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Studies

Seeds of change: trait shifts over time in wild plant populations revealed using *ex situ* Seeds of Success collections

Laura C. Shriver [1]*, **Sarah C. Barga** [2], **Elizabeth A. Leger** [1]

[1]Ecology, Evolution, & Conservation Biology, University of Nevada Reno, 1664 N. Virginia Street, Reno, NV 89557, United States
[2]USDA Forest Service, Rocky Mountain Research Station, RMRS Shrub Science Lab, 1770 Kitty Hawk Drive, Cedar City, UT 84721, United States
*Corresponding author. Ecology, Evolution, & Conservation Biology, University of Nevada Reno, 1664 N. Virginia Street, Reno, NV 89557, USA. E-mail: lcshriver@gmail.com

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Abstract

Seed banking supports conservation, but freshly collected and stored seed may differ in important characteristics. Our resurrection study assessed differences in seedling traits from stored and fresh populations of six native plant species in the Great Basin, where invasive annual grasses increase fire frequency to the detriment of native plants. We evaluated stored seed collected through the Seeds of Success programme and contemporary re-collections from the same population 3–11 years later, including sites that burned between collection dates and paired, unburned sites. We sowed seeds in a common garden and measured differences in seed mass, emergence (timing and total), survival, and multiple size traits. We observed temporal changes in trait means for at least one trait in every species irrespective of burn history. The direction of change varied among species, and very few traits changed in variance. Seed mass and emergence traits changed most frequently (12 of 17 measures changed over time), with fewer changes in mortality and size traits (6 of 24). Changes may reflect sampling, ageing, or maternal effects, or changes in gene frequency from drift or natural selection. Evidence consistent with adaptive evolutionary response to disturbance was observed in *Elymus elymoides*, with burned sources shifting towards smaller plant size and earlier emergence, with lower variance. Regardless of cause, widespread differences in seed and seedling traits between wild populations and seed banked seeds provide support for continued seed banking efforts, as intra-population phenotypes often differ between *ex situ* seed collections and *in situ* wild populations.

Keywords fire, Great Basin, native plants, rapid evolution, resurrection study

Introduction

Seed banking supports native plant conservation (Schoen and Brown 2001, Guerrant et al. 2004, Pritchard et al. 2014), but traits in *ex situ* collections may diverge from their original *in situ* source population (Franks et al. 2008, 2018, Etterson et al. 2016). For *ex situ* populations, divergence can stem from initial sampling effects and storage effects (Franks et al. 2018, Weis 2018). Sampling effects occur when seeds are non-randomly collected across phenotypes, space, and time (Franks et al. 2018, Weis 2018). Storage can shift traits via maternal effects, plastic responses to storage conditions, or non-random mortality reducing phenotypes relevant to survival during storage and associated traits (Franks et al. 2018, Weis 2018, Pennington et al. 2026). Meanwhile, *in situ* populations phenotypes or gene frequencies may shift over time through maternal effects or evolutionary change (Hamilton 1994, Franks et al. 2018, Braasch et al. 2021). Assessing trait divergence can inform seed banking strategies, especially in an era of widespread anthropogenic change where *in situ* populations may undergo rapid evolution in response to environmental pressures that *ex situ* populations do not face (Franks et al. 2018). For instance, competition with invasive plants may exert selection pressures and prompt rapid evolutionary response in some native plant populations (Strauss et al. 2006, Oduor 2013, Brafford et al. 2021). If divergence between *ex situ* and *in situ* populations is widespread, seed banking strategies may need to incorporate repeated visits to extant populations to accurately represent wild plant trait variation (Hoban et al. 2020).

Resurrection studies that grow past and contemporary seeds from the same population in a common garden are a key method to assess trait divergence and change over time (Franks et al.

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2018, Pennington et al. 2026). These studies have revealed temporal changes in flowering phenology, size, and mating system in crop weeds (Cheptou et al. 2022); changes in leaf morphology in response to drought (Anstett et al. 2021); and potential rapid adaptation within populations of invasive plants in their new ranges (Whitney and Gabler 2008, Sultan et al. 2013, Hernández et al. 2019). A recent synthesis found phenotypic change in almost every resurrection study conducted on flowering plants (50 out of 52 reviewed studies), for just over 50% of measured traits (Pennington et al. 2026). These results suggest that rapid evolution is common in plants, particularly for annuals, which demonstrated greater, more rapid temporal change and were more studied than perennials (Pennington et al. 2026). Furthermore, changes were adaptive across many studies and thus consistent with rapid evolution in response to natural selection, such as the evolution of earlier phenology, which may be an adaptive response to drought (Franks et al. 2008, Weis et al. 2014, Pennington et al. 2026). However, genetic drift can also prompt rapid, sometimes maladaptive evolutionary change, particularly in small populations or via population bottlenecks (Jump and Peñuelas 2005, Pennington et al. 2026).

