, in *Pedicularis* (Guo, Mazer, & Du, 2010a), *Euptelea pleiospermum* (Wu et al., 2018) and *Picea mariana* (Liu et al., 2013), seed size decreases with elevation, whereas in *Heteromeles arbutifolia* (Martijena & Bullock, 1997) and *Nothofagus nervosa* (in 1 of 4 years: Marchelli & Gallo, 1999), seed size increases with elevation (see also Wu & Du, 2009 for contrasting patterns). These studies demonstrate that environmental factors are associated with differences among communities and populations in seed size; none of these studies, however, were designed to detect independent effects on seed size of temperature, precipitation and elevation.

In addition to the effects of these extrinsic factors on the evolution of seed size, attributes intrinsic to species and populations may also affect seed size evolution. For example, within genera comprised of species that differ in mating system, the mean seed mass of selfing taxa has been reported to be lower than that of their outcrossing congeners in *Arabidopsis* (Mitchell-Olds, 2001), *Plantago* (De Jong, Dijk, & Klinkhamer, 2005) and *Clarkia* (Knies, Delesalle, & Cavaliere, 2004). Self-fertilization regularly co-evolves (from outcrossing progenitors) with traits associated with more efficient resource allocation and/or more rapid development—the 'selfing syndrome'—presumably due to the reversal of selection favouring genotypes with energetically expensive traits that attract or reward pollinators (Primack, 1987; Sicard & Lenhard, 2011; Vallejo-Marín, 2009; Wyatt, 1984). Accordingly, attributes that have evolved in selfing taxa include smaller flowers (Duncan & Rausher, 2013; but see de Vos, Wüest, & Conti, 2014), shorter floral life spans (Dudley, Mazer, & Galusky, 2007), a reduction in pollen production per flower (Delesalle, Mazer, & Paz, 2008) and lower pollen:ovule ratios (Mazer, Dudley, Delesalle, Paz, & Galusky, 2009). The effect of shifts in mating system on the evolution of seed size, however, has not been widely studied. If the evolution of self-fertilization is consistently associated with an evolutionary reduction in seed size, then this would be a previously unrecognized component of the selfing syndrome.

1.1 | The potential for the co-evolution of self-fertilization and small seeds

Self-fertilization may be expected to co-evolve with small seeds because both attributes may increase the probability of the colonization of new sites. Self-fertilizing genotypes are more likely to establish new populations than pollinator-dependent genotypes because the former do not require pollen vectors to produce seeds (Baker, 1955, 1959). This inference has been corroborated by Grossenbacher, Runquist, Goldberg, and Brandvain (2015), who found that within many genera, self-fertilizing taxa have broader geographical distributions than their outcrossing congeners. Small-seeded genotypes may have two advantages over large-seeded genotypes with respect to colonization. First, small-seeded genotypes and taxa are expected to have higher fecundity per individual than large-seeded ones (Smith & Fretwell, 1974); second, among taxa with wind- or passively dispersed seeds, small seeds are expected to disperse farther than large ones (Greene & Johnson, 1993; Tamme et al., 2014). Consistent with these predictions, Sonkoly et al. (2017) found that among 1,600 Central European herbaceous species, range size is inversely correlated with mean individual seed mass; and Thomson, Moles, Auld, and Kingsford (2011) reported that, among 181 species collectively distributed world-wide, mean seed mass is negatively correlated with both mean and maximum dispersal distances, controlling for variation in plant height.

In sum, genotypes (or populations) that are both self-fertilizing and produce small, wind- or passively dispersed seeds are expected to be more likely to colonize new sites than conspecific genotypes (or populations) that are large-seeded and outcrossing, although the long-term persistence of small-seeded taxa is not ensured. The patterns cited above within *Arabidopsis*, *Plantago* and *Clarkia* provide evidence that this association between mating system and seed mass may be common. These studies, however, did not control for the possible confounding effects of abiotic factors on seed size. Self-fertilization may also co-evolve with small seeds due to the effects of chronic selfing on the intensity of genetic conflict (Haig & Westoby, 1991); this mechanism is not addressed in this study, but see Section 4, below.

The current study was designed with two primary objectives. First, we aimed to determine whether, independent of climate conditions and elevation, the evolution of self-fertilization in *Clarkia* is associated with the evolution of relatively small seeds. Second, we sought evidence that the observed geographical variation in seed size reflects evolutionary adaptation in response to long-term abiotic conditions versus plastic responses to conditions in the year of collection. One may distinguish between these causes of population differentiation by comparing the effects of long-term mean climate conditions on population mean seed size to the effects of deviations between conditions in the year of collection and long-term means (i.e. short-term
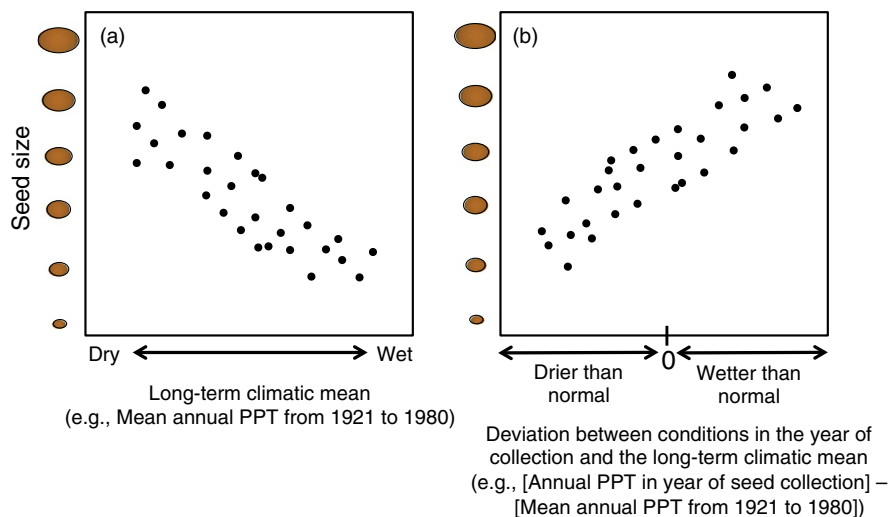

FIGURE 1 Conceptual diagram illustrating how the relationship among population means between seed size and local climate may depend on long-term climatic conditions, on the deviation between current and long-term conditions (i.e. climate anomalies) or on both. (a) represents the case where the optimum seed size declines under increasingly wet conditions and the response to selection results in a negative relationship among population means between seed size and mean, long-term annual precipitation (PPT). Under this scenario, in chronically dry sites, relatively large seeds evolve because they give rise to seedlings that can access soil moisture and withstand drought stress more readily than those derived from small seeds. In chronically wet sites, by contrast, small seeds evolve because germinants experience low drought stress, and small-seeded individuals may achieve higher fecundity (and higher individual fitness) than large-seed genotypes due to a size-number trade-off. (b) illustrates how conditions during a given growing season may affect the size of seeds produced in that year. In this example, populations experiencing unusually wet conditions relative to long-term means (where the *x*-axis >0) exhibit environmentally induced increases in plant size that result in the production of larger ovaries and seeds than populations experiencing unusually dry conditions (where the *x*-axis <0). By contrast, populations experiencing unusually dry conditions may be sufficiently drought-stressed to produce relatively small plants, ovaries and seeds. These plastic responses to precipitation anomalies generate the positive relationship shown here

'anomalies'; Figure 1). For example, if population mean seed size is more strongly correlated with long-term climate conditions than with short-term climate anomalies, then natural selection can be interpreted to be more influential than phenotypic plasticity in generating the association. Several recent studies have used this approach to infer the role of evolutionary adaptation versus phenotypic plasticity in generating variation among populations in phenology, reproductive output, seed size and/or floral traits (Bontrager & Angert, 2016; Diskin, Roctor, Jebb, Sparks, & Donnelly, 2012; Munson & Sher, 2015; Ramírez-Valiente, Valladares, Gil, & Aranda, 2009; Soper Gorden et al., 2016). Alternatively, the effect on seed size of long-term climatic conditions may differ qualitatively from the effect of the climate anomalies, indicating that the direction of the evolutionary response to high values of a particular variable contrasts with the direction of the plastic response (e.g. Figure 1).

We collected maternal families of seeds from 58 wild populations representing three pairs of sister taxa in the genus *Clarkia*, with each pair consisting of one predominantly outcrossing and one mixed mating or selfing taxon. We examined variation in seed size among these populations to address the following questions: (a) Is geographical variation in seed size associated with mating system, taxon pair, elevation, historical climate conditions or the climate experienced during the year of seed maturation and collection (relative to historical conditions)? If so, does each factor affect seed size independent of variation in the other factors? (b) Do historical or recent climate anomalies better explain variation among populations in seed size, allowing inferences concerning the efficacy of natural selection in moulding seed size variation in response to abiotic conditions?

2 | MATERIALS AND METHODS

2.1 | Study species

Clarkia is a genus of erect, annual, self-compatible, late spring-flowering herbs native to the western U.S. (Lewis, 1955). *Clarkia concinna* (Fisch. & C. A. Mey.) Greene and *C. xantiana* each contain subspecies of contrasting mating systems, including the predominantly outcrossing subspecies, *C. concinna* ssp. *concinna* and *C. xantiana* ssp. *xantiana*, and their facultatively autogamous counterparts, *C. concinna* ssp. *automixa* and *C. xantiana* ssp. *parviflora* (Allen, Gottlieb, & Ford, 1991; Bowman, 1987; Gottlieb, 1984; Moore & Lewis, 1965; Pettengill & Moeller, 2013; Runions & Geber, 2000). *Clarkia unguiculata* and *C. exilis* are predominantly outcrossing and selfing sister species, respectively, although there is considerable variation among populations of the latter with respect to outcrossing rates (Hove, Mazer, & Ivey, 2016; Ivey, Dudley, Hove, Emms, & Mazer, 2016; Vasek, 1958, 1964, 1965, 1967, 1976; Vasek & Harding, 1976). The predominantly outcrossing species are highly protandrous and herkogamous (Dudley et al., 2007). All of these taxa are diploid and occupy Mediterranean

climates characterized by cool, wet winters and hot and dry spring and summer months.

