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Germination responses to changing rainfall timing reveal potential climate vulnerability in a clade of wildflowers

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Abstract

The seasonal timing of life history transitions is often critical to fitness, and many organisms rely upon environmental cues to match life cycle events with favorable conditions. In plants, the timing of seed germination is mediated by seasonal cues such as rainfall and temperature. Variation in cue responses among species can reflect evolutionary processes and adaptation to local climate and can affect vulnerability to changing conditions. Indeed, climate change is altering the timing of precipitation, and germination responses to such change can have consequences for individual fitness, population dynamics, and species distributions. Here, we assessed responses to the seasonal timing of germination-triggering rains for eleven species spanning the *Streptanthus*/*Caulanthus* clade (Brassicaceae). To do so, we experimentally manipulated the onset date of rainfall events, measured effects on germination fraction, and evaluated whether responses were constrained by evolutionary relationships across the phylogeny. We then explored the possible consequences of these responses to contemporary shifts in precipitation timing. Germination fractions decreased with later onset of rains and cooler temperatures for all but three *Caulanthus* species. Species' germination responses to the timing of rainfall and seasonal temperatures were phylogenetically constrained, with *Caulanthus* species appearing less responsive. Further, four species are likely already experiencing significant decreases in germination fractions with observed climate change, which has shifted the timing of rainfall towards the cooler, winter months in California. Overall, our findings emphasize the sensitivity of germination to seasonal conditions, underscore the importance of interacting environmental cues, and highlight vulnerability to shifting precipitation patterns with climate change, particularly in more northern, mesic species.

KEYWORDS
Caulanthus, climate change, germination cues, germination niche, germination responses, Mediterranean climate, rainfall onset, *Streptanthus*

INTRODUCTION

The timing of life cycle transitions, such as birth, emergence, and reproduction, can have profound effects on individual performance, fitness, and population dynamics (Bradshaw & Holzapfel, 2008; Cohen, 1976; Lane et al., 2012; Varpe, 2017). Strategies to time these critical life history functions with favorable conditions are expected to be under strong selection, and often entail responses to environmental cues that signal such conditions are approaching (McNamara et al., 2011; Shave et al., 2019). However, climate change is altering seasonal conditions, affecting both the availability and reliability of cues, and potentially creating mismatches between life history timing and environmental conditions (Abrahms et al., 2022; Bernhardt et al., 2020; Bonamour et al., 2019; Parmesan & Hanley, 2015).

For plants, the seasonal timing of seed germination is critical to seedling establishment, seasonal phenology, and ultimately plant fitness (Donohue et al., 2010; Gremer, Chiono, et al., 2020; Kalisz, 1986). Germination timing depends critically on a species' germination niche, the range of environmental conditions under which germination can occur. Precipitation and temperature are critical cues for germination (Barga et al., 2017; Burghardt et al., 2015; Finch-Savage & Leubner-Metzger, 2006; Probert, 2000; Puglia et al., 2018), in particular, the timing of precipitation interacts with temperature to drive germination timing (Huang et al., 2016; Kimball et al., 2010; Levine et al., 2008; Mayfield et al., 2014; Walck et al., 2011; Went, 1949). Thus, climate change-induced shifts in precipitation regimes may affect the timing of germination and the amount of seeds that do germinate (germination fraction) (Martínez-Berdeja et al., 2023). The degree to which the germination niche is constrained by evolutionary history could, in part, determine how species respond to shifting climate, with implications for individual fitness and population dynamics (Arène et al., 2017; Fang et al., 2017; Fernández-Pascual et al., 2021).

Germination timing determines the abiotic and biotic environments seedlings will experience, influencing performance during one of the most vulnerable plant life stages (Gremer et al., 2016; Matías et al., 2011). To time germination with favorable conditions, germination cues may evolve such that seeds respond to partially or wholly reliable cues signaling favorable conditions for germination and establishment (Bonamour et al., 2019; Cohen, 1967; Donohue et al., 2010; Gremer et al., 2016). For example, a global-scale meta-analysis of 661 alpine species revealed their strong propensity to germinate in response to warm, wet conditions (Fernández-Pascual et al., 2021), which signal the onset of the summer growing season. On the other hand, in variable and changing environments, seeds may not germinate either because appropriate conditions or cues are unavailable, or because seeds may remain dormant even in the presence of those cues. Seed dormancy can act to distribute germination through time, spreading the risk of germinating into unfavorable conditions and acting as a bet hedging strategy (Cohen, 1966; Hoyle et al., 2015). Bet-hedging through germination is often found in unpredictable environments like deserts, where environmental cues are unreliable (Gremer & Venable, 2014; Venable, 2007). If seeds fail to germinate because of the absence of appropriate cues and conditions, or due to seed dormancy, they must survive in the soil seedbank in order to germinate in future conditions.

Understanding variation among species' germination strategies and responses to environmental cues for germination can reveal vulnerability or resilience to climate change (Kimball et al., 2010; Liu et al., 2013). Climate change is increasing temperature and variability in both temperature and precipitation (IPCC, 2021; Pathak et al., 2018; Swain et al., 2018; Wright et al., 2016). Indeed, climate change is already increasing seasonal temperatures and shifting the timing of germination-triggering rains, which will likely interact to affect germination conditions (Levine et al., 2011; Luković et al., 2021; Mayfield et al., 2014). Temperature cues are critical for germination, which is typically expected to increase with temperature until a threshold is reached (Alvarado & Bradford, 2002; Dwyer & Erickson, 2016; Finch-Savage & Leubner-Metzger, 2006) unless species have cold-cued germination (Mayfield et al., 2014). However, shifting rainfall timing may counteract or overwhelm effects of rising temperatures. For example, later arrival of seasonal rain may result in cooler germination temperatures for species with winter growing seasons (Huang et al., 2016; Kimball et al., 2010, 2011). Climate change has already shifted patterns of seasonal precipitation in Mediterranean climates (Barredo et al., 2018; Giorgi & Lionello, 2008; Walck et al., 2011). In California, the timing of first seasonal rains has shifted to later in the fall and winter growing season, now occurring under cooler conditions (Luković et al., 2021). Moreover, climate change may create mismatches between germination cues and conditions, such that seeds may germinate in unfavorable conditions or not germinate at all if they do not receive appropriate environmental cues (Donohue et al., 2010; Walck et al., 2011). Thus, shifting temperature and precipitation with climate change have implications for germination processes.