Resurrection studies are a potentially powerful tool to examine temporal trait change, including in seed banking programmes (Mattana et al. 2025). However, it can be challenging to determine whether trait shifts result from maternal effects, storage effects, or evolutionary change (Franks et al. 2018, Weis 2018, Pennington et al. 2026). Growing a 'refresher generation' of past and contemporary seed collections together is a common strategy to reduce maternal and storage effects (Franks et al. 2018, Pennington et al. 2026, Sheth et al. 2026). However, this can be difficult for perennial species with slower reproduction timelines than annuals: indeed, while ∼80% of resurrection studies on annual species include a refresher generation, ∼60% of studies on perennials or multiple species with mixed longevity do not (Pennington et al. 2025). Additionally, resurrection studies alone cannot determine evolutionary mechanisms, but complementary genetic, experimental, or observational studies can help identify cause(s) (i.e. adaptive natural selection, gene flow, or genetic drift, Franks et al. 2018, Pennington et al. 2026). For instance, a resurrection study with populations collected across a range of drought severity paired with a water limitation experiment revealed evidence of rapid evolution in traits associated with drought avoidance that occurred only in populations that had experienced severe drought (Anstett et al. 2021). It is also possible to infer adaptive natural selection by examining trait change in light of known environmental changes and evolutionary patterns (Franks et al. 2018). In observational studies, stronger trait shifts in regions that have experienced greater environmental change could suggest natural selection (i.e. trait shifts correlated with drought intensity suggesting drought as a selective agent, Rauschkolb et al. 2023). Similarly, trait shifts towards earlier phenology could be consistent with natural selection in response to climatic warming, as advanced phenology appears common across experimental warming studies (Stuble et al. 2021), observational studies (Cleland et al. 2007, Thackeray et al. 2016), and resurrection studies inferring natural selection in response to climate change (Pennington et al. 2026). Further evidence for trait change driven by directional selection include shifts in trait means along with decreases in trait variance (Franks et al. 2018, Bishop et al. 2023). Despite uncertainty over the causes of trait changes in some resurrection studies, especially with perennial plants, conducting such studies is important to understand the changes in phenotypic diversity between *ex situ* and *in situ* populations, and contribute to a broader understanding of trait change in wild plants.

We used a resurrection study to explore trait shifts between *ex situ* and *in situ* populations of six widespread native plant species in the Great Basin USA, an area of intense environmental change, restoration, and seed banking activity (Pilliod et al. 2017, 2021, Barga et al. 2020). The spread of flammable invasive annual grasses (including *Bromus tectorum* L.) across the Great Basin fuels a positive feedback cycle in which increased wildfire size and frequency transforms native shrubland habitats into invasive-dominated grasslands (Svejcar et al. 2017, Fusco et al. 2019, Pilliod et al. 2021, Strand et al. 2025). The combination of altered fire regimes and intense competition from invasive annual grasses displaces native plants, many of which have difficulty recovering after fire, especially when fires are repeated (Pilliod et al. 2021). There is evidence that some populations of 'remnant' native plants may have undergone rapid adaptive evolution in response to strong selection pressures, allowing them to persist in invaded, burned, and altered Great Basin landscapes (Leger 2008, Goergen et al. 2011, Rowe and Leger 2011, Leger and Goergen 2017). If these populations harbour beneficial adaptations, they could be managed to preserve *in situ* diversity, protected from gene flow and outcrossing with non-local and non-adapted genotypes, and targeted as seed sources for restoration (Leger 2008, Leger and Espeland 2010). The latter approach may be of particular interest to land managers, as large-scale post-fire restoration is frequently implemented in the Great Basin, often with limited success (Pilliod et al. 2017, Svejcar et al. 2017), but could potentially benefit from prioritizing seed sources that are locally adapted to contemporary environmental stressors (Leger and Baughman 2015, Baughman et al. 2019, Leger et al. 2024).