In two of these pairs of sister taxa (*C. unguiculata* vs. *C. exilis* and *C. xantiana* ssp. *xantiana* vs. ssp. *parviflora*), the predominantly outcrossing taxon is known to produce flowers with higher pollen:ovule ratios, higher pollen production, fewer ovules per flower, larger corollas and longer styles than its selfing counterpart (Delesalle & Mazer, 2009; Delesalle et al., 2008; Mazer et al., 2009; Vasek & Weng, 1988). Where populations of *C. unguiculata* and *C. exilis* or *C. xantiana* ssp. *xantiana* and ssp. *parviflora* occur sympatrically, the selfing taxon typically completes its flowering before its outcrossing sister taxon begins. Among the field populations of the six taxa studied here, Knies et al. (2004) found that the facultative selfing taxa produced smaller seeds than their outcrossing sister taxa. However, Knies et al. examined only one population of *C. concinna* ssp. *automixa* and did not investigate or control statistically for the effects of abiotic factors on seed size.

2.2 | Seed collection and the estimation of seed size per population

Seeds were collected from 58 wild populations distributed in the Coastal Ranges and in the southern Sierra Nevada (Figure 2; Figure A1 in Appendix 1; Table A1 in Appendix 2) between 1999 and 2014. Sampling efforts reflected the distribution and abundance of each taxon (*C. concinna* ssp. *automixa*: $n = 2$ populations; *C. concinna* ssp. *concinna*: $n = 4$ populations; *C. exilis*: $n = 11$ populations; *C. unguiculata*: $n = 27$ populations; *C. xantiana* ssp. *parviflora*: $n = 3$ populations; *C. xantiana* ssp. *xantiana*: $n = 11$ populations). Seeds from 8 to 119 maternal families per population (mean = 32.72, SD = 13.78 families per population) were collected when fruits were dry and dehiscing and placed in paper coin envelopes within zip-lock plastic bags with silica gel and stored at 6.4°C prior to weighing. From each family, *c.* 20 seeds were counted and weighed (to 0.01 mg) to estimate mean seed size per family. The maternal family means from each population were then used to estimate its mean seed size.

2.3 | Effects of population-specific climate means versus deviations from long-term means during the year of seed collection

ClimateNA v5.0 (Wang, Hamann, Spittlehouse, & Carroll, 2016) was used to estimate the historical and current climate conditions experienced by each sampled population. ClimateNA is an application that extracts and downscales the monthly climate data for a large number of climate variables estimated from 1901 to the present. Climate normals from 1961 to 1990 are based on a 4 × 4 km grid throughout the United States and downscaled to generate scale-free point locations for which climate parameters are estimated across multiple or individual months, years or other time periods,
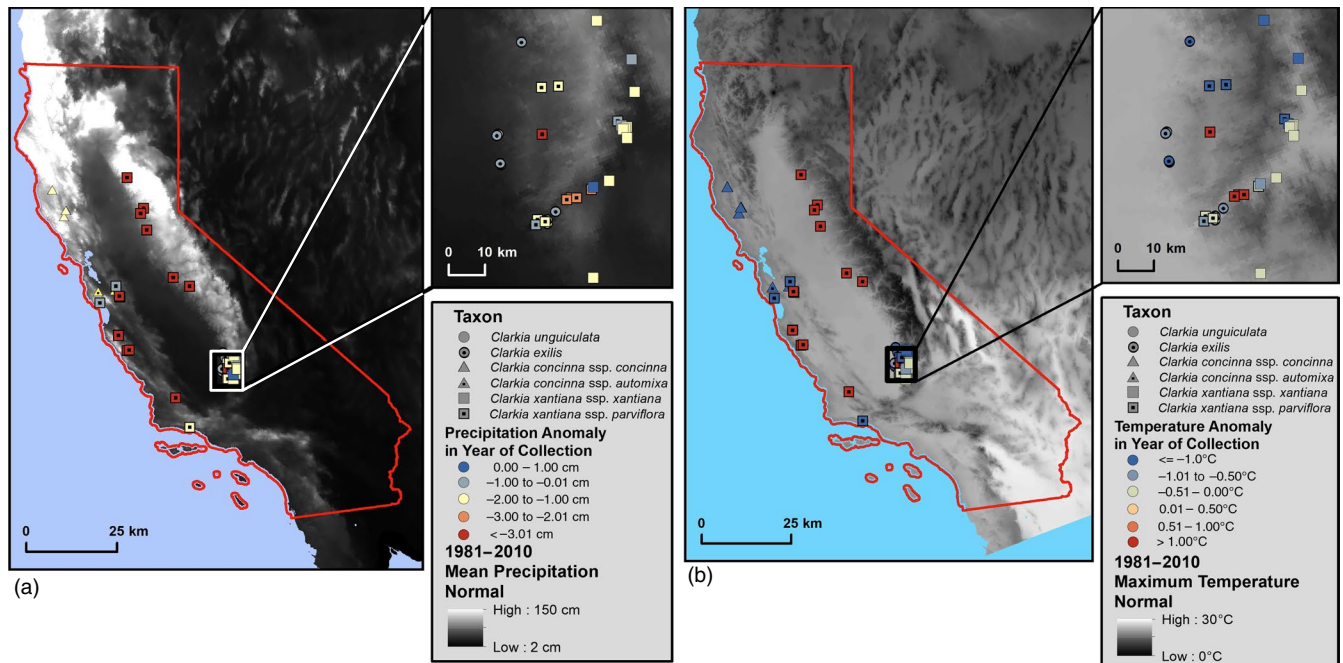
FIGURE 2 Locations of the 58 georeferenced populations included in this study, with long-term mean climatic conditions across the region represented by grey-scale shading, and the colour of each point representing the magnitude and direction of the climate anomaly for a given population in the year in which seeds were collected. (a) Grey-scale shading represents long-term mean annual fall-winter-spring precipitation, and the colour of each point indicates the value of the anomaly for precipitation for a given population in the year in which seeds were collected; (b) Grey-scale shading represents long-term mean monthly fall-winter-spring T_{max}, and the colour of each point indicates the value of the anomaly for T_{max} for a given population in the year in which seeds were collected. Population-specific symbols indicate whether the population is a member of a predominantly selfing taxon (symbols include black dots in their centre) or a predominantly outcrossing taxon (symbols include no internal dot)

as specified by the user. ClimateNA also uses these scale-free data as a baseline used to downscale historical climate variables for individual months, years or other time periods between 1901 and 2016.

To detect the effects of historical climate conditions on seed size, we used the climate norms for mean monthly maximum temperature (T_{max}), cumulative moisture deficit (CMD) and cumulative precipitation (PPT, which includes rain and snow [the latter when melted]) during fall, winter and spring. For each of these climate parameters, we calculated mean conditions during two climate periods, one for 1921–1980 (1980, the point after which recent climate change has accelerated: National Oceanic & Atmospheric Administration, 2017) and another for 1981–2000 (representing climate conditions in the recent past, which incorporates more recent climate change), in order to determine whether both sets of historical climate conditions have similar effects on seed size. For each population, we calculated the values for mean monthly T_{max}, CMD, and cumulative PPT during the growing season (the prior fall, followed by winter and spring) of the year of seed collection. To test for differences between the effects of relatively long-term climate conditions on seed size of populations and the effects of conditions during the year of collection, we calculated the deviation, for each set of mean climate conditions (1921–1980 and 1981–2000) between the historical mean conditions and the conditions during the growing season of the year of collection for each population. For each climate parameter, the

historical means were subtracted from the mean value in the year of collection; positive values for the deviation (i.e. the anomaly) indicate that conditions during the year of collection were represented by higher CMD, T_{max} or PPT than the historical means.

2.3.1 | Correlations among climate parameters

To determine whether the five sets of climate parameters (climate means for 1921–1980 and for 1981–2000; climate conditions during the year-of-collection; and the deviations between the two) varied independently among sites, Pearson correlation coefficients were calculated between each pair of parameters (Table A2 in Appendix 3). CMD, T_{max} and cumulative PPT during the year of collection were strongly positively correlated with both sets of historical climate means (Table A2 in Appendix 3; $r > .75$ in all cases, $p < .0001$) for all pairs of variables (Figures A2–A4 in Appendix 1). Due to these strong correlations, any statistical effects of climate conditions during the year of collection on seed size cannot be interpreted to be caused by these recent conditions alone. Consequently, to isolate the effects of recent climate conditions on seed size from the effects of historical climate means, we used the deviations between the climate means and the conditions during the year of seed collection.

For CMD and T_{max}, the deviations varied independently of the long-term climate means (Figures A2 and A3 in Appendix 1; Table A2 in Appendix 3). For cumulative PPT, however, the deviations were moderately negatively correlated with both sets of climate means ($r = -.33$ for the correlation between the 1921–1980 means and the deviations, $p < .0017$; $r = -.49$ for the correlation between the 1980–2000 means and the deviations). That is, among the populations sampled here, locations that were historically relatively wet were unusually dry in the year of collection (Figure A4 in Appendix 1).

2.4 | Statistical analyses

2.4.1 | Variation in seed size among populations versus within populations

To assess the magnitude of variation in mean seed mass among versus within populations, we compared the estimates of variation among population means to the mean values (across populations) of their corresponding estimates among individuals within populations. These parameters included the variance, the standard deviation, the CV, and the range of mean individual seed mass among versus within populations. We compared these metrics calculated using the 58 population means to the mean values (among the 58 populations) of within-population metrics. We also conducted a series of GLMs to detect the proportion of variance in mean seed mass among individuals explained by population alone, by taxon alone, and by both taxon and population (nested within taxon).

2.4.2 | Seed size of selfing versus outcrossing taxa within each pair of sister taxa

Using the population means for seed size, we conducted one-way analyses of variance within each pair of sister taxa to determine whether the raw values of seed size differ between selfing and outcrossing taxa. All analyses were conducted using JMP®, Version 13. SAS Institute Inc., 1989–2019.

2.4.3 | Model testing and selection

Among sampled populations of *Clarkia* taxa, we conducted standard least squares regressions (GLMs) to detect the independent effects of mating system (selfing vs. outcrossing), taxon pair (*exilis/unguiculata*, *xantiana/parviflora* and *concinna/automixa*), elevation, historical climate norms and population-specific deviations from climate norms on seed size. Least squared means were used to compare taxon pairs and mating systems with respect to seed size. Two-way interactions between the main effects were included when they were statistically significant; otherwise, they were excluded from the analyses presented here.