The *Streptanthus* (s.l.) clade of Brassicaceae is an ideal system to ask how shifting rainfall onset will alter germination patterns. The clade has desert origins and diversified as it moved northward (Axelrod, 1958; Cacho et al., 2021) across the Mediterranean climate of California. As these species spread from the desert, many of their traits diversified along the phylogeny, with closer relatives having more similar traits (Cacho & Strauss, 2014; Christie & Strauss, 2018). For example, Pearse et al. (2020) found phylogenetically conserved fitness responses to water availability, suggesting that diversification of those responses was constrained by evolutionary history. However, much less is known about their germination responses and how they vary across the clade.

To investigate how the timing of rainfall affects germination fraction for *Streptanthus* and *Caulanthus* species across the *Streptanthus* (s.l.) clade, we experimentally varied only the date of rainfall onset. We decoupled this germination trigger from other multivariate seasonal cues, including temperature, to better understand the consequences of shifting rainfall timing in a complex seasonal environment. Further, shifting rainfall timing with climate change (Luković et al., 2021; Pathak et al., 2018; Swain et al., 2018) is likely to be one of the strongest, most direct effects on germination timing for plants with a winter growing season in this region. We asked three questions: (1) How does variation in the timing of germination-triggering precipitation and corresponding seasonal temperature affect germination fraction? (2) What are the possible effects of contemporary shifts in precipitation timing on germination fraction of species across the clade? And (3) how have germination responses to seasonal conditions diversified across these closely related species? We expected that seeds would germinate at higher fractions with earlier rainfall events that occur during warmer fall temperatures, which are known to facilitate germination. We also expected that species adapted to divergent climates of origin would vary in germination response to rainfall onset timing. Specifically, we predicted that *Caulanthus* species that occupy drier, more variable environments would be less affected by the timing of germination-triggering rains and corresponding temperatures (Golodets et al., 2013; Figure 1). Correspondingly, we also expected to see lower germination fractions, suggesting higher dormancy in *Caulanthus* species from variable and less predictable local environments.

MATERIALS AND METHODS

Study system

To investigate how climatic shifts may influence germination fractions, we used 13 populations from 11 species spanning the *Streptanthus clade* (s.l.; Thelypodieae Brassicaceae),

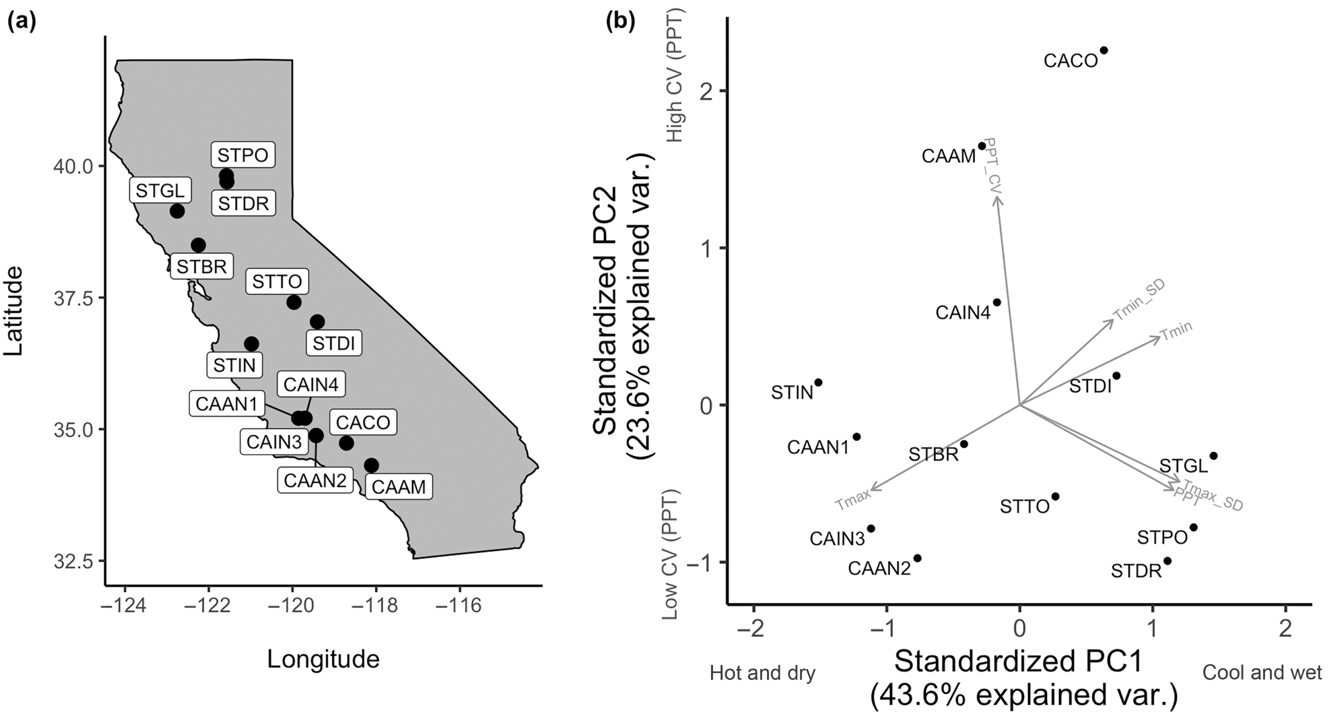

FIGURE 1 Location and climate for study species. (a) Seeds were collected from 13 populations of 11 species from across California. (b) Principal components (PC) analysis of mean germination season (September–December) climate for 1991–2015 for the location of each population. The first two principal components are illustrated on the *x* and *y* axes (Appendix S1: Table S11). The first PC was negatively associated with maximum temperature (Tmax) and positively associated with precipitation (PPT), minimum temperature (Tmin), and variability in maximum temperature (SD, Tmax_SD). The second PC was positively associated with variability in precipitation (CV, PPT_CV). These climate variables describe variation among the habitats occupied by these populations ranging from hot and dry to cold and wet with low or high precipitation variability. Data source was Flint and Flint (2014). See species abbreviations in Table 1.

which includes nonmonophyletic genera *Streptanthus* and *Caulanthus* (Table 1; Cacho et al., 2014). Henceforth, we refer to all species by the abbreviations given in Table 1. As a group, these species span the latitudinal range of the California Floristic Province and typically inhabit relatively barren, dry substrates ranging from sandy deserts to rocky and serpentine outcrops (Figure 1a; Cacho & Strauss, 2014). The clade occupies habitats with a range of mean temperature and precipitation, and a range of variability in these measures (Figure 1b, Table 1; Cacho et al., 2021; Pearse et al., 2020). All species in this study experience the Mediterranean climate in California, in which the growing season begins with germination-triggering rain events in the fall or early winter and ends with the onset of summer drought.