We investigated change over time using *ex-situ* seeds sources from the Seeds of Success (SOS) programme, a Bureau of Land Management (BLM)-led effort which has been collecting and storing seeds from the Great Basin since 2000 (Haidet and Olwell 2015). Over 600 SOS sites have burned since collection (Barga et al. 2020), creating a unique opportunity to re-collect seeds and ask if fire affects trait change over time. Using a paired framework, we compared plant traits within populations collected before (past) and after fires (contemporary), along with sites collected in similar timeframes that had not burned in over 20 years. Our objective was to assess trait change in *ex situ* and *in situ* populations, and ask if divergent fire history affected change. We asked: (i) Have plant traits (means and variance) diverged between past and contemporary collections? (ii) Does change over time differ between burned and unburned populations?

We hypothesized that fire could alter the evolutionary trajectory of native plants via natural selection or genetic drift associated with a sudden reduction in population size. Accordingly, we expected trait means to shift in potentially adaptive directions and trait variance to decrease over time in burned populations, indicative of directional selection (Bishop et al. 2023) reducing or eliminating genotypes that were not favoured in burned landscapes. Alternatively, decreases in trait variance without shifts in

trait means over time could indicate stabilizing selection towards an adaptive trait mean (Franks et al. 2018). Given the association between invasive annual grasses and fire, we expected to see shifts in burned populations towards traits that are potentially adaptive for native Great Basin plants growing in invaded and disturbed environments (Leger and Baughman 2015). These include earlier emergence, which is associated with seedling survival in invaded Great Basin environments (Kulpa and Leger 2013, Leger et al. 2019, Ploughe et al. 2020, Agneray et al. 2022); larger seed mass, which is sometimes associated with increased survival in the Great Basin (Kulpa and Leger 2013, Leger et al. 2019, Agneray et al. 2022) and drylands globally (Shackelford et al. 2021); and smaller plant size, which may be associated with increased survival and competitive abilities in the Great Basin (Goergen et al. 2011, Kulpa and Leger 2013). Conversely, consistent trait shifts regardless of burn status across species could suggest selection from a global actor, such as climate change, or indicate that strong maternal effects are driving change over time. While we hypothesized that temporal trait changes would be driven by rapid evolution due to selection or drift, we cannot rule out the possibility that differences in seed collection techniques, seed storage conditions/duration, or maternal effects could result in trait change, and we consider all of these potential mechanisms in our interpretation.

Methods

Source populations and site characteristics

We studied six species—three forbs and three grasses—native to Great Basin sagebrush ecosystems: *Chaenactis douglasii* (Hook.) Hook. and Arn., *Elymus elymoides* (Raf.) Swezey, *Erigeron linearis* (Hook.) Piper, *Poa secunda* J. Presl, *Pseudoroegneria spicata* (Pursh) Á. Löve, and *Sphaeralcea grossulariifolia* (Hook. and Arn.) Rydb. We chose species that were present in burned and unburned sites and for *E. elymoides* and *P. secunda*, were examined in previous trait research in the Great Basin (Leger and Baughman 2015, Leger et al. 2021). Forbs were perennials (*E. linearis* and *S. grossulariifolia*) or annual, biennial, or short-lived perennial (*C. douglasii*). *Chaenactis douglasii* is mostly outcrossing (Cane et al. 2012), *E. linearis* has an unknown mating system but its importance to pollinators implies some degree of outcrossing (Gucker and Shaw 2019), and *S. grossulariifolia* is strongly outcrossing and possibly self-sterile (Gucker and Shaw 2024a). Grasses were perennials and self-pollinating (*E. elymoides*, Jones 1998), self-pollinating or apomictic (*P. secunda*, Kellogg 1987, Kelley et al. 2009), or outcrossing (*P. spicata*, Bradley St. Clair et al. 2013).