Four sets of linear models were constructed and tested to identify those that best explain the variation among populations in seed size and to test specific hypotheses concerning the effects of historical

versus recent conditions on seed size (see Table A3 in Appendix 4 for the full list of 24 models). Each set of models included taxon pair and mating system as independent variables and most models included elevation as an independent variable. Each set, however, included a different combination of climate variables. The first set included one or more of the following variables estimated across all fall, winter and spring months: 1921–1980 means for CMD, mean T_{max} and Log10(Cumulative PPT). The second set included one or more of the following: 1981–2000 fall-winter-spring means for CMD, T_{max} and Log10(Cumulative PPT). The third set included one or more of the following: the deviation between the 1921–1980 fall-winter-spring means and the conditions from the fall prior to the year of collection through the spring of the year of collection for CMD, T_{max} and Cumulative PPT. The fourth set included one or more of the following: the deviation between the 1981–2000 fall-winter-spring means and the annual mean conditions from the fall prior to the year of collection through the spring of the year of collection for CMD, T_{max} and Cumulative PPT. AIC values were examined to identify the optimal model for each set of variables tested. The models constructed to test the particular hypotheses of interest or with the lowest AIC values are presented in the main text; all models are summarized in Table A3 (Appendix 4). Type III sums of squares were used for significance testing for all main effects; this approach reports the significance of each independent factor when placed last into the model.

3 | RESULTS

3.1 | Variation in seed size among populations versus within populations

All measures of variation among populations exceed the mean values of these parameters among individuals within populations (Table A4a in Appendix 5). In addition, a one-way ANOVA of mean individual seed mass among all individuals ($n = 1892$) sampled to obtain population means shows that population explains over half (57%) of the total variance in mean individual seed mass (Table A4b in Appendix 5). Moreover, a one-way ANOVA testing for the effect of taxon (species or subspecies) on mean individual seed mass indicates that differences among the six taxa explain only 24% of the variance in mean individual seed mass (Table A4c in Appendix 5). Finally, a two-way fixed effect ANOVA that includes taxon and population (nested within taxon) as independent variables shows that population explains a highly significant ($p < .0001$) proportion of the variance in mean individual seed mass within taxa (Table A4d in Appendix 5). This model also demonstrates that including population (nested within taxon) in the model more than doubles the adjusted model R^2, from 24% (Table A4c) to 57% (Table A4d).

3.2 | Seed size of selfing versus outcrossing taxa

Within each pair of sister taxa, the raw value of mean seed size among the populations of the predominantly selfing taxon is lower than that

of its outcrossing counterpart, but this difference is only statistically significant between the selfing *C. xantiana* ssp. *parviflora* and the outcrossing *C. xantiana* ssp. *xantiana* (Figure 3; one-way ANOVA: $F_{1,12} = 42.65$, $p < .0001$; adjusted $R^2 = .76$; $n = 14$ populations).

3.3 | Effects of taxon pair, elevation and long-term climate means on seed size

A total of 24 models were tested to estimate the independent effects of mating system, taxon pair, elevation and either 1921–1980 or 1981–2000 climate means on seed size (Table A3 in Appendix 4); several of these models also included the climate conditions in the year of collection (relative to climate means), the effects of which are discussed below (Models 10, 12, 13, 14, 15, 16, 22 and 26). The models presented in detail in Tables 1 and 2 have the highest R^2 and the lowest AIC values of these models.

In 19 of the 24 models that included long-term climate means as independent variables, there were significant differences among the three taxon pairs, with *C. concinna* ssp. *concinna* and ssp. *automixa* producing significantly larger seeds than either of the other two taxon pairs. In all 24 models, outcrossing taxa produced significantly larger seeds than selfing taxa. In the models
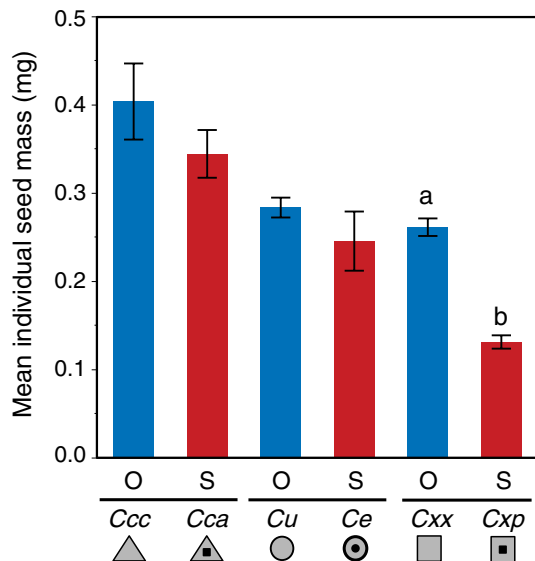

FIGURE 3 Least square means (±*SE*) of population means for mean individual seed mass, estimated from a GLM that included (as independent variables) taxon pair, species (nested within taxon pair), elevation, mean T_{max} (1981–2001) and mean precipitation during the growing season (fall, winter and spring, 1981–2000). Cca: *Clarkia concinna* ssp. *automixa*; Ccc: *Clarkia concinna* ssp. *concinna*; Ce: *C. exilis*; Cu: *C. unguiculata*; Cxp: *C. xantiana* ssp. *xantiana*; Cxx: *C. xantiana* ssp. *xantiana*. Only within *C. xantiana* do the sister taxa differ significantly with respect to population mean seed mass. O = predominantly outcrossing; S = predominantly selfing. Within taxon pairs (Cxx vs. Cxp), significant differences between sister taxa in mean individual seed mass are indicated by distinct letters (a vs. b; $F_{1,12} = 42.65$, $p < .0001$). Symbols below abbreviated taxon names correspond to population locations in Figure 2

of best fit (Tables 1, 2), elevation had a significant negative effect on seed size, controlling for all other variables (Figure 4a). In four other models (Models 9, 10, 11 and 12), elevation also had a significant negative effect on seed size; in all other models, the effect of elevation was non-significant regardless of the other independent variables included.

Populations at sites characterized by relatively warm fall-winter-spring temperatures and by high precipitation produced seeds of relatively low seed size. The 1981–2000 means for T_{max} and for cumulative PPT in fall, winter and spring had significant negative effects on seed size independent of all other factors (Table 1a; Figure 4b,c). The same patterns are observed for the 1921–1980 climate means (Table 1b; Figure A6 in Appendix 1). All models that detected significant effects on seed size of either set of means for T_{max} exhibited negative relationships between T_{max} and seed size (Models 3, 4, 9, 10, 11 and 12; Table A3 in Appendix 4). Similarly, all models that detected

TABLE 1 Summary of GLMs designed to detect the independent effects of taxon pair, mating system, elevation, historical mean monthly T_{max} and cumulative precipitation for fall, winter and spring on mean individual seed mass. Precipitation was log10-transformed to improve normality. Interactions were non-significant and were excluded from the model

Source	df	Sum of squares	F ratio	p value
(a) Effects of historical conditions using 1981–2000 climate norms				
Taxon pair	2	0.0377	4.73	**.0130**
Mating system	1	0.0540	13.56	**.0006**
Elevation	1	0.0218	5.49	**.0231**
Mean T_{max} FWS (1981–2000)	1	0.0372	9.34	**.0036**
Mean PPT FWS (1981–2000)	1	0.0556	13.97	**.0005**
Model	6	0.1962	8.22	**<.0001**
Error	51	0.2029		
Corrected total	57	0.3991		
Adjusted $R^2 = .43$				
AIC = −144.475				
(b) Effects of historical conditions using 1921–1980 climate norms				
Taxon pair	2	0.0431	5.36	**.0077**
Mating system	1	0.0543	13.51	**.0006**
Elevation	1	0.0206	5.12	**.0279**
Mean T_{max} FWS (1921–1981)	1	0.0352	8.77	**.0046**
Mean PPT FWS (1921–1981)	1	0.0544	13.55	**.0006**
Model	6	0.1942	8.06	**<.0001**
Error	51	0.2049		
Corrected total	57	0.3991		
Adjusted $R^2 = .43$				
AIC = −143.921				

p-values < .05 appear in boldface.

Term	Estimate	SE	t-ratio	Prob > t
(a) Parameter estimates based on model shown in Table 1a				
Mating system (outcrossing)	0.0415	0.0113	3.68	**0.0006**
Elevation	−0.0002	6.75×10^{-5}	−2.34	**0.0231**
Mean T_{max} FWS (1981–2000)	−0.0385	0.0126	−3.06	**0.0036**
Mean PPT FWS (1981–2000)	−0.1153	0.0309	−3.74	**0.0005**
Mean individual seed mass least squares means (LSM) and raw means				

Taxon pair	LSM (mg)	SE	Raw mean (mg)	
C. concinna ssp. concinna/automixa	0.3669[a]	0.0360	0.3837	
C. exilis/unguiculata	0.2553[b]	0.0115	0.2723	
C. xantiana ssp. parviflora/xantiana	0.2096[b]	0.0253	0.2332	
Mating system				
Outcrossing	0.3187[a]	0.0140	0.2889	
Selfing	0.2358[b]	0.0185	0.2362	

Independent variable	Estimate	SE	t-ratio	Prob > t
(b) Parameter estimates based on model shown in Table 1b				
Mating system (outcrossing)	0.0416	0.0113	3.68	**0.0006**
Elevation	−0.0002	6.75×10^{-5}	−2.26	**0.0279**
Mean T_{max} FWS (1981–2000)	−0.0375	0.0127	−2.96	**0.0046**
Mean PPT FWS (1981–2000)	−0.2636	0.0716	−3.68	**0.0006**
Mean individual seed mass least squares means (LSM) and raw means				

Taxon pair	LSM (mg)	SE	Raw mean (mg)	
C. concinna ssp. concinna/automixa	0.3717[a]	0.0354	0.3837	
C. exilis/unguiculata	0.2557[b]	0.0115	0.2723	
C. xantiana ssp. parviflora/xantiana	0.2061[b]	0.0252	0.2332	
Mating system				
Outcrossing	0.3194[a]	0.0140	0.2889	
Selfing	0.2363[b]	0.0186	0.2362	

TABLE 2 Parameter estimates: Means and regression coefficients for the models that tested for the independent effects of mating system, elevation and long-term climate conditions on mean individual seed mass (see Tables 1a and 1b). Precipitation was log10-transformed to improve normality. Interactions were non-significant and were excluded from the model

For main effects, p-values < .05 appear in boldface. Least square means (LSM) of individual seed mass that differ significantly between taxon pairs (p = .0130) or between mating systems (p = .0231) are indicated by distinct superscripts (a vs. b).

significant effects of either set of long-term climate means for PPT exhibited negative relationships between PPT and seed size (Models 3–6, 10, 12–16, 22 and 26: Table A3 in Appendix 4; Figure 4c; Figure A6 in Appendix 1).