Phylogeny estimation

Full methods for phylogeny estimation can be found in Cacho et al. (2014). In brief, the phylogenetic hypothesis was generated using six single-copy nuclear genes, three identified specifically for this group in combination with three traditionally used nuclear regions (phyA, ITS, PEPC), and two chloroplast regions (trnL, trnH-psbA). The hypothesis was based on Bayesian MCMC runs consisting of three 50-million-generation independent runs with sampling every 5000 generations. Here, for the two species with two populations, additional populations were added to the phylogeny at the same node with the same edge length as the other population of the species using the phytools (Revell, 2012) and ape (Paradis & Schliep, 2019) packages in R programming language (R Core Team, 2021).

TABLE 1 Species (11) and populations (13) included in this study from the *Caulanthus* and *Streptanthus* genera of Brassicaceae.

Species	Abbreviation	PPT	Tmax	Tmin
Caulanthus amplexicaulis	CAAM	39.90	21	9
Caulanthus anceps	CAAN1	16.42	23	6
Caulanthus anceps	CAAN2	19.00	22	6
Caulanthus coulteri	CACO	21.74	19	8
Caulanthus inflatus	CAIN3	19.97	22	6
Caulanthus inflatus	CAIN4	18.07	21	9
Streptanthus breweri	STBR	66.99	22	8
Streptanthus diversifolius	STDI	58.07	21	8
Streptanthus drepanoides	STDR	100.18	22	10
Streptanthus glandulosus	STGL	124.75	18	8
Streptanthus insignis	STIN	30.53	22	5
Streptanthus polygaloides	STPO	142.42	20	8
Streptanthus tortuosus	STTO	50.76	22	8

Note: Mean germination season (September to December) climate data from 1991 to 2015 are also reported for each population's location: Precipitation (PPT, in millimeters), maximum temperature (Tmax, in degrees Celsius), and minimum temperature (Tmin, in degrees Celsius). Climate data sourced from Flint and Flint (2014). Populations were chosen for their approximate central location within the range-wide climate space for each species (Appendix S1: Figure S1).

Experimental design

This experiment was conducted in a "screenhouse" with a clear plastic roof that allowed for controlled watering, but exposed seeds to seasonal temperature fluctuations and changes in ambient light, located on campus at the University of California, Davis. This design replicated natural field conditions where, if rains come later in the season, plants experience cooler temperatures and different light regimes. To assess species differences in germination responses to variation in the timing of germination-triggering rains, we experimentally imposed seven rainfall onset events throughout the germination season. Distinct germination cohorts were created by simulating germination-triggering rain events every 2 weeks: September 17, October 2, October 16, October 30, November 13, November 27, and December 11, 2020. On each of these dates, a distinct cohort of pots with seeds was intensively watered for the first time to simulate germination-triggering rain. The timing of watering events included the average historical (October 2) and contemporary (October 30) rainfall onset dates in California (Luković et al., 2021) as well as dates beyond this range, encompassing natural interannual variation and projected future shifts in arrival time of rains (Gremer, Chiono, et al., 2020; Luković et al., 2021).

Seeds were collected as maternal families from field locations in 2019, June to August depending on the population, and pooled for this experiment (Appendix S1: Table S1). For nine of the species, seeds were collected from one population approximately centrally located within the species' range-wide temperature and precipitation space (Appendix S1: Figure S1). For two species (CAAN and CAIN), for which we had more seed, we included seeds from two sites (Appendix S1: Figure S1). Seeds after-ripened while stored dry, in the dark, at room temperature (~21°C) until the start of the experiment in September 2020. Mean viability of seeds from the original pools was estimated as

96% by tetrazolium assays, suggesting ungerminated seeds in the study were more likely dormant or dead, not initially inviable (Appendix S1: Table S1).

For each of the seven cohorts, individual seeds were sown into 107 mL cone-tainer pots (Stuewe and Sons SC7) filled with a mix of 2/3 UC Davis potting soil (1:1:1 parts sand, compost, peat moss with dolomite), and ⅓ coarse 16 grit sand. For each species, except CACO, 16 pots were placed in each of three replicate blocks for a total of 48 seeds/pots per cohort. For CACO, for which we had limited seed, there were four pots per replicate block, 12 total seeds/pots per cohort. Each of the three blocks was on a separate screenhouse bench and contained randomly assigned pots of each species and each cohort within species.

We simulated initial germination-triggering rain events for each cohort by bottom-watering pots to saturation, adding an individual seed to each pot, and then intensely misting pots for one week (Appendix S1: Table S2). Pots in previously deployed cohorts also received intense misting for one week during new cohort deployment, as seeds would experience subsequent rainstorms in the field. After that time, each pot in each cohort received lower levels of watering between simulated rainstorms to maintain moist soil conditions (Appendix S1: Table S2). Watering amounts following germination-triggering rain events reduced as the experiment progressed because of cooler seasonal temperatures. One week after the last cohort was sown, all pots were subjected to maintenance watering until germination surveys ceased. Germination was assessed daily until January 11, 2021, by the appearance of cotyledons, when germination had slowed and, thereafter, germination surveys were reduced to twice weekly and then further reduced on February 1, 2021, to once per week. All surveys and watering were completely stopped on April 16, 2021, after no germination had been observed in the previous two weeks. Earlier cohorts were allowed to germinate over a longer period of time during the study to contribute to their total germination as would naturally occur in the field.