Each species had a paired burned and unburned population (Table 1). We determined burn status using GIS fire perimeters (National Interagency Fire Center (NIFC) 2025), selecting unburned populations that had not burned since 1995, and burned populations that burned after their initial SOS collection date. We focused on fires occurring in 1995 and later due to improvements in tools for measuring fire perimeters in the early 90s and to allow at least 15 years between the last fire and seed collection for unburned populations. We matched burned–unburned pairs by Level III Ecoregions (Environmental Protection Agency (EPA) 2025), geographic distance, and past collection dates (Table 1). We retrieved 30-year climate normals (1991–2020) for each site (PRISM Climate Group 2014), and burned sites were generally warmer and drier than unburned sites (except for *P. secunda* and *S. grossulariifolia*, Table 1).

From this experimental design, each population had two types of seed: past seed collected through SOS and obtained via the Germplasm Resources Information Network (ars-grin.gov) and contemporary seed collected in 2020–2021 in Nevada, Oregon, and Idaho (Table 1, Supplementary Table S1, Fig. 1). Both collections followed the SOS protocol, including collecting from at least 50 plants, recording the approximate number of plants collected and found (Supplementary Table S2), and pooling seed within the population (i.e. not separating seed by maternal lines, Bureau of Land Management (BLM) 2023). Contemporary collections were generally smaller than past collections, but we sampled randomly and equally across the entire population when feasible (following SOS protocol, BLM 2023), or within 100 m of the collection's GPS point for large populations (Supplementary Table S2). While the SOS protocol recommends collecting seed throughout the dispersal season (BLM 2023), most past collections were made during a single visit in June or July, and contemporary collections were made during a single visit in June (during 2020, 2021, or both years, Table 1, Supplementary Table S2). We collected plant cover data at each site following a modified version of the rangeland Assessment, Inventory, and Monitoring programme protocol (Herrick et al. 2017). Specifically, we recorded vegetation types intersecting a pin flag dropped every paced metre along three 50-m transects radiating from the collection GPS point at 0°, 120°, and 240°. We recorded vegetation by habit (shrub, perennial or annual forb or grass) combined with native status (native or non-native). We also recorded *Bromus tectorum* L. cover at the species level as we were interested in its relationship to burn status and trait change, but still included it in the non-native and non-native annual grass categories (along with less common non-native annual grasses *Bromus racemosus* L., *Taeniatherum caput-medusae* L., and *Vulpia bromoides* L., Supplementary Table S2).

Greenhouse planting

We grew four sources per species (burned/unburned + past/contemporary) in a common greenhouse environment at the Valley Road Greenhouse Complex in Reno, Nevada. We grouped species and randomized sources within to accommodate different planting times and watering needs. We watered plants daily during emergence, then biweekly once seedlings were established. Greenhouse temperatures fluctuated with ambient conditions, with greenhouse controls set to 2–20°C in winter/early spring and up to 25°C in late spring/summer. We planted 100 pots per source with 2–3 contemporary seeds or one past seed per pot, as we had more contemporary than past seed. We randomly thinned pots with multiple seedlings 3 days after the last seedling emerged. We directly seeded the grasses (*E. elymoides*, *P. secunda*, *P. spicata*) and *E. linearis* into pots without treatment. We scarified then stratified *S. grossulariifolia* seeds at 3.8°C for 15 days (Dunn 2011), then transplanted seeds (most of which germinated) into

Table 1 Collection location information for each species, population (represented by burn status), year burned (from 1995 to 2021, NIFC 2025), Level III Ecoregion (EPA 2025), the distance between paired sites, mean annual precipitation (MAP) and mean annual temperature (MAT, both; 30-year normals from, 1990–2020, PRISM Climate Group 2014), elevation, past and contemporary (contemp.) collection years, the difference in past/contemporary collection years, and number of years between fire(s) and contemporary collection years.