The effect of CMD on seed size depended on which other variables were included in the model. When CMD was included instead of T_{max} (Models 5 and 6; Table A3 in Appendix 4), CMD had a significant negative effect on seed size (as expected, given that CMD and T_{max} are strongly positively correlated; r > .77; Table A2 in Appendix 3). In these models, however, elevation did not have a significant effect on seed size. When CMD, T_{max} and PPT were all included (Models 7 and 8; Table A3 in Appendix 4), neither CMD nor T_{max} had a significant effect on seed size (an expected consequence of the positive correlation between them). The negative effect of cumulative PPT on seed size was detected in most of the models that also included CMD (Models 5, 6, 13, 16, 22 and 26; Table A3 in Appendix 4),

even though CMD and cumulative PPT are strongly negatively correlated among sites (r < −.92; Table A2 in Appendix 3).

3.4 | Effect on seed size of climate anomalies

A total of 24 GLMs were run to estimate the independent effects on seed size of mating system, taxon pair, elevation and climate anomalies (the deviation between climate conditions in the year of seed collection and either the 1921–1980 or 1981–2000 climate means; Table A3 in Appendix 4). In 21 of the 24 models that included climate means as independent variables, the three taxon pairs differed significantly in mean seed size. In all 24 models, outcrossing taxa produced larger seeds than selfing taxa. Among the models that included the anomalies (but not the long-term climate means) as independent variables, a significant effect of elevation was never detected.
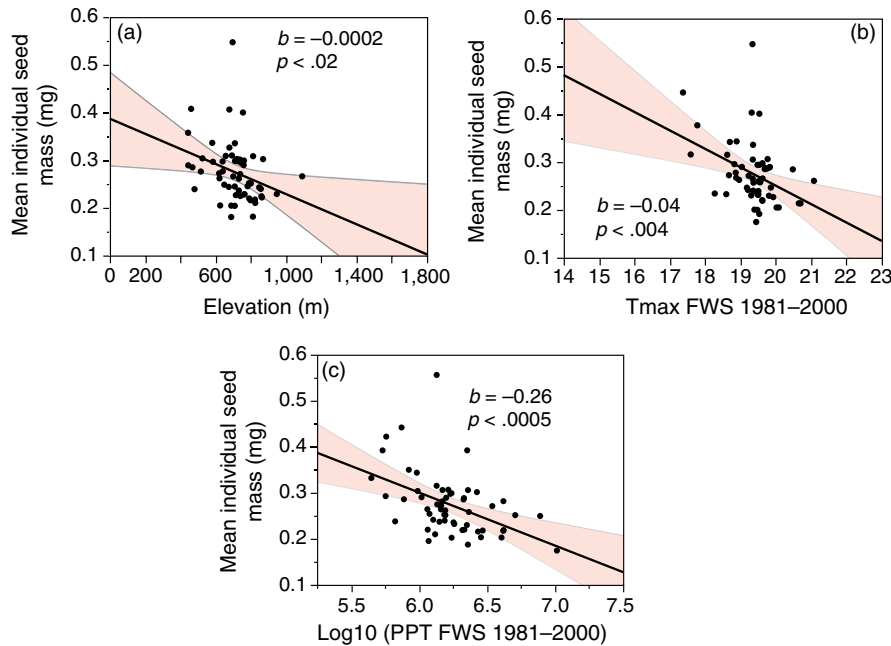
FIGURE 4 Bivariate plots derived from the GLM designed to detect the effects on population mean seed mass of taxon pair, mating system, elevation, and mean T_{max} and cumulative precipitation (PPT) for fall, winter and spring (FWS) from 1981 to 2000. (a) Mean individual seed mass vs. elevation, among sampled populations; (b) Mean individual seed mass vs. long-term mean Tmax (°C), among sampled populations; (c) Mean individual seed mass vs. the Log_{10} (Long-term cumulative annual precipitation), among sampled populations. Each panel illustrates the relationship between the y- and x-variables independent of the other variables in the model. The slope of each line represents the regression coefficient estimated for the independent variable by the GLM (see Table 2 for all parameter estimates). The pink shading represents the 95% confidence interval of the slope

The model presented in detail in Table 3 (Model 18 in Appendix 4) is the only one to detect a significant effect of any of the climate anomalies on seed size. Sites that experienced higher-than-average PPT during the growing season of the year of seed collection produced larger seeds than populations at sites that were drier than average (based on 1981–2000 climate means) during the year of seed collection (Figure 5). This positive effect of the precipitation anomaly on seed size contrasts with the negative effect on seed size of mean PPT from 1981 to 2000 or from 1961 to 1980 (Figure 4c and Figure A6 in Appendix 1 respectively).

For a given climate parameter (CMD, T_{max} and PPT), when both long-term climate means and the anomalies during the year of collection were included in a given model, only the long-term mean climate conditions had significant effects on seed size (Models 10, 12, 13, 14, 15, 16, 22 and 26; Table A3 in Appendix 4). That is, independent of variation in the climate anomalies, the long-term mean conditions had significant effects on seed size; by contrast, independent of variation in the long-term climate means, the anomalies did not explain significant variation in seed size.

long-term mean monthly T_{max}, precipitation during the growing season and CMD are each associated with variation in seed size among *Clarkia* taxa and populations. The direction of the effect of precipitation on population mean seed size, however, differed between the response to long-term precipitation and the response to the precipitation anomaly in the year of seed collection. Increases in long-term precipitation are associated with reductions in population mean seed size (Figure 4c), while increases in the precipitation anomaly in the year of seed collection are associated with increases in population mean seed size (Figure 5).

The effects of the deviation between long-term and contemporary climate conditions on reproductive traits have been evaluated in several previous studies designed to detect evidence of adaptation and/or of environmental effects on plant phenotype (Bontrager & Angert, 2016; Diskin et al., 2012; Munson & Sher, 2015). Similarly, two studies have compared the effects of long-term versus contemporary climate conditions on seed size to distinguish between adaptation and maternal environmental effects (Ramírez-Valiente et al., 2009; Soper Gorden et al., 2016), although these studies did not take into account the correlation between historical versus current climate conditions.

4 | DISCUSSION

By simultaneously examining the effects of both intrinsic (mating system) and extrinsic (long-term climate, climate anomalies and elevation) factors on seed size (estimated as a population's mean individual seed mass), we found that mating system, elevation and

4.1 | Effects of mating system on seed size: Seed size of selfing versus outcrossing taxa

Previous reports that self-fertilizing taxa produce smaller seeds than their outcrossing counterparts (De Jong et al., 2005; Knies

Source	df	Sum of squares	F ratio	p value
Taxon pair	2	0.0751	8.02	**.0009**
Mating system	1	0.0569	12.13	**.0010**
Elevation	1	1.6×10^{-5}	3.5×10^{-3}	.9530
Deviation between precipitation in the year-of-collection and 1981–2000	1	0.0193	4.12	**.0474**
Model	5	0.1554	6.64	**<.0001**
Error	52	0.2436		
Corrected total	57	0.3991		
Adjusted R^2 = .33				
AIC = −136.57				

Independent variable	Estimate	SE	t-ratio	Prob > t
Mating system (outcrossing)	0.0411	0.0118	3.48	**.0010**
Elevation	2.40×10^{-6}	4.05×10^{-5}	0.06	.9530
Deviation (precipitation)	0.0001	6.82×10^{-5}	**2.03**	**.0474**

Mean individual seed mass least squares means (LSM) and raw means			
Taxon pair	LSM (mg)	SE	Raw mean (mg)
C. concinna ssp. concinna/automixa	0.3549[a]	0.0317	0.3837
C. exilis/unguiculata	0.2616[b]	0.0124	0.2723
C. xantiana ssp. parviflora/xantiana	0.1982[b]	0.0230	0.2332
Mating system			
Outcrossing	0.3127[a]	0.0130	0.2889
Selfing	0.2305[b]	0.0223	0.2362

For main effects, p-values < .05 appear in boldface. Least square means (LSM) of individual seed mass that differ significantly between taxon pairs (p = .0009) or between mating systems (p = .0010) are indicated by distinct superscripts (a vs. b).

et al., 2004; Mitchell-Olds, 2001; Sharma, Koul, & Kaul, 1999) may be interpreted to indicate that relatively small seeds are a feature of the 'selfing syndrome' (Duncan & Rausher, 2013; Ornduff, 1969; Sicard & Lenhard, 2011). However, these reports of divergence in seed size with mating system did not account for potentially confounding extrinsic factors (such as climate) that could independently influence the evolution of seed size. Here, we have documented for the first time a consistent difference between predominantly selfing versus outcrossing taxa independent of multiple, population-specific environmental factors.

Within each pair of *Clarkia* sister taxa examined here, the mean seed size of the populations of the predominantly selfing taxon is smaller than that of its outcrossing counterpart, although this difference is statistically significant only between the selfing *C. xantiana* ssp. *parviflora* and the outcrossing *C. xantiana* ssp. *xantiana* (Figure 3). The generality of the relationship, however, is supported by the observation that outcrossing taxa produced larger seeds than their selfing counterparts in all 24 of the models examined here that estimated the independent effects of mating system,

taxon pair, elevation and either the 1921–1980 or the 1981–2000 climate means on seed size. In *Clarkia*, the production of relatively small seeds appears to be a component of the selfing syndrome.

4.2 | Alternative explanations for the co-evolution of seed size and mating system

The association between the evolution of self-fertilization and a reduction in seed size is consistent with the hypothesis that both traits promote successful colonization and may therefore be expected to evolve together. However, chronic self-fertilization may promote an evolutionary reduction in seed size through two additional, non-mutually exclusive, mechanisms as well.