After Year 1 of the study was completed, all pots with ungerminated seeds were allowed to dry out and kept in the screenhouse to expose seeds to natural temperatures over the summer. The following fall, we simulated a germination-triggering early season rain event to investigate seed dormancy strategies of these species and compare germination responsiveness with rainfall timing between years. This provided an estimate of how many seeds possibly remained dormant in Year 1 by quantifying the number of seeds that germinated in the second year in response to simulated rainfall and early season temperatures. Pots were re-randomized, bottom-watered, and then received one week of high-frequency watering, as in the previous year, starting on September 15, 2021, to simulate the beginning of the next growing season (year 2). Germination surveys were then conducted daily until November 5, 2021, when they were reduced to three times weekly. On November 22, 2021, surveys decreased to once per week and were stopped on December 27, 2021, after a two-week period without any germination.

Thermal germination conditions

We determined the temperature each seed experienced prior to germination by calculating the mean temperature between the day of rainfall onset (cohort deployment date) and day of germination. Mean temperature was calculated from hourly values measured by loggers (Thermochron DS1921G iButtons), seven in each block, buried in soil-filled pots (Figure 2a; Appendix S1: Figure S2). In models of Year 1 germination fractions, the average was taken of the mean temperatures experienced by each seed in each block, within each cohort. This procedure gave a block-level estimate of mean temperature experienced by seeds in each block between rainfall onset date and germination date to match block-level estimates of germination fractions. Throughout the experiment, ambient temperatures decreased through time such that seeds in earlier rainfall onset events experienced warmer temperatures than seeds in later rainfall onset events as would occur in natural field conditions (Figure 2a). Temperature during Year 2 of the experiment followed a similar pattern to that of Year 1 (Appendix S1: Figure S2). Our unpublished findings from thermal germination experiments show the importance of temperature as a germination cue in these species (see Gremer, Chiono, et al., 2020 for *S. tortuosus*). Mean temperature in the screenhouse during the experiment was ~15°C (9–20°C) in Year 1 and ~14°C (9–19°C) in Year 2, comparable to both historical and contemporary field mean temperatures populations experienced (Appendix S1: Table S3).

Data analysis

Germination fraction

Relationships between germination fraction and the timing of rainfall onset (date coded as continuous) were evaluated for each species separately. Both linear and quadratic models were fit with binomial error and logit link function, and likelihood ratio tests (lmtest package, Zeileis & Hothorn, 2002) were used to determine the significance of factors in the models. Only linear model results are presented as their conclusions were

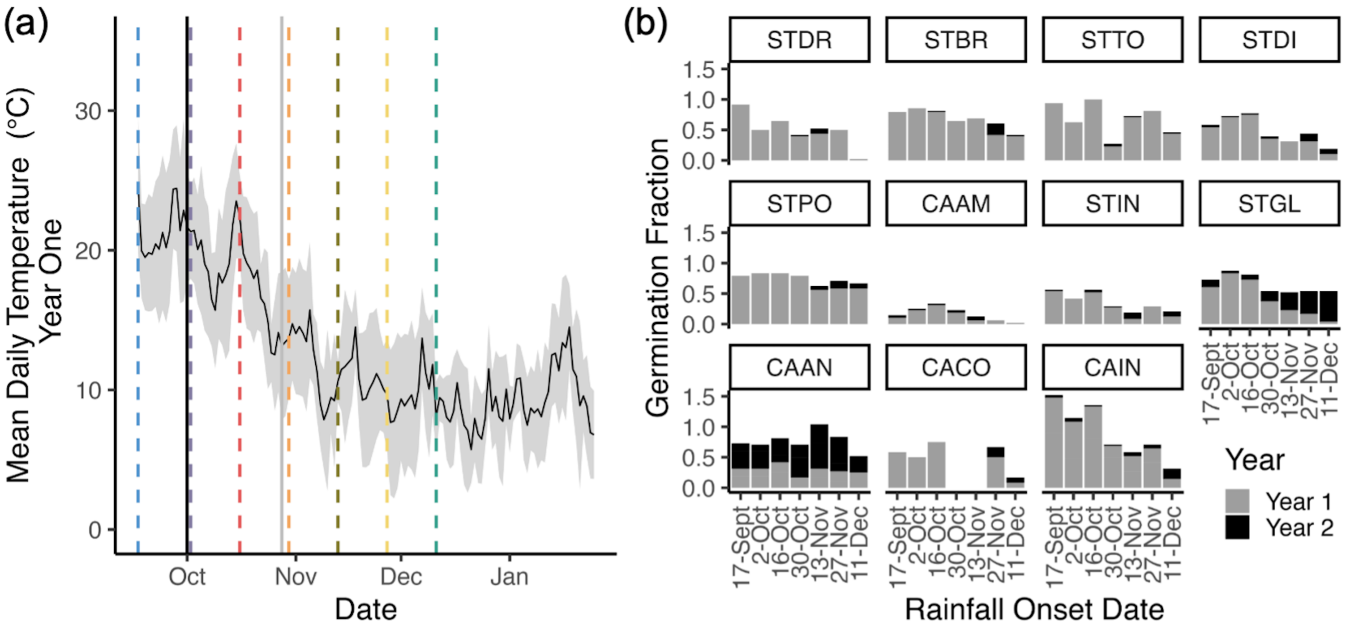

FIGURE 2 Temperatures seeds experienced during the study and germination fractions in each year of the study. (a) Mean and SD of daily temperatures (in degrees Celsius) from the first rainfall onset date (September 17, 2020) to the last day of observed germination (January 25, 2021) in Year 1 of the experiment. Dashed lines represent each rainfall onset date. The solid black line corresponds to the date of historic onset of rainfall (October 1) and the solid gray line represents the 27-day shift to the contemporary date of rainfall onset (October 28) in California according to Luković et al. (2021). (b) Amount of total germination fraction for each species during Year 1 (gray) versus Year 2 (black) of the study at each rainfall onset date. Plots are in the same order as branch tips of the phylogeny (Figure 5). See species abbreviations in Table 1.

not distinguishable from quadratic models. A grouped logistic regression was used to evaluate the relationships between germination fraction and seasonal temperature. A generalized linear mixed-effects model (lme4 package; Bates et al., 2015) was built with groups for each of the three blocks, and successes indicating germination, with block included as a random effect. Marginal means were estimated for each species using the emmeans package (Lenth, 2022) for use in post hoc comparisons. We also tested whether species differ in their germination responsiveness to rainfall onset between years. A Pearson's Chi-squared test with three contingencies (Year 1, Year 2, Never) was used to evaluate germination timing. We performed post hoc analyses using the chisq.posthoc.test package (Ebbert, 2019) in R with a Bonferroni p-value adjustment.