Species	Burn status	Year burned	Ecoregion (Level III)	Distance apart (km)	MAP (mm)	MAT (°C)	Elevation (m)	Past collection year	Contemp. collection year	Years between collections	Years between fire and contemp. collection
C. douglasii	Burned	2015	Snake River Plain	88.8	228.8	11.6	739	2011	2021	10	6
C. douglasii	Unburned	NA	Snake River Plain	—	398.9	10	968	2013	2021	8	—
E. elymoides	Burned	2015	Northern Basin and Range	201.8	253.1	10	1164	2015	2020	5	5
E. elymoides	Unburned	NA	Northern Basin and Range	—	361.5	8.9	1567	2017	2020	3	—
E. linearis	Burned	2012	Northern Basin and Range	53.5	410.5	8.5	1963	2012	2021	9	9
E. linearis	Unburned	NA	Northern Basin and Range	—	469.2	8.3	1932	2016	2021	5	—
P. secunda	Burned	2015	Northern Basin and Range	94.4	346.3	8.5	1292	2011	2021	10	6
P. secunda	Unburned	NA	Northern Basin and Range	—	300.5	9.1	1394	2011	2021	10	—
P. spicata	Burned	2015	Northern Basin and Range	194.9	253.1	10	1164	2015	2020	5	5
P. spicata	Unburned	NA	Northern Basin and Range	—	318.6	9.8	1512	2016	2020	4	—
S. grossulariifolia	Burned	2015	Snake River Plain	24.9	244.1	10.3	841	2015	2020 and 2021	3–4	5–6
S. grossulariifolia	Unburned	NA	Snake River Plain	—	232.0	10.3	1032	2017	2020 and 2021	5–6	NA

The past collection year and year burned are the same for several species, but the past seed collections were completed before each fire occurred. Additional information on population locations, fire history, population and collection size, and seed collection timing can be found in Supplementary Table S1.