First, mating system influences the intensity of genetic conflict among co-developing seeds (Haig & Westoby, 1991). In outcrossing populations, maternal and paternal genotypes conflict with respect to the optimum allocation of resources distributed among developing offspring (Raunsgard et al., 2018; Willi, 2013). Where seed size

$b = -0.0001$
$p < .05$

Mean individual seed mass (mg)

Precipitation anomaly (mm)
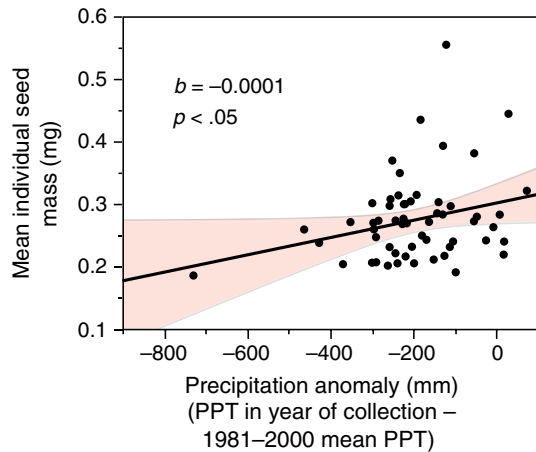(PPT in year of collection –
1981–2000 mean PPT)

FIGURE 5 Relationship between mean individual seed mass and the anomalies for precipitation (i.e. the deviation between cumulative precipitation during the growing season of the year of seed collection and the long-term mean from 1981 to 2000). This bivariate plot is derived from the GLM summarized in Table 3, illustrating the relationship between the *y*- and *x*-variables independent of the other variables in the model (taxon pair, mating system, elevation and the fall-winter-spring T_{max} anomalies (relative to the mean for 1981–2000). The slope of the line represents the regression coefficient for the precipitation anomaly estimated by the model (see Table 3 for parameter estimates)

positively affects seedling survival, for example, a paternal parent (i.e. a pollen donor) that sires seeds that acquire a disproportionate share of maternal resources will be favoured by selection among donors, even if this allocation reduces the fecundity of the maternal plant. By contrast, in self-fertilizing populations, maternal and paternal contributions to seeds are equal, so the optimum seed size does not differ between them. During an evolutionary shift from outcrossing to selfing, as the selfing rate increases, so does the relatedness among developing seeds within a maternal plant, reducing parental conflict and weakening selection favouring paternally inherited genes that produce larger seeds. This relaxation of selection should result in an evolutionary reduction in seed size (De Jong et al., 2005), particularly where the production of smaller seeds results in higher fecundity. Second, as selfing rates increase, the occurrence of genomic imprinting is also reduced, which also leads to decreased investment per offspring (De Jong et al., 2005; Raunsgard et al., 2018).

4.3 | Effects of extrinsic factors on seed size: evolutionary adaptation versus phenotypic plasticity

Interpreting geographical variation in seed size and climate to infer the processes that generate such variation begins with an understanding of the environmental conditions that may favour relatively large (or small) seeds. Seed size can affect many fitness-related characteristics of seeds and seedlings (Foster, 1986; Moles & Westoby, 2004; Vaughton & Ramsey, 1998), and, within species, large seeds often improve these attributes, particularly when water or nutrients are

limiting (Stock, Pate, & Delfs, 1990; Tungate, Burton, Susko, Sermons, & Rufty, 2006) and when seedling density is high (Susko & Cavers, 2008). Despite these advantages to large seeds, geographical variation in seed size remains common within and among wild species. This persistent variation may be the result of conflicting selective pressures, as large seeds may not be beneficial in all conditions.

In this study, we evaluated the independent effects of several features of local climate (cumulative PPT, T_{max} and CMD) on population mean seed size. We examined variation in both long-term climate conditions and climate anomalies among sampled sites to determine whether differences in seed size among populations in *Clarkia* are better explained by the process of evolutionary adaptation to long-term conditions or by phenotypic plasticity. Climate anomalies have been used in several recent studies to determine whether the timing of flowering or other phenological events are affected by unusual conditions in the year of observation (Diskin et al., 2012; Munson & Sher, 2015). This approach has also been used to examine and to compare the effects of long-term climate means, of contemporary climate conditions and/or of climate anomalies on floral traits, reproductive output and seed size (Bontrager & Angert, 2016; Ramírez-Valiente et al., 2009; Soper Gorden et al., 2016). For example, in a study of herbarium specimens of *Clarkia pulchella*, Bontrager and Angert (2016) examined the effects of 30-year climate means, site-and-year-specific climate conditions and site-and-year-specific anomalies on petal length, herkogamy and reproductive output. Plants collected at sites with higher-than-average precipitation had higher reproductive output than those collected at drier-than-average sites. Bontrager and Angert (2016) concluded that reproductive output is highly plastic and responds positively to recent water availability in this annual herb. Bontrager and Angert (2016) also detected negative effects on herkogamy of 30-year spring and summer temperatures (warmer climates are associated with a higher potential for self-fertilization), but no effect of spring or summer temperature anomalies on this floral trait. Accordingly, the authors interpreted these results to mean that the degree of herkogamy represents an adaptation to long-term climate conditions but does not show evidence of phenotypic plasticity.

Among all of the models tested here, the strength of the effects of long-term climate conditions on seed size consistently exceeded the effects of short-term climate anomalies (Table A3 in Appendix 4). Long-term climatic conditions are a reliable predictor of seed size in *Clarkia*, consistent with the interpretation that the seed size of the sampled populations evolved as an adaptation to long-term climate regimes. *Clarkia* populations that experienced relatively high T_{max} and PPT in fall, winter and spring from 1981 to 2000 (Table 1a; Figure 4b,c) and from 1921 to 1980 (Table 1b; Figure A6 in Appendix 1) produce significantly smaller seeds than cool and dry sites, independent of the other factors tested in our models.

Geographical variation in seed size in association with precipitation and temperature has been found in many species, but the direction of the relationship differs among taxa. Precipitation has been shown to have both positive (Gallagher & Leishman, 2012) and negative (Tautenhahn et al., 2008) effects on seed size within species.

Soper-Gorden et al. (2016) examined the relationships between seed size and both long-term (30-year normals) and current temperature and precipitation within and between several herbaceous and grass species distributed across the central and eastern United States. Both long-term temperature and current temperature had a positive effect on seed mass across all species, but the relationships between seed mass and precipitation differed among taxa. However, Soper-Gorden et al. (2016) analysed the independent effects on seed size due to conditions in May–July rather than in fall, winter spring (as examined here). Temperature and precipitation may influence seed mass differently during different stages of plant growth and development, and these effects may be highly taxon-specific.

In the current study, in the case of PPT during the growing season, seed size is negatively correlated with long-term mean precipitation during both 20-year periods (1961–1980 and 1981–2000; Figures A4 and A6 in Appendix 1; Table A3, Models 3 and 4, in Appendix 4), but positively correlated with precipitation anomalies in the growing season of the year of collection (Figure 5; Table A3, Model 18, Appendix 4). This contrast supports two interpretations. First, populations adapted to chronically mesic conditions evolve to produce smaller seeds than those adapted to more xeric conditions. One hypothesis for the negative relationship between seed size and long-term precipitation means observed in *Clarkia* is that in historically mesic locations, seeds may not require as much maternal provisioning (relative to xeric sites) to produce seedlings whose roots can grow quickly enough to reach sufficient soil moisture to support them throughout their juvenile and adult stages. Under these conditions, genotypes with relatively small seeds (but higher fertility due to a size-number trade-off) should exhibit a selective advantage relative to those of relatively high seed size (but lower fertility). By contrast, where the environment during and after germination has been historically xeric, selection favouring high seed size is expected to be relatively strong due to the competitive advantage it confers to seedlings (Cochrane et al., 2016; Stock et al., 1990).

Second, populations that experience wetter-than-average conditions in the year of seed production produce larger seeds than those experiencing drier-than-average conditions. The production of relatively large seeds in wetter-than-average years may be the result of a plastic response to greater soil moisture, resulting in faster growth, the achievement of greater plant size and the production of larger ovaries and seeds (Figure 1). In sum, both local adaptation and short-term responses to precipitation may contribute to variation among populations in seed size.

4.4 | Effects of elevation on seed size

Elevation gradients are commonly used to examine variation and adaptation in wild plant species (Baker, 1972; Blionis & Vokou, 2002; Guo et al., 2010a, 2010b, 2011), as elevation may serve as a proxy for climate variables such as annual precipitation, temperature, length of the frost-free period and growing season length. To our knowledge, this study is the first to identify significant effects of elevation

on seed size independent of both long-term and contemporary precipitation and temperature. Seed size has been predicted either to increase among populations at higher elevations due to the advantage of large seeds during seedling establishment in stressful environments (the 'stress tolerance' hypothesis) or to decline at higher elevations due a reduction in photosynthetic rates and maternal provisioning caused by low temperatures and a shorter growing season (the 'energy constraints' hypothesis; Qi et al., 2014). Some studies have detected an increase in seed size with elevation (Boulli, Baaziz, & M'Hirit, 2001; Pleuss et al., 2005) while others have detected a negative relationship between seed size and elevation (Baker, 1972; Bu et al., 2007; Guo et al., 2010a).

In the current study, seed size declines with increasing elevation (Figure 4a), which supports the 'energy constraints' hypothesis (Qi et al., 2014). In addition, among the sites sampled in this study, the partial pressure of oxygen ranges from 20.8 kPa (at 137 m elev.) to 17.4 kPa (at 1,618 m elev.). Experimental studies of several species have found that embryo growth and seed production decline, while seed abortion rates increase, with declining partial pressure of oxygen (Akita & Tanaka, 1973; Borisjuk & Rolletschek, 2009; Kuang, Crispi, & Musgrave, 1998). Consequently, the production of smaller seeds, which have higher surface:volume ratios than large ones and may therefore allow more rapid oxygen diffusion during development, may represent an adaptation to low atmospheric pressure. An alternative hypothesis is that higher elevations are associated with higher incident sunlight and lower vegetation cover, both of which would reduce competition for light and soil resources, thereby favouring small-seeded genotypes (which may have higher fecundity than large-seeded ones).