Potential effects of climate change

To understand how climate change-induced shifts in precipitation timing affect germination responses, we compared germination fractions on dates that represent mean historical and contemporary rainfall onset based on Luković et al. (2021), who showed that rainfall onset date has shifted approximately 27 days later into the fall from an average rainfall onset date of October 1 (1960–1989) to an average onset date of October 28 (1990–2019). These dates align closely with our rainfall onset dates of October 2 (historical date) and October 30 (contemporary date). In order to contrast responses at these two specific dates, we fit species-specific generalized linear models similar to those described above but treated timing of rainfall onset date as a factor to facilitate contrasts. Marginal means were estimated, and comparisons between historical (October 2) and contemporary (October 30) rainfall onset dates were made using the emmeans package (Lenth, 2022) with p-values adjusted using the Tukey method for multiple comparisons.

Phylogenetic analyses of Species' responses

Phylogenetic generalized linear mixed models (PGLMMs) were fitted to evaluate how germination responses to rainfall onset date and seasonal temperatures diversified across the phylogeny using the phyr package (Ives et al., 2020). This approach allowed us to explore responses while incorporating variance explained by phylogenetic structure as well as variance explained by species-specific (random variation) properties simultaneously (Ives et al., 2020). These models took on the same structure as the generalized linear mixed models above, one fixed effect and block as a random effect, but included additional random effects.

An overall phylogenetic random effect of species was included to account for non-independence among species while a non-phylogenetic random effect of species was included to account for random differences among species. We also included a rainfall onset date-by-phylogenetic species random effect or temperature-by-phylogenetic species random effect to estimate the degree to which more phylogenetically related species have more similar germination responses. Lastly, a random effect was included for rainfall onset date-by-species or temperature-by-species, without phylogenetic covariance, to account for species-specific relationships independent of phylogeny. Models were used to evaluate the contribution of the random effects to variation in germination responses, with significance evaluated with likelihood ratio tests. The phylogeny in this study included two populations of two of the species (CAAN and CAIN), so in addition to this phylogeny being included in these models, additional models were fit, each including a different pairwise combination of populations of the two species.

RESULTS

In general, later rainfall onset had a negative effect on germination fraction (Figure 3, Appendix S1: Table S4), though responses varied among species. Germination fraction also significantly decreased at cooler temperatures for all but three species (CAAM, CAAN, and CACO) (Figure 4; Appendix S1: Tables S5 and S6). In addition, germination fraction significantly decreased between rainfall onset dates representing historical (October 2, 20°C mean) and contemporary (October 30, 14°C mean) dates of rainfall timing for STDI, STGL, STTO, and one of the populations of CAIN (CAIN4; Figure 3; Appendix S1: Table S7).

Species also differed in the fates of their seeds across the study (germination in Year 1, fall Year 2, or never; $\chi^2 = 1006.1$, df $= 24$, $p < 0.0001$; Figure 2b). While most species germinated much less in the second year, three species had different responses (Figure 2b; Appendix S1: Table S8). Both populations of CAAN, a desert dwelling species, had higher germination in Year 2 than in Year 1. Seeds of STGL experiencing later rainfall onset events in Year 1 had low germination, but then germinated in high fractions in the early season rainfall event of Year 2 (Figure 2b: 27 November, 11 December). The mid- high elevation, lower latitude species CAAM was not as responsive to the timing of rainfall onset or temperature, with significantly lower germination in both years (Figure 2b; Appendix S1: Table S8).

Similarity among species in germination responses to rainfall onset date and seasonal temperatures was congruent with phylogenetic relationships among the species (Appendix S1: Tables S9 and S10). In other words, closely related species were more likely to share the same germination responses (Figure 5). These results were consistent among models with different combinations of populations of CAAN and CAIN except for three of the models of rainfall onset date. In these models, significant variance in the global slope including all species was still explained by phylogenetic relationships, but variation in species-specific slopes of the relationship between germination fraction and rainfall onset date due to phylogenetic relationships was not significant (Appendix S1: Table S9). Despite some combinations of populations lacking significance for models including rainfall onset date, populations within the species do have similar responses to each other (Figure 3), suggesting this difference could be an artifact of small sample size.

DISCUSSION

Life history timing is critically linked to environmental conditions such that mistimed life cycle transitions may expose individuals to unfavorable conditions (Bonamour et al., 2019; Bradshaw & Holzapfel, 2008; Lane et al., 2012). For plants, timing germination with appropriate precipitation and temperature cues is vital for their performance, fitness, and population persistence (Donohue et al., 2010; Martínez-Berdeja et al., 2023). Here, we assessed how variation in the timing of rainfall onset events affected seasonal timing of germination for closely related species that have radiated into different geographic regions within Mediterranean climates of California. This study focuses on the impacts of shifting rainfall timing on germination by exposing seeds to ambient variation in other germination cues, such as temperature and daylength, that they would naturally experience in the field. Our results indicate that later onset of seasonal rains during cooler seasonal temperatures generally decreases germination fractions, though species vary in their responsiveness to these cues. *Caulanthus* species were generally less responsive to the timing of rainfall onset events or their associated temperatures than *Streptanthus* species and had lower germination overall. Further, results indicate that four species may already be experiencing negative effects of contemporary shifts in the timing of rainfall. Variation in responses to the timing of rainfall and corresponding temperatures across the clade show phylogenetic signal, which may indicate that diversification of germination responses was constrained by evolutionary history as species radiated into different climates.