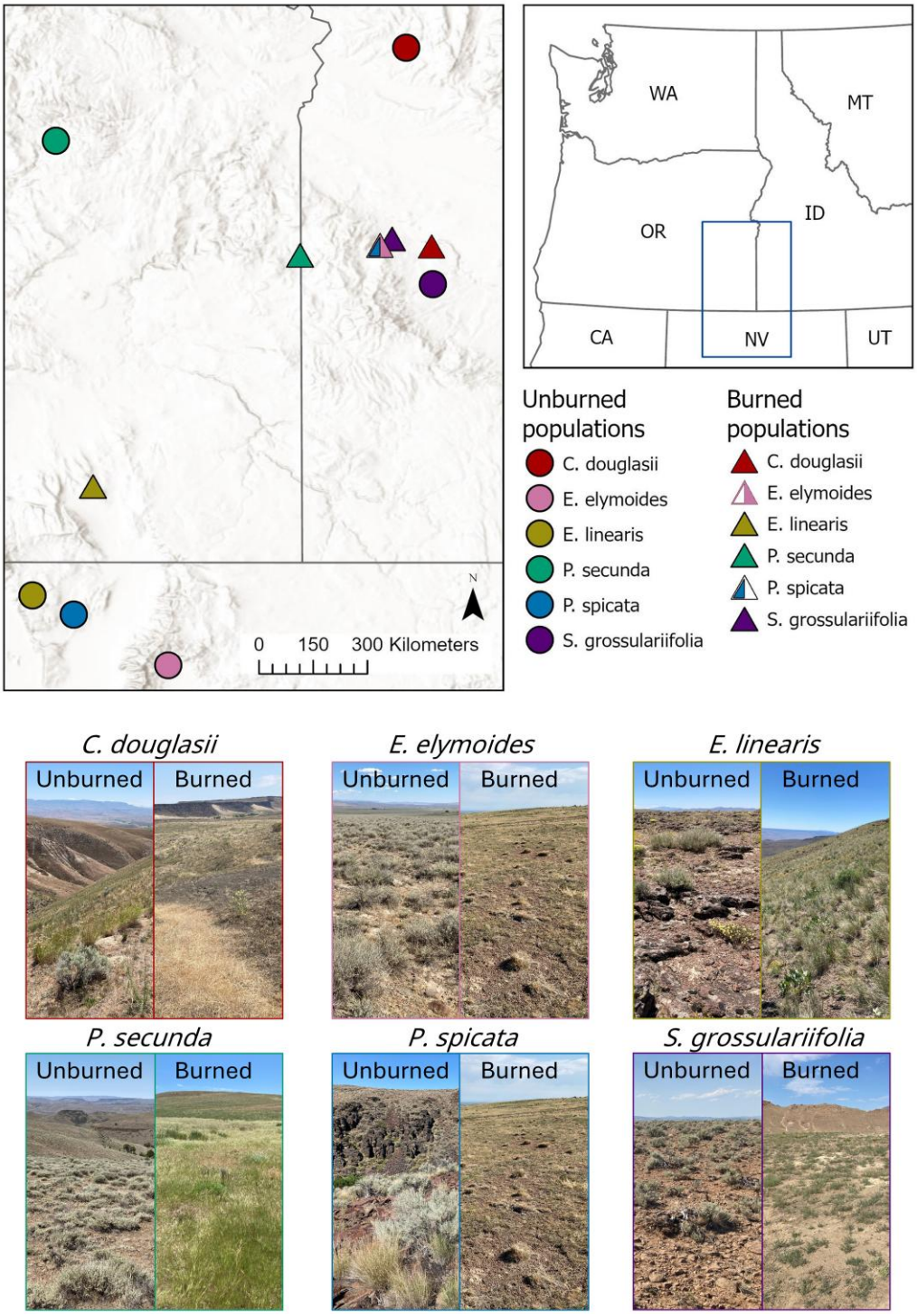

Figure 1 Seed collection site locations and photos for our six study species in Oregon, Idaho, and Nevada. Site locations are colour-coded by species and unburned sites are represented by circles while burned sites are represented by triangles. The triangle with two colours represents the *P. spicata* and *E. elymoides* burned populations that were collected from the same location. Collection site photos show the unburned site on the left, and burned site on the right, for each species.

pots. We also stratified *C. douglasii* seeds at 3.8°C for 30 days before planting (Gucker and Shaw 2024b). We planted seeds in 6.3 cm × 25.4 cm pots (Heavyweight Deepot Cells, Stuewe and Sons, Inc.) with 33% decomposed granite and 67% topsoil (mixed) in February (or March 2021 after stratification for *C. douglasii*) then harvested plants in September 2022.

Data collection

We were unable to grow a refresher generation as few plants produced seed within our study timeframe, so traits were measured from initial seed collections (seed mass) or plants grown from initial seed (other traits). Before planting, we weighed seed mass to

0.1 mg from 10 lots of 5 randomly chosen seeds. In the greenhouse, we recorded total emergence, emergence timing, mortality, height, leaf number, and collected aboveground biomass. We assessed total emergence and emergence timing using all planted seeds, including seeds that were thinned if multiple seeds germinated per pot. Other responses (mortality, height to 0.1 cm, leaf number, and aboveground biomass to 0.1 mg) were recorded only for plants that emerged and were not thinned. We recorded emergence and mortality daily for 4 weeks after planting (from the week of March 14–25 April 2022 for *E. elymoides*, *E. linearis*, *P. secunda*, *P. spicata*, and *S. grossulariifolia*, or from April 23–3 June 2022 for *C. douglasii*) then biweekly for the remainder of the experiment. We measured height from the soil to the tallest part of any green plant structure and leaf number as the total number of green leaves per plant. We recorded height and leaf number the week of 26 September 2022. Aboveground biomass was harvested at the soil surface the week of 2 October 2022, dried in an oven at 40°C for 5 days, and weighed in October and November 2022.

Data analysis

We analysed data with R version 4.4.0 (R Core Team 2024) and based significance on $P < 0.05$ for analyses, but also present and discuss differences of $P < .10$ for some metrics. We calculated Pearson correlation coefficients to assess association among sets of traits measured per plant (emergence timing, height, leaf number, and aboveground biomass), and all correlations were under 0.65 with most under 0.50, so we consider and present traits as independent variables.

First, we asked whether plant community composition differed between burned and unburned sites, comparing the per cent cover of aggregated native and non-native species, non-native annual grasses, and *B. tectorum*. We used mixed linear models to determine how burn status, species, and their interaction affected per cent cover with transect number as a random effect (model: lmer(cover ~ burn * species + (1|transect)). We assessed the distribution of residuals (visually through Q–Q plots and histograms), then log transformed *B. tectorum* per cent cover (with a small constant added to each 0 value) to meet assumptions of normality. We calculated test statistics and *P* values using Wald analysis of deviance tests with the R package 'car' (Fox and Weisberg 2019), then used post-hoc Tukey tests with the R package 'emmeans' (Lenth 2025) to examine pairwise differences between burned and unburned collection sites for each species.

Next, we asked how trait averages and variance differed between past to contemporary sources and if the direction or magnitude of change over time differed between burned and unburned populations. We initially included species identity in models and found significant species effects, and for most trait interactive species effects with time (Supplementary Table S3), so we ran separate models per species, using each plant as an independent replicate. Ideally, we would have included multiple burned and unburned sites per species to enable generalization beyond our study sites, but we were constrained by past collection locations so such replicates were not possible with these species in this region.