4.5 | Independent effects of taxon pair on seed size

Taxonomic membership often predicts seed size (Qi et al., 2014), and among the *Clarkia* sister pairs studied here, taxon pair explained a significant proportion of variation in seed size in all but two of the 24 linear models used to examine the relationship between mating system, climate, elevation and seed mass (Table A3 in Appendix 4). While these results are consistent with a phylogenetic component to seed size in *Clarkia*, a multi-generation common garden study that eliminates environmentally induced maternal effects on seed size would be required to establish unambiguously whether the population differentiation in seed size observed here represents genetic differentiation rather than phenotypic plasticity (Etterson & Shaw, 2001).

5 | CONCLUSIONS

Drought conditions and arid environments are commonly considered to favour large-seeded genotypes and taxa (Baker, 1972; Mazer, 1990; Salisbury, 1975; Wulff, 1986), and this hypothesis is supported by the geographical patterns observed in *Clarkia*. Climate change predictions

for North America include an overall increase in temperature and less predictable precipitation (IPCC, 2014). In California, droughts are predicted to become more frequent, longer and more severe (Loarie et al., 2008). Based on the geographical relationships between seed size and climate reported here, taxa with relatively small seeds may be less likely to persist through long-term reductions in precipitation. In contrast, if climate change also results in a reduction in wild pollinator abundances, then self-fertilizing populations and taxa will have a strong ecological advantage over pollinator-dependent taxa. If these self-fertilizing, pollinator-independent taxa are also small-seeded, however, then their ability to adapt to increasingly competitive abiotic conditions may be compromised.

This study and others have shown that the strength and direction of the relationships between seed size and temperature, precipitation or mating system can be used to inform predictions of future evolutionary change in seed size. Moreover, alterations in temperature and precipitation in California may influence not only the evolution of seed size, but also the evolution of subsequently expressed and interrelated traits such as germination (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011), seed dormancy, phenology, dispersal, survival and reproduction. Early developmental stages of plants (seeds) are expected to be more sensitive to climate change than adult stages, and as such may represent a major bottleneck to population and species' persistence (Dalgleish, Koons, & Adler, 2010; Fay & Schultz, 2009; Lloret, Peñuelas, & Ogaya, 2004). Understanding the effects of climate change on the stability and evolution of wild plant populations requires an integrated assessment of both intrinsic and extrinsic sources of variation in seed size and related traits, which directly and indirectly influence survival and reproduction.

AUTHORS' CONTRIBUTIONS

S.J.M. conceived the ideas, and S.J.M. and I.M.P. designed the methodology; S.J.M., M.K., E.M.M., A.M.Y. and K.P. collected or weighed the seeds; I.M.P. extracted and assembled the climate data and produced Figure 2; S.J.M. conducted analyses and created all other figures and tables; S.J.M. and K.P. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.25349/D93888 (Mazer et al., 2019). Raw data for population mean seed mass, geographical variables and climate parameters are also provided in Appendix 2.

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REFERENCES

Agrawal, A. A. (2001). Transgenerational consequences of plant responses to herbivory: An adaptive maternal effect? *The American Naturalist*, *157*, 555–569. https://doi.org/10.1086/319932

Akita, S., & Tanaka, I. (1973). Studies on the mechanism of differences in photosynthesis among species III. Influence of low oxygen concentration on dry matter production and grain fertility of rice. *Proceedings of the Crop Science Society of Japan*, *42*, 18–23. https://doi.org/10.1626/jcs.42.18

Allen, G. A., Gottlieb, L. D., & Ford, V. S. (1991). Electrophoretic evidence for the independent origins of two self-pollinating subspecies of *Clarkia concinna* (Onagraceae). *Canadian Journal of Botany*, *69*, 2299–2301.

Andersson, S. (1996). Seed size as a determinant of germination rate in *Crepis tectorum* (Astseraceae): Evidence from a seed burial experiment. *Canadian Journal of Botany*, *74*, 568–572.

Arellano, G., & Peco, B. (2012). Testing the role of seed size in annual legume seedling performance under experimental autumn moisture conditions. *Journal of Vegetation Science*, *23*, 690–697. https://doi.org/10.1111/j.1654-1103.2012.01394.x

Armstrong, D. P., & Westoby, M. (1993). Seedlings from large seeds tolerate defoliation better: A test using phylogenetically independent contrasts. *Ecology*, *74*, 1092–1100. https://doi.org/10.2307/1940479

Azcarte, F. M., Manzano, P., & Peco, B. (2010). Testing seed-size predictions in Mediterranean annual grasslands. *Seed Science Research*, *20*, 179–188. https://doi.org/10.1017/S0960258510000176

Baker, H. G. (1955). Self-compatibility and establishment after 'long distance' dispersal. *Evolution*, *9*, 347–348. https://doi.org/10.2307/2405656

Baker, H. G. (1959). Reproductive methods as factors in speciation in flowering plants. *Cold Spring Harbor Symposia on Quantitative Biology*, *24*, 177–191. https://doi.org/10.1101/SQB.1959.024.01.019

Baker, H. G. (1972). Seed mass in relation to environmental conditions in California. *Ecology*, *53*, 997–1010. https://doi.org/10.2307/1935413

Bartlow, A. W., Agosta, S. J., Curtis, R., Yi, X., & Steele, M. A. (2018). Acorn size and tolerance to seed predators: The multiple roles of acorns as food for seed predators, fruit for dispersal and fuel for growth. *Integrative Zoology*, *13*, 251–266.

Benard, R. B., & Toft, C. A. (2007). Effect of seed size on seedling performance in a long-lived desert perennial shrub (*Ericameria nauseosa*: Asteraceae). *International Journal of Plant Sciences*, *168*, 1027–1033. https://doi.org/10.1086/518942

Blionis, G., & Vokou, D. (2002). Structural and functional divergence of *Campanula spatulata* subspecies on Mt Olympos (Greece). *Plant Systematics and Evolution*, *232*, 89–105. https://doi.org/10.1007/s006060200029

Bonfil, C. (1998). The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *American Journal of Botany*, *85*, 79–87. https://doi.org/10.2307/2446557

Bontrager, M., & Angert, A. L. (2016). Effects of range-wide variation in climate and isolation on floral traits and reproductive output of *Clarkia pulchella*. *American Journal of Botany*, *103*, 10–21. https://doi.org/10.3732/ajb.1500091

Boriskjuk, L., & Rolletschek, H. (2009). The oxygen status of the developing seed. *New Phytologist*, *1982*, 17–30. https://doi.org/10.1111/j.1469-8137.2008.02752.x

Boulli, A., Baaziz, M., & M'Hirit, O. (2001). Polymorphism of natural populations of *Pinus halepensis* Mill. in Morocco as revealed by morphological characters. *Euphytica*, *119*, 309–316.

Bowman, R. N. (1987). *Clarkia concinna* subsp. *automixa* (Onagraceae), a new subspecies from the South Bay Region, central California. *Madroño*, *34*, 41–47.

Bu, H., Chen, X., Xu, X., Liu, K., Jia, P., & Du, G. (2007). Seed mass and germination in an alpine meadow on the eastern Tsinghai–Tibet plateau. *Plant Ecology*, *191*, 127–149. https://doi.org/10.1007/s11258-006-9221-5

Carón, M. M., De Frenne, P., Brunet, J., Chabrerie, O., Cousins, S. A. O., De Backer, L., … Verheyen, K. (2014). Latitudinal variation in seeds characteristics of *Acer platanoides* and *A. pseudoplatanus*. *Plant Ecology*, *215*, 911–925. https://doi.org/10.1007/s11258-014-0343-x

Chacon, P., & Bustamante, R. O. (2001). The effects of seed size and pericarp on seedling recruitment and biomass in *Cryptocarya alba* (Lauraceae) under two contrasting moisture regimes. *Plant Ecology*, *152*, 137–144.

Chávez-Pesqueira, M., & Núñez-Farfán, J. (2016). Habitat fragmentation changes the adaptive value of seed mass for the establishment of a tropical canopy tree. *Biotropica*, *48*, 628–637. https://doi.org/10.1111/btp.12346

Cochrane, A., Hoyle, G. L., Yates, C. J., Neeman, T., & Nictra, A. B. (2016). Variation in plant functional traits across and within four species of Western Australian *Banksia* (Proteaceae) along a natural climate gradient. *Austral Ecology*, *41*, 886–896. https://doi.org/10.1111/aec.12381

Dalgleish, H. J., Koons, D. N., & Adler, P. B. (2010). Can life-history traits predict the response of forb populations to changes in climatic variability? *Journal of Ecology*, *98*, 209–217.

De Jong, T. J., Dijk, H. V., & Klinkhamer, P. G. L. (2005). Hamilton's rule, imprinting and parent-offspring conflict over seed mass in partially selfing plants. *Journal of Evolutionary Biology*, *18*, 676–682. https://doi.org/10.1111/j.1420-9101.2004.00856.x

De Vos, J. M., Wüest, R. O., & Conti, E. (2014). Small and ugly? Phylogenetic analyses of the "selfing syndrome" reveal complex evolutionary fates of monomorphic primrose flowers. *Evolution*, *68*, 1042–1057. https://doi.org/10.1111/evo.12331

Delesalle, V. A., & Mazer, S. J. (2009). Size-dependent pollen: Ovule ratios and the allometry of floral sex allocation in *Clarkia* (Onagraceae) taxa with contrasting mating systems. *American Journal of Botany*, *96*, 968–978.

Delesalle, V. A., Mazer, S. J., & Paz, H. (2008). Temporal variation in the pollen: Ovule ratios of *Clarkia* (Onagraceae) taxa with contrasting mating systems: Field populations. *Journal of Evolutionary Biology*, *21*, 310–323.

Diskin, E., Roctor, H., Jebb, M., Sparks, T., & Donnelly, A. (2012). The phenology of *Rubus fruticosus* in Ireland: Herbarium specimens provide evidence for the response of phenophases to temperature, with implications for climate warming. *International Journal of Biometerology.*, *56*, 1103–1111.