In systems with winter growing seasons, like lower elevation habitats of California, earlier onset of seasonal

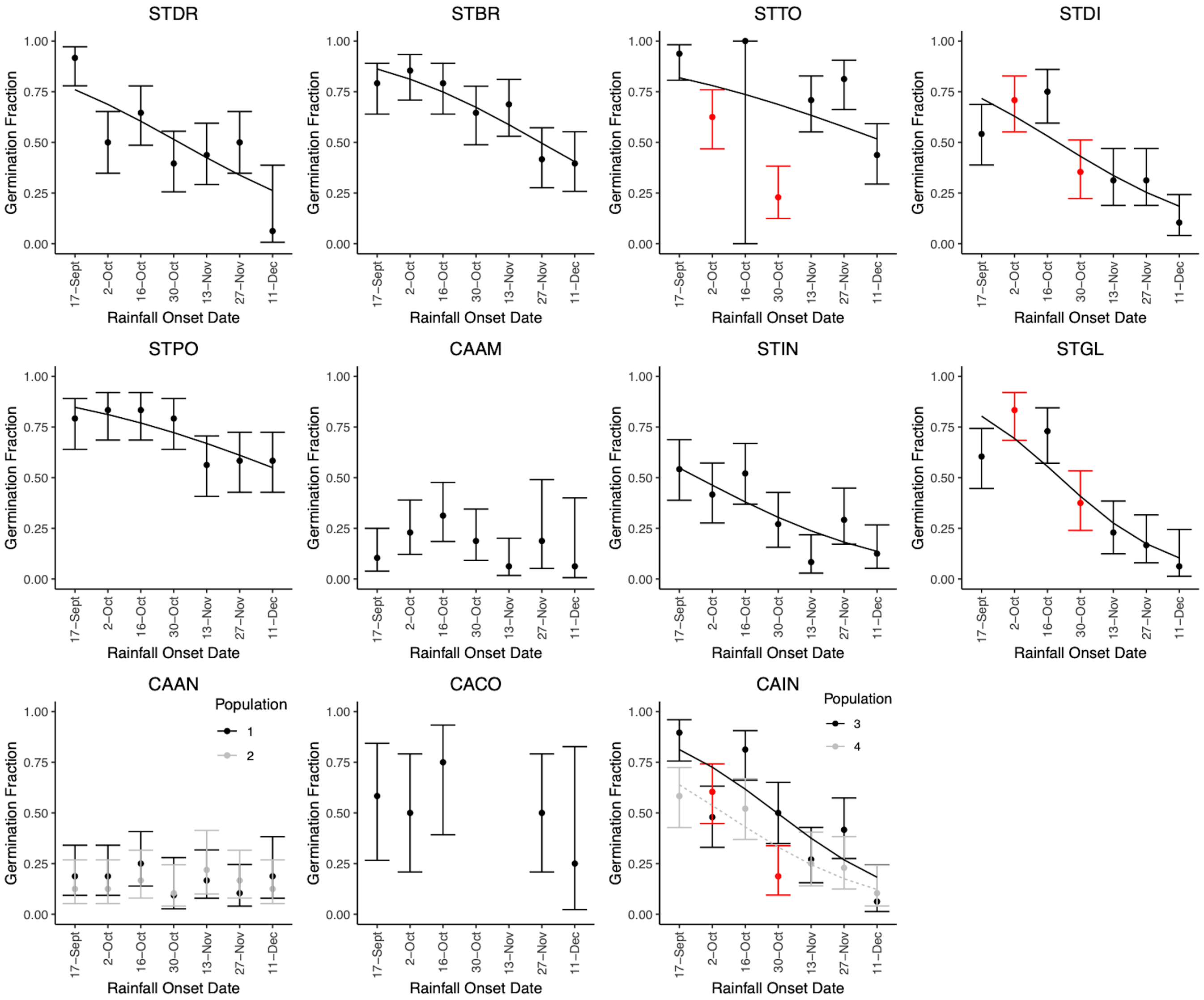

FIGURE 3 Relationships between germination fraction and rainfall onset date and comparison of germination fraction between October 2 (historical onset of rainfall) and October 30 (contemporary onset of rainfall), during Year 1 of the study. Plots where regression lines are present had significant relationships between germination fraction and rainfall onset date (back transformed from logit scale). For all significant relationships, germination fraction decreased as rainfall onset occurred later in the season. Points are the mean predicted germination fraction for each cohort with 95% CIs back transformed from logit scale. In plots where points and bars are red, a significant decrease in germination fraction was found between the historical onset date of rainfall (October 2) and the contemporary onset date of rainfall (October 30; Luković et al., 2021). Plots are in the same order as branch tips of the phylogeny (Figure 5). See species abbreviations in Table 1.

rains typically corresponds with warmer temperatures. Thus, earlier rains may drive higher germination simply due to thermal requirements for germination, or may be an adaptive response in which seeds are tuned to early conditions for germination to take advantage of a longer growing season. Similar observations have been made in bird systems, where birds that time egg-laying with warmer spring temperatures fledge more young (Hoover & Schelsky, 2020; Shave et al., 2019). On the other hand, there may be advantages to germinating later in the season during cooler temperatures that may indicate reliable cool, wet weather has arrived (Mayfield et al., 2014). Here, germination fraction significantly decreased for most species with later onset of precipitation that occurred under cooler temperatures. Huang et al. (2016) reported similar results in a Sonoran Desert plant community finding lower germination percentages later in the season under cooler conditions. Further, work in that same system demonstrated that, despite warming temperatures over 25 years, changes in species composition were primarily due to shifting rainfall timing and the cooler temperatures associated with later germination rains (Kimball et al., 2010). Our findings and previous research highlight how important the interaction of