For trait averages, we used generalized linear (or generalized linear mixed) models with data-specific distributions to account for non-normally distributed residuals that were not improved by transformation. For emergence traits, we used generalized linear mixed models to determine how burn status, time, and their interaction affected trait averages with pot number as a random effect (models: glmer(trait ~ burn * time + (1|pot_number)). We analysed total emergence as binary values on a per-seed basis with a binomial distribution and emergence timing as count data (number of days to emergence) with a negative binomial distribution to account for overdispersion. We did not analyse emergence timing for *S. grossulariifolia* because seeds germinated rapidly during cold stratification. We analysed non-emergence traits with generalized linear models to determine how burn status, time, and their interaction affected trait averages (models: glm(trait ~ burn * time). We analysed mortality as binary values on a per-plant basis with a binomial distribution, leaf number as count data (number of leaves) with a negative binomial distribution to account for overdispersion, and seed mass, height, and aboveground biomass with generalized linear models with Gamma distributions. We do not present figures for leaf number or aboveground biomass as there was little variation among sources. We calculated test statistics and *P* values using Wald analysis of deviance tests with the R package 'car' (Fox and Weisberg 2019). For trait variance, we performed Levene's Test for Homogeneity of Variance to assess trait variance changes from past to contemporary sources for each burned and unburned population per species (excluding total emergence and mortality). We use standard error to represent variance in the results and figures.

Results

Source population community composition

The per cent cover of native species, non-native species, non-native annual grasses, and *B. tectorum* was significantly affected by burn status (native: $\chi 21 = 44.45$, $P < .0001$; non-native: $\chi^2_1 = 28.17$, $P < .0001$; non-native annual grasses: $\chi^2_1 = 5.73$, $P < .05$; *B. tectorum*: $\chi^2_1 = 50.94$, $P < .0001$), species (native: $\chi^2_1 = 98.62$, $P < .0001$; non-native: $\chi^2_1 = 22.75$, $P < .001$; non-native annual grasses: $\chi^2_1 = 31.10$, $P < .0001$; *B. tectorum*: $\chi^2_1 = 72.03$, $P < .0001$), and the burn by species interaction (native: $\chi^2_1 = 124.70$, $P < .0001$; non-native: $\chi^2_1 = 39.40$, $P < .0001$; non-native annual grasses: $\chi^2_1 = 44.85$, $P < .0001$; *B. tectorum*: $\chi^2_1 = 92.65$, $P < .0001$, Supplementary Table S4). There were significant species effects and species by burn status interactions for all cover responses (Supplementary Table S4), indicating that while burned sites had overall higher cover of non-native species (18 percentage points higher) and lower cover of native species than unburned sites (17 percentage points lower, Supplementary Table S4, Fig. 2), the strength of these effects differed among species pairs (Supplementary Tables S4 and S5, Supplementary Figure S1). A post-hoc analysis found that neither *B. tectorum* nor total invasive annual grass cover predicted the magnitude nor direction of trait change in native plants over time, so we continued analysing burn/unburned as binary factors.

Overview of trait change

We saw significant change over time from past to contemporary sources for at least one trait mean in every species, while trait