Dudley, L. S., Mazer, S. J., & Galusky, P. (2007). The joint evolution of mating system, floral traits and life history in *Clarkia* (Onagraceae): Genetic constraints vs. independent evolution. *Journal of Evolutionary Biology*, *20*, 2200–2218. https://doi.org/10.1111/j.1420-9101.2007.01421.x

Duncan, T. M., & Rausher, M. D. (2013). Evolution of the selfing syndrome in *Ipomoea*. *Frontiers in Plant Science*, *4*, 301. https://doi.org/10.3389/fpls.2013.00301

Eriksson, O. (1999). Seed size variation and its effect of germination and seedling performance in the clonal herb *Convallaria majalis*. *Acta Oecologica-International Journal of Ecology*, *20*, 61–66. https://doi.org/10.1016/s1146-609x(99)80016-2

Etterson, J. R., & Shaw, R. G. (2001). Constraint to adaptive evolution in response to global warming. *Science*, *294*, 151–154. https://doi.org/10.1126/science.1063656

Fay, P. A., & Schultz, M. J. (2009). Germination, survival, and growth of grass and forb seedlings: Effects of soil moisture variability. *Acta Oecologica*, *35*, 679–684. https://doi.org/10.1016/j.actao.2009.06.007

Foster, S. A. (1986). On the adaptive value of large seeds from tropical moist forest trees: A review and synthesis. *Botanical Review*, *52*, 260–299. https://doi.org/10.1007/bf02860997

Gallagher, R. V., & Leishman, M. R. (2012). A global analysis of trait variation and evolution in climbing plants. *Journal of Biogeography*, *39*, 1757–1771. https://doi.org/10.1111/j.1365-2699.2012.02773.x

Gomaa, N. H., & Xavier Pico, F. (2011). Seed germination, seedling traits, and seed bank of the tree *Moringa peregrina* (Moringaceae) in a hyper-arid environment. *American Journal of Botany*, *98*, 1024–1030. https://doi.org/10.3732/ajb.1000051

Gottlieb, L. D. (1984). Electrophoretic analysis of the phylogeny of the self-pollinating populations of *Clarkia xantiana*. *Plant Systematics*, *147*, 91–102. https://doi.org/10.1007/BF00984582

Greene, D. F., & Johnson, E. A. (1993). Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos*, *67*, 69–74. https://doi.org/10.2307/3545096

Gross, K. L. (1984). Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology*, *72*, 369–387. https://doi.org/10.2307/2260053

Grossenbacher, D., Runquist, R. B., Goldberg, E. E., & Brandvain, Y. (2015). Geographic range size is predicted by plant mating system. *Ecology Letters*, *18*, 706–713. https://doi.org/10.1111/ele.12449

Guo, H., Mazer, S. J., & Du, G.-Z. (2010a). Geographic variation in seed mass within and among nine species of *Pedicularis* (Orobanchaceae): Effects of elevation, plant size and seed number per fruit. *Journal of Ecology*, *98*, 1232–1242. https://doi.org/10.1111/j.1365-2745.2010.01688.x

Guo, H., Mazer, S. J., & Du, G.-Z. (2010b). Geographic variation in primary sex allocation per flower within and among 12 species of *Pedicularis* (Orobanchaceae): Proportional male investment increases with elevation. *American Journal of Botany*, *98*, 1334–1341. https://doi.org/10.3732/ajb.0900301

Guo, H., Weiner, J., Mazer, S. J., Zhao, Z., Du, G., & Li, B. O. (2011). Reproductive allometry in *Pedicularis* species changes with elevation. *Journal of Ecology*, *100*, 452–458. https://doi.org/10.1111/j.1365-2745.2011.01884.x

Haig, D., & Westoby, M. (1991). Genomic Imprinting in Endosperm: Its effect on seed development in crosses between species, and between different ploidies of the same species, and its implications for the evolution of apomixis. *Philosophical Transactions: Biological Sciences*, *333*, 1–13.

Hallett, L. M., Standish, R. J., & Hobbs, R. J. (2011). Seed mass and summer drought survival in a Mediterranean-climate ecosystem. *Plant Ecology*, *212*, 1479–1489. https://doi.org/10.1007/s11258-011-9922-2

Halpern, S. L. (2005). Sources and consequences of seed size variation in *Lupinus perennis* (Fabaceae): Adaptive and non-adaptive hypotheses. *American Journal of Botany*, *92*, 205–213. https://doi.org/10.3732/ajb.92.2.205

Houssard, C., & Escarré, J. (1991). The effects of seed weight on growth and competitive ability of *Rumex acetosella* from two successional old-fields. *Oecologia*, *86*, 236–242. https://doi.org/10.1007/BF00317536

Hove, A. A., Mazer, S. J., & Ivey, C. T. (2016). Seed set variation in wild *Clarkia* populations: Teasing apart the effects of seasonal resource depletion, pollen quality, and pollen quantity. *Ecology and Evolution*, *6*, 6524–6536.

IPCC. (2014). Climate change 2014: Synthesis report. In Core Writing Team, R. K. Pachauri, & L. A. Meyer (Eds.), *Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC. 151 pp.

Ivey, C. T., Dudley, L. S., Hove, A. A., Emms, S. K., & Mazer, S. J. (2016). Outcrossing and photosynthetic rates vary independently within two *Clarkia* species: Implications for the joint evolution of drought escape physiology and mating system. *Annals of Botany*, 118, 897–905. https://doi.org/10.1093/aob/mcw134

Kalisz, S. (1989). Fitness consequences of mating system, seed weight, and emergence date in a winter annual, *Collinsia verna*. *Evolution*, 43, 1263–1272. https://doi.org/10.1111/j.1558-5646.1989.tb02573.x

Khan, M. L. (2004). Effects of seed mass on seedling success in *Artocarpus heterophyllus* L., a tropical tree species of north-east India. *Acta Oecologica*, 25, 103–110. https://doi.org/10.1016/j.actao.2003.11.007

Knies, J. L., Delesalle, V. A., & Cavaliere, A. R. (2004). Seed mass and morphology in outcrossing and selfing species of *Clarkia* (Onagraceae): An SEM Study. *International Journal of Plant Sciences*, 165, 85–96. https://doi.org/10.1086/380979

Konarzewski, T. K., Murray, B. R., & Godfree, R. C. (2012). Rapid development of adaptive, climate-driven clinal variation in seed mass in the invasive annual form *Echium plantagineum* L. *PLoS ONE*, 7, e49000. https://doi.org/10.1371/journal.pone.0049000

Kuang, A., Crispi, M., & Musgrave, M. E. (1998). Control of seed development in *Arabidopsis thaliana* by atmospheric oxygen. *Plant, Cell and Environment*, 21, 71–78.

Larios, E., Burquez, A., Becerra, J. X., & Venable, D. L. (2014). Natural selection on seed size through the life cycle of a desert annual plant. *Ecology*, 95, 3213–3220. https://doi.org/10.1890/13-1965.1

Lázaro, A., & Traveset, A. (2009). Does spatial variation in selective pressures explain among-site differences in seed mass A test with *Buxus balearica*. *Evolutionary Ecology*, 23, 847–865.

Lemke, I. H., Kolb, A., Graae, B. J., De Frenne, P., Acharya, K. P., Blandino, C., ... Diekmann, M. (2015). Patterns of phenotypic trait variation in two temperate forest herbs along a broad climatic gradient. *Plant Ecology*, 216, 1523–1536. https://doi.org/10.1007/s11258-015-0534-0

Lewis, H. (1955). *The genus* Clarkia, 20 (4). Berkeley, CA; Los Angeles, CA: University of California Press.

Liu, J., Bai, Y., Lamb, E. G., Simpson, D., Liu, G., Wei, Y., ... Papadopol, P. (2013). Patterns of cross-continental variation in tree seed mass in the Canadian Boreal Forest. *PLoS ONE*, 8, e61060. https://doi.org/10.1371/journal.pone.0061060

Llanderal-Mendoza, J., Gugger, P. F., Oyama, K., Uribe-Salas, D., & González-Rodríguez, A. (2017). Climatic determinants of acorn size and germination percentage of *Quercus rugosa* (Fagaceae) along a latitudinal gradient in Mexico. *Botanical Sciences*, 95, 37–45. https://doi.org/10.17129/botsci.640

Lloret, F., Peñuelas, J., & Ogaya, R. (2004). Establishment of co-existing Mediterranean tree species under a varying soil moisture regime. *Journal of Vegetation Science*, 15, 237–244.

Loarie, S. R., Carter, B. E., Hayhoe, K., McMahon, S., Moe, R., Knight, C. A., & Ackerly, D. D. (2008). Climate change and the future of California's endemic flora. *PLoS ONE*, 3, e2502. https://doi.org/10.1371/journal.pone.0002502

Marchelli, P., & Gallo, L. A. (1999). Annual and geographic variation in seed traits of Argentinean populations of southern beech *Nothofagus nervosa* (Phil.) Dim. et Mil. *Forest Ecology and Management*, 121, 239–250. https://doi.org/10.1016/S0378-1127(99)00004-3

Martijena, N. E., & Bullock, S. H. (1997). Geographic variation in seed mass in the chaparral shrub *Heteromeles arbutifolia* (Rosaceae). *The Southwestern Naturalist*, 42, 119–121.

Mazer, S. J. (1987). The quantitative genetics of life-history and fitness components in *Raphanus raphanistrum* L. (Brassicaceae): Ecological and evolutionary consequences of seed weight variation. *The American Naturalist*, 130, 891–914. https://doi.org/10.1086/284754

Mazer, S. J. (1989). Ecological, taxonomic, and life-history correlates of seed mass among Indiana Dune angiosperms. *Ecological Monographs*, 59, 153–175.

Mazer, S. J. (1990). Seed mass of Indiana Dune genera and families: Taxonomic and ecological correlates. *Evolutionary Ecology*, 4, 326–357. https://doi.org/10.1007/BF02270931

Mazer, S. J., Dudley, L. S., Delesalle, V. A., Paz, H., & Galusky, P. (2009). Stability of pollen–ovule ratios in pollinator-dependent versus autogamous *Clarkia* sister taxa: Testing evolutionary predictions. *New Phytologist*, 183, 630–648. https://doi.org/10.1111/j.1469-8137.2009.02886.x

Mazer, S. J., Park, I. M., Kimura, M., Maul, E. M., Yim, A. M., & Peach, K. (2019). Data from: Mating system and historical climate conditions affect population mean seed mass: Evidence for adaptation and a new component of the selfing syndrome in *Clarkia*. *Dryad Digital Repository*, https://doi.org/10.25349/D93888

Mitchell-Olds, T. (2001). *Arabidopsis thaliana* and its wild relatives: A model system for ecology and evolution. *Trends in Ecology & Evolution*, 16, 693–700. https://doi.org/10.1016/S0169-5347(01)02291-1

Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology*, 92, 372–383. https://doi.org/10.1111/j.0022-0477.2004.00884.x

Moore, D. M., & Lewis, H. (1965). The evolution of self-pollination in *Clarkia xantiana*. *Evolution*, 19, 104–114.