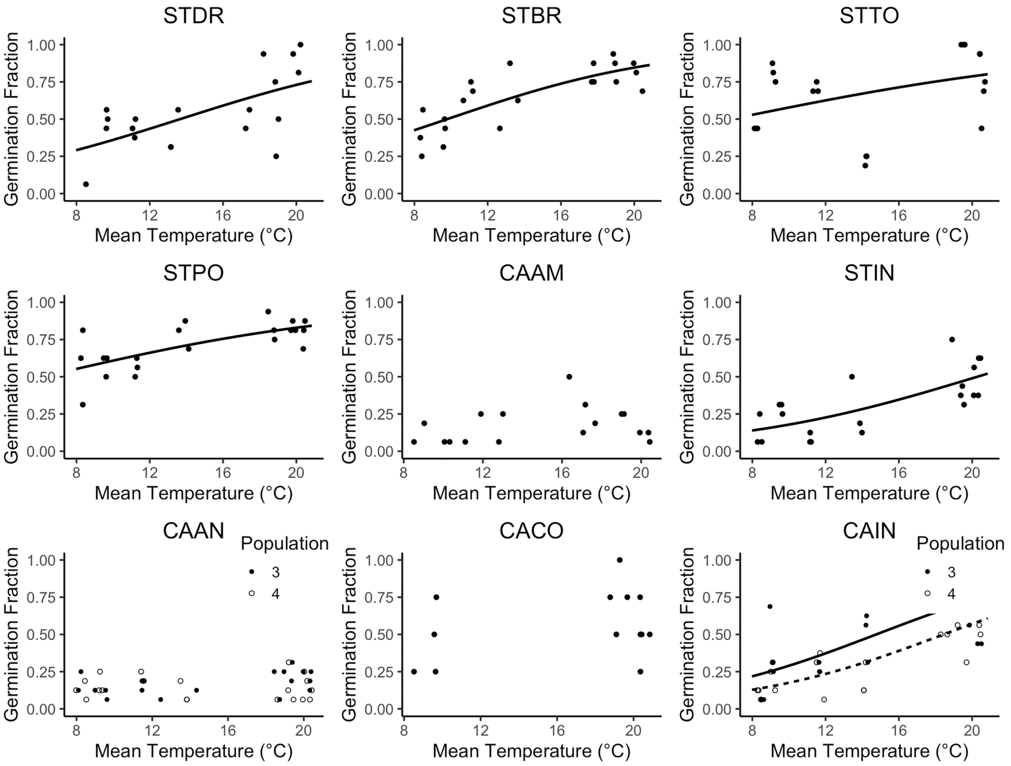

FIGURE 4 Relationships between germination fraction and mean temperature seeds experienced between their rainfall onset date and germination date during Year 1 of the study. Regression lines represent significant, positive relationships between germination fraction and mean temperature seeds experienced (back transformed from logit scale). Points are observed values of germination fraction for the three blocks in each cohort. Plots are in the same order as branch tips of the phylogeny (Figure 5). See species abbreviations in Table 1.

precipitation timing and temperature is for driving germination patterns and suggest that shifting rainfall timing could overwhelm effects of increasing temperatures with climate change.

Indeed, a growing body of literature has found that germination cues interact to drive climate change effects on germination timing and fractions (Donohue et al., 2010; Huang et al., 2016; Kimball et al., 2010; Levine et al., 2008; 2011). While the timing of precipitation onset has shifted later since 1960 in California (Luković et al., 2021), mean temperature has not followed the same trend as sharply as precipitation (Pathak et al., 2018; Rapacciuolo et al., 2014; Wright et al., 2016), suggesting a recent and continuing mismatch between the timing of precipitation and the temperature following rain events relative to historic patterns. This may be particularly detrimental for systems in which temperature is an important germination cue like the one studied here (Cochrane, 2020; Dwyer & Erickson, 2016; Gremer, Chiono, et al., 2020; Huang et al., 2016). In this study, four species showed decreases in germination fractions between estimates of historic and contemporary onset dates of precipitation. This result highlights species-specific sensitivities to climate change, calling for species-level restoration and conservation plans (Barga et al., 2017; Finch-Savage & Footitt, 2017).

Previous work has found strong phylogenetic signal in germination cues (Arène et al., 2017; Baskin et al., 2022; Fernández-Pascual et al., 2021), consistent with our results. In the *Streptanthus* (s.l.) clade, divergence and spread of these species has been linked to edaphic and climatic adaptations, including soil nutrients and precipitation quantity (Cacho & Strauss, 2014; Christie & Strauss, 2018; Pearse et al., 2020). We found that germination of many *Caulanthus* species is much less responsive to rainfall timing and corresponding temperatures than *Streptanthus* species, contributing to overall lower germination. Lower latitude *Caulanthus* species have typically evolved in drier, warmer, and more variable habitats than higher latitude *Streptanthus* species (Figure 1b; Christie & Strauss, 2018), potentially contributing to divergence in their germination responsiveness to rainfall onset timing. With continued climate change, seeds may either not germinate or germinate under suboptimal conditions based on formerly adaptive germination cues, unless they are able to shift germination timing by tracking conditions through time or space (Catelotti et al., 2020), adapt to respond to new