Munson, S. M., & Sher, A. A. (2015). Long-term shifts in the phenology of rare and endemic Rocky Mountain plants. *American Journal of Botany*, 102, 1–9. https://doi.org/10.3732/ajb.1500156

Murray, B. R., Brown, A. H. D., Dickman, C. R., & Crowther, M. S. (2004). Geographical gradients in seed mass in relation to climate. *Journal of Biogeography*, 31, 379–388. https://doi.org/10.1046/j.0305-0270.2003.00993.x

National Oceanic and Atmospheric Administration, National Centers for Environmental Information. (2017). Global Climate Report – Annual 2017. Retrieved from https://www.ncdc.noaa.gov/sotc/global/201713

Ornduff, R. (1969). Reproductive biology in relation to systematics. *Taxon*, 18, 121–133. https://doi.org/10.2307/1218671

Pettengill, J. B., & Moeller, D. A. (2013). Tempo and mode of mating system evolution between incipient *Clarkia* species. *Evolution*, 66, 1210–1225. https://doi.org/10.1111/j.1558-5646.2011.01521.x

Pleuss, A. R., Schütz, W., & Stöcklin, J. (2005). Seed weight increases with altitude in the Swiss Alps between related species but not among populations of individual species. *Oecologia*, 144, 55–61. https://doi.org/10.1007/s00442-005-0047-y

Primack, R. B. (1987). Relationships among flowers, fruits, and seeds. *Annual Reviews of Ecology and Systematics*, 18, 409–430. https://doi.org/10.1146/annurev.es.18.110187.002205

Qi, W., Guo, S., Chen, X., Cornelissen, J. H. C., Bu, H., Du, G., ... Liu, K. (2014). Disentangling ecological, allometric and evolutionary determinants of the relationship between seed mass and elevation: Insights from multiple analyses of 1355 angiosperm species on the eastern Tibetan Plateau. *Oikos*, 123, 23–32. https://doi.org/10.1111/j.1600-0706.2013.00448.x

Ramírez-Valiente, J. A., Valladares, F., Gil, L., & Aranda, I. (2009). Population differences in juvenile survival under increasing drought are mediated by seed size in cork oak (*Quercus suber* L.). *Forest*

Ecology and Management, *257*, 1676–1683. https://doi.org/10.1016/j.foreco.2009.01.024

Raunsgard, A., Opedal, Ø. H., Ekrem, R. K., Wright, J. W., Bolstad, G. H., Armbruster, W. S., & Pélabon, C. (2018). Intersexual conflict over seed size is stronger in more outcrossed populations of a mixed-mating plant. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 11561–11566. https://doi.org/10.1073/pnas.1810979115

Runions, C. J., & Geber, M. A. (2000). Evolution of the self-pollinating flower in *Clarkia xantiana* (Onagraceae). I. Size and development of floral organs. *American Journal of Botany*, *67*, 1439–1450.

Sage, R. D., Koenig, W. D., & McLaughlin, B. C. (2011). Fitness consequences of seed size in the valley oak *Quercus lobata* Née (Fagaceae). *Annals of Forest Science*, *68*, 477–484. https://doi.org/10.1007/s13595-011-0062-6

Salisbury, E. J. (1942). *The reproductive capacity of plants*. London, UK: G. Bell and Sons.

Salisbury, E. (1975). Seed size and mass in relation to environment. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *186*, 83–88.

Sharma, N., Koul, A., & Kaul, V. (1999). Pattern of resource allocation of six *Plantago* species with different breeding systems. *Journal of Plant Research*, *112*, 1–5. https://doi.org/10.1007/PL00013850

Sicard, A., & Lenhard, M. (2011). The selfing syndrome: A model for studying the genetic and evolutionary basis of morphological adaptation in plants. *Annals of Botany*, *107*, 1433–1443. https://doi.org/10.1093/aob/mcr023

Simons, A., & Johnston, M. O. (2000). Variation in seed traits of *Lobelia inflata* (Campanulaceae): Sources and fitness consequences. *American Journal of Botany*, *87*, 124–132.

Simpson, A. H., Richardson, S. J., & Laughlin, D. C. (2016). Soil-climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography*, *25*, 964–978. https://doi.org/10.1111/geb.12457

Smith, C. C., & Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *The American Naturalist*, *108*, 499–506. https://doi.org/10.1086/282929

Sonkoly, J., Deák, B., Valkó, O., Molnár, V. A., Tóthmérész, B., & Török, P. (2017). Do large-seeded herbs have a small range size? The seed mass-distribution range trade-off hypothesis. *Ecology and Evolution*, *7*, 11204–11212. https://doi.org/10.1002/ece3.3568

Soper-Gorden, N. L., Winkler, K. J., Jahnke, M. R., Marshall, E., Horky, J., Huddelson, C., & Etterson, J. R. (2016). Geographic patterns of seed mass are associated with climate factors, but relationships vary between species. *American Journal of Botany*, *103*, 60–72.

Stanton, M. L. (1984). Seed variation in wild radish: Effect of seed size on components of seedling and adult fitness. *Ecology*, *65*, 1105–1112. https://doi.org/10.2307/1938318

Stock, W., Pate, J. S., & Delfs, J. (1990). Influence of seed size and quality on seedling development under low nutrient conditions in five Australian and South African members of the Proteaceae. *Journal of Ecology*, *78*, 1005–1020. https://doi.org/10.2307/2260949

Susko, D. J., & Cavers, P. B. (2008). Seed size effects and competitive ability in *Thlaspi arvense* L. (Brassicaceae). *Botany-Botanique*, *86*, 259–267.

Tamme, R., Götzenberger, L., Zobel, M., Bullock, J. M., Hooftman, D. A. P., Kaasik, A., & Pärtel, M. (2014). Predicting species' maximum dispersal distances from simple plant traits. *Ecology*, *95*, 505–513. https://doi.org/10.1890/13-1000.1

Tardella, F. M., Piermarteri, K., Malatesta, L., & Catorci, A. (2016). Environmental gradients and grassland trait variation: Insight into the effects of climate change. *Acta Oecologica*, *76*, 47–60. https://doi.org/10.1016/j.actao.2016.08.002

Tautenhahn, S., Heilmeier, H., Gotzenberger, L., Klotz, S., Wirth, C., & Kuhn, I. (2008). On the biogeography of seed mass in Germany: Distribution patterns and environmental correlates. *Ecography*, *31*, 457–468. https://doi.org/10.1111/j.0906-7590.2008.05439.x

Thomson, F. J., Moles, A. T., Auld, T. D., & Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, *99*, 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Tungate, K., Burton, M., Susko, D., Sermons, S., & Rufty, T. (2006). Altered weed reproduction and maternal effects under low-nitrogen fertility. *Weed Science*, *54*, 847–853. https://doi.org/10.1614/WS-05-145R.1

Vallejo-Marín, M., & Barrett, S. C. H. (2009). Modification of flower architecture during early stages in the evolution of self-fertilization. *Annals of Botany*, *103*, 951–962. https://doi.org/10.1093/aob/mcp015

Vasek, F. C. (1958). The relationships of *Clarkia exilis* to *Clarkia unguiculata*. *American Journal of Botany*, *45*, 150–162.

Vasek, F. C. (1964). Outcrossing in natural populations. I. Breckinridge Mountain population of *Clarkia exilis*. *Evolution*, *21*, 213–218.

Vasek, F. C. (1965). Outcrossing in natural populations. II. *Clarkia unguiculata*. *Evolution*, *19*, 152–156.

Vasek, F. C. (1967). Outcrossing in natural populations. 3. Deer Creek population of *Clarkia exilis*. *Evolution*, *21*, 241–248.

Vasek, F. C. (1976). Outcrossing in natural populations. 5. Analysis of outcrossing, inbreeding, and selection in *Clarkia exilis* and *Clarkia tembloriensis*. *Evolution*, *30*, 403–411.

Vasek, F. C., & Harding, J. (1976). Outcrossing in natural populations. 5. Analysis of outcrossing, inbreeding, and selection in *Clarkia exilis* and *Clarkia tembloriensis*. *Evolution*, *30*, 403–411. https://doi.org/10.1111/j.1558-5646.1976.tb00920.x

Vasek, F. C., & Weng, V. (1988). Breeding systems of *Clarkia* sect. *Phaeostoma* (Onagraceae): I. Pollen-ovule ratios. *Systematic Botany*, *13*, 336–350. https://doi.org/10.2307/2419297

Vaughton, G., & Ramsey, M. (1998). Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). *Journal of Ecology*, *86*, 563–573.

Volis, S., Mendlinger, S., & Ward, D. (2002). Adaptive traits of wild barley plants of Mediterranean and desert origin. *Oecologia*, *133*, 131–138. https://doi.org/10.1007/s00442-002-0999-0

Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, *17*, 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Willi, Y. (2013). The battle of the sexes over seed size: Support for both kinship genomic imprinting and interlocus contest evolution. *The American Naturalist*, *181*, 787–798. https://doi.org/10.1086/670196

Winn, A. A. (1988). Ecological and evolutionary consequences of seed size in *Prunella vulgaris*. *Ecology*, *69*, 1537–1544. https://doi.org/10.2307/1941651

Wu, G., & Du, G. (2009). Seed mass in *Kobresia*-dominated communities in alpine meadows at two different elevations. *Israel Journal of Ecology and Evolution*, *55*, 31–40. https://doi.org/10.1560/IJEE.55.1.31

Wu, H., Meng, H., Wang, S., Wei, X., & Jiang, M. (2018). Geographic patterns and environmental drivers of seed traits of a relict tree species. *Forest Ecology and Management*, *422*, 59–68. https://doi.org/10.1016/j.foreco.2018.04.003

Wulff, R. D. (1986). Seed size variation in *Desmodium paniculatum*: II. Effects on seedling growth and physiological performance. *Journal of Ecology*, *74*, 99–114. https://doi.org/10.2307/2260351

Wyatt, R. (1984). The evolution of self-pollination in granite outcrop species of *Arenaria* (Caryophyllaceae). I. Morphological correlates. *Evolution*, *38*, 804–816. https://doi.org/10.2307/2408392

SUPPORTING INFORMATION

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