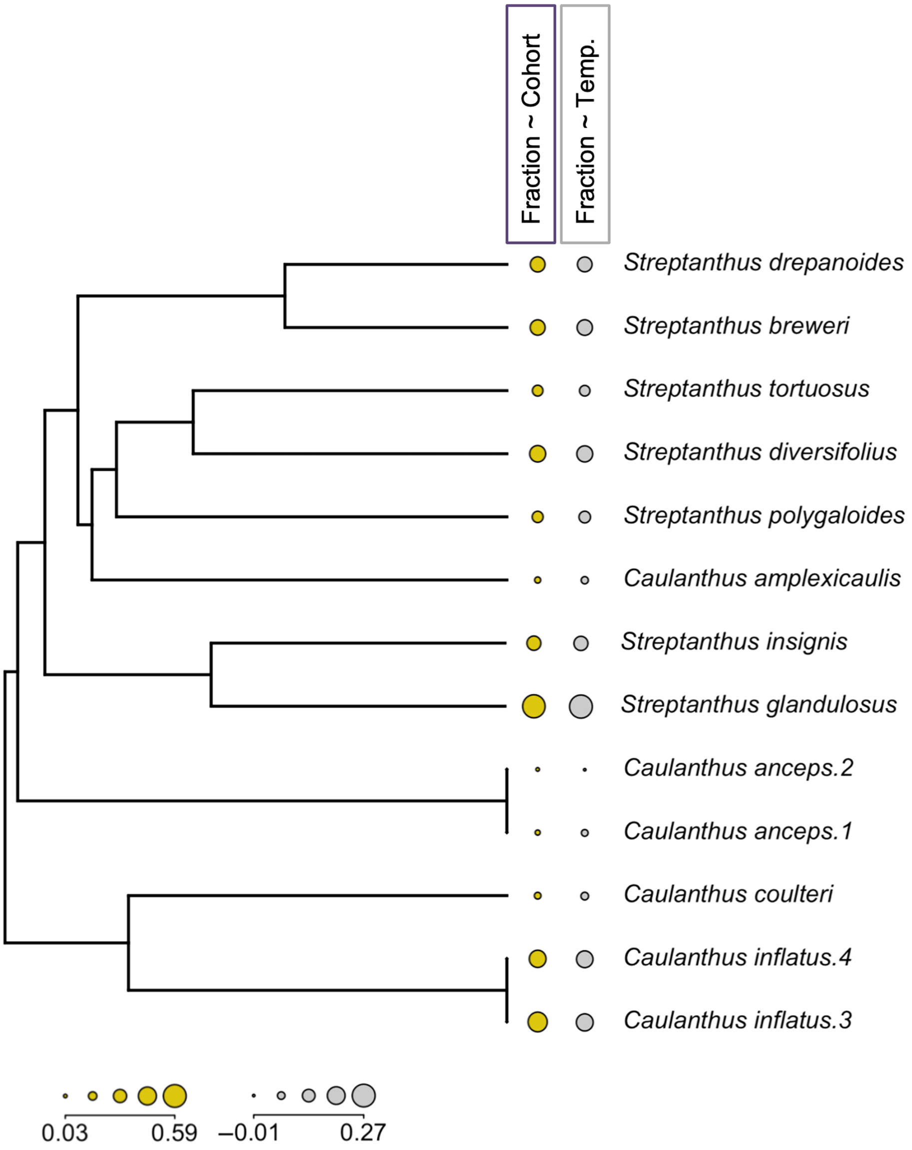

FIGURE 5 Slopes of the relationships evaluated in this study displayed across the phylogeny. For both relationships, more closely related species were more likely to share the same germination response. Yellow dots display the slopes of the relationship between germination fraction and rainfall onset date (Figure 3; phylogenetic generalized linear mixed model: Variance 0.001 ± 0.12, $p = 0.0008$). All slopes are negative except for *Caulanthus anceps.2* (0.03). Gray dots display the slopes of the relationship between germination fraction and mean temperature experienced by seeds (Figure 4; variance 0.002 ± 0.05, $p < 0.00001$). All slopes are positive except for *Caulanthus anceps.2* (−0.01).

combinations of germination cues (Donohue et al., 2010; Walck et al., 2011), or use a combination of these strategies (Gremer et al., 2016; Gremer, Wilcox, et al., 2020).

Life history evolution has led to a variety of strategies to adjust timing of key life stage transitions (Bernhardt et al., 2020; Bradshaw & Holzapfel, 2008; Stenseth & Mysterud, 2002; Varpe, 2017). For plants, germination strategies can include using cues to time germination with appropriate conditions, not germinating in a given year if germination conditions or cues are unavailable, or remaining dormant in the soil. Species in this study encompassed all these germination strategies. First, most species were quite responsive to precipitation and temperature germination cues. On the other hand, STGL had much lower germination in later cohorts, instead waiting until the following fall to germinate in warmer temperatures, indicating that appropriate cues may not have been available in later cohorts of the first year. Such patterns can be achieved through secondary dormancy, which can prevent germination under unfavorable conditions and must be released under favorable conditions in subsequent years (Finch-Savage & Footitt, 2017; Hawkins et al., 2017; Probert, 2000; Walck et al., 2011). In contrast, three *Caulanthus* species had similar low germination fractions regardless of the timing of rainfall onset or corresponding temperatures. Low germination across conditions is consistent with bet-hedging strategies to spread germination across years, particularly in harsh and temporally variable environmental conditions (Cohen, 1966; Gremer & Venable, 2014; Venable, 2007). Together, these patterns suggest that a range of germination strategies have evolved along the phylogeny to mitigate the negative consequences of reduced germination for fitness.

Overall, our findings shed further light on the sensitivity of germination, a key life history transition in plant life cycles, to changing temperature and precipitation, and suggest responses have evolved as the clade diversified into different climatic conditions. While populations were chosen for their approximate central location within climate space for their species, as well as availability of seed from naturally occurring populations, a caveat is that these represent one to two populations per species. Indeed, our study trades-off replicating populations within species for comparing species across the clade; however, we can still infer some species-level properties. For instance, a population of CAAN (CAAN2) and a population of CAIN (CAIN3) were collected from the same field location (Appendix S1: Table S1), but each of these populations responded more similarly to the other conspecific population of its species than to the population of the other species collected at the same locality (Figures 3 and 4). Moreover, one would be unlikely to detect phylogenetic signal in germination properties if intra- and interspecific variations were similar (Pearse et al., 2020). Our focus on precipitation in this study may be viewed as a limitation since we did not manipulate other germination cues such as temperature, photoperiod, or chilling (Baskin & Baskin, 2014). However, this dynamic allowed for a more realistic understanding of how later rainfall onset will affect germination in the field where other germination cues are variable. We are complementing our understanding gained in this study with controlled environment experiments to dissect specific cues for germination among these species.

Mismatches of phenology with environmental conditions are known to have major implications for population persistence and species dynamics across a range of organisms (Abrahms et al., 2022; Bernhardt et al., 2020; Gremer et al., 2020a; Levine et al., 2011; Samplonius et al., 2016). Together, our results support previous work highlighting how climate change is creating mismatches between formerly adaptive cues and optimal seasonal conditions (Bernhardt et al., 2020; Lindén, 2018; McNamara et al., 2011). In particular, our results underscore the importance of temperature in mismatched responses and allow us to identify which species may be more sensitive to current and future shifts associated with climate change. The next critical steps are to link these responses with fitness and population dynamics, using experiments, demographic data, and process-based models that can predict life cycle timing in response to current and future climates (Burghardt et al., 2015; Hamann et al., 2021; Huang et al., 2016). These directions are vital to further our understanding of how climate factors impact life history timing and scale to affect population persistence and species distributions.

AUTHOR CONTRIBUTIONS

Jennifer R. Gremer, Johanna Schmitt, Sharon Y. Strauss, and Julin N. Maloof conceived and designed the study. Arquel Miller, Eda Ceviker, Sarah R. Ashlock, and Johanna Schmitt performed the experiment, with help from Jennifer R. Gremer and Sharon Y. Strauss in data collection. Samantha J. Worthy, Jennifer R. Gremer, Sharon Y. Strauss, and Johanna Schmitt designed the data analyses. Samantha J. Worthy and Jennifer R. Gremer analyzed the data with assistance from Johanna Schmitt, Sharon Y. Strauss, Arquel Miller, Sarah R. Ashlock, and Eda Ceviker. Samantha J. Worthy, Jennifer R. Gremer, Arquel Miller, and Johanna Schmitt wrote the manuscript with contributions from all other authors. All authors contributed to the development of ideas, analyses, and interpretation of results.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Worthy, 2024) are available on Zenodo at https://doi.org/10.5281/zenodo.12753087.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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