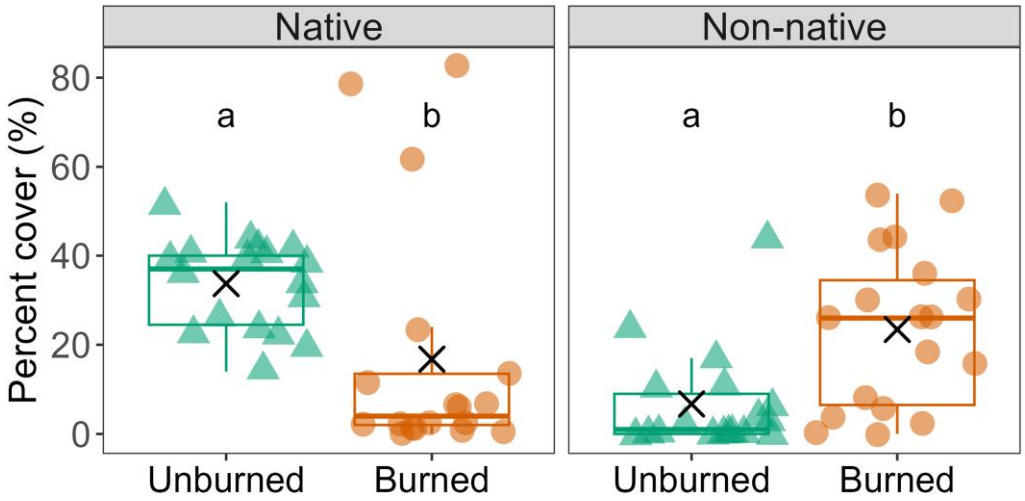

Figure 2 Density (per cent cover) of native and non-native plants by burn status across seed collection sites. Boxes represent the interquartile range with whiskers representing upper and lower quartiles; the horizontal line inside each box represents the median; 'X' symbols represent the mean; and points represent average cover per transect (three transects per site across six unburned and six burned sites). Different letters within panels represent significant differences in cover ($P < .05$) between the burned and unburned populations (Supplementary Table S4).

Table 2 Overview of significant mean trait differences between burned and unburned populations (B), change over time (T), time by burn interactions (BxT), and trait variance change over time in the burned (VB) or unburned (VU) populations for our six study species; full statistical results are reported in the text and supplement (Supplementary Tables S2, S5, S6).

Species	Seed mass	Total emergence	Emergence timing	Mortality	Height	Leaf number	Aboveground biomass
C. douglasii		T		B			
E. elymoides	B, T, BxT, VU		T, **B**xT, VB		T		B
E. linearis	T, **B**xT	B	T	T			B
P. secunda	T, BxT	B, T, BxT	T	**B**xT	BxT		
P. spicata	B, T		T		B		
S. grossulariifolia	B, T	B, **B**xT	—	T	BxT		VU

A bold 'B' in BxT interactions indicates that change was stronger in burned populations, as we predicted. Traits include seed and seedling traits (seed mass, total emergence, and emergence timing), mortality, and size traits (height, leaf number, and aboveground biomass). A dash (–) indicates that the trait was not measured or analysed for that species. Trait variance was not measured for total emergence or mortality.

variance remained similar for all species except *E. elymoides* and *S. grossulariifolia* (Table 2, Supplementary Tables S6 and S7). Changes in trait means were concentrated in seed and seedling emergence stages (12 of 17 seed and seedling emergence measures changed over time) with fewer changes in mortality, height, leaf number, or aboveground biomass (6 of 24 mortality and size traits changed over time; Table 2). The magnitude or direction of changes in trait means over time differed among species (Figs 3, 4, 5) and sometimes differed between burned and unburned populations (indicated by a significant burn by time interaction), particularly for *P. secunda* and *E. elymoides* (Table 2).

Seed mass

Seed mass changed significantly over time for five of six species (*E. elymoides*: $\chi^2_1 = 4.28$, $P < .05$; *E. linearis*: $\chi^2_1 = 9.58$, $P < .01$, *P. secunda*: $\chi^2_1 = 59.24$, $P < .0001$, *P. spicata*: $\chi^2_1 = 30.42$, $P < .0001$, *S. grossulariifolia*: $\chi^2_1 = 9.07$, $P < .01$, Table 2, Supplementary Table S6), though the direction of change differed among species (Fig. 3a). Burn status influenced change for three species (burn × time interactions; *E. elymoides*: $\chi^2_1 = 6.88$, $P < .01$, *E. linearis*: $\chi^2_1 = 5.65$, $P < .05$, *P. secunda*: $\chi^2_1 = 4.16$, $P < .05$, Table 2, Supplementary Table S6). *Erigeron linearis* and *P. secunda* seed mass decreased over time, and this decrease was stronger in the *E. linearis* burned population (0.13 ± 0.00 mg decline in average seed mass) than unburned population (0.02 ± 0.00 mg decline) and stronger in the *P. secunda* unburned population (0.27 ± 0.00 mg decline) than burned population (0.19 ± 0.01 mg decline, Fig. 3a). *Elymus elymoides* seed mass averages and variance decreased over time in the unburned population (0.36 ± 0.02 mg decline, $F_{1,28} = 4.30$, $P < .05$), while changing little in the burned population (0.07 ± 0.03 mg increase, Fig. 3a, Supplementary Table S7). *Pseudoroegneria spicata* and *S. grossulariifolia* seed mass increased over time regardless of burn status (Fig. 3a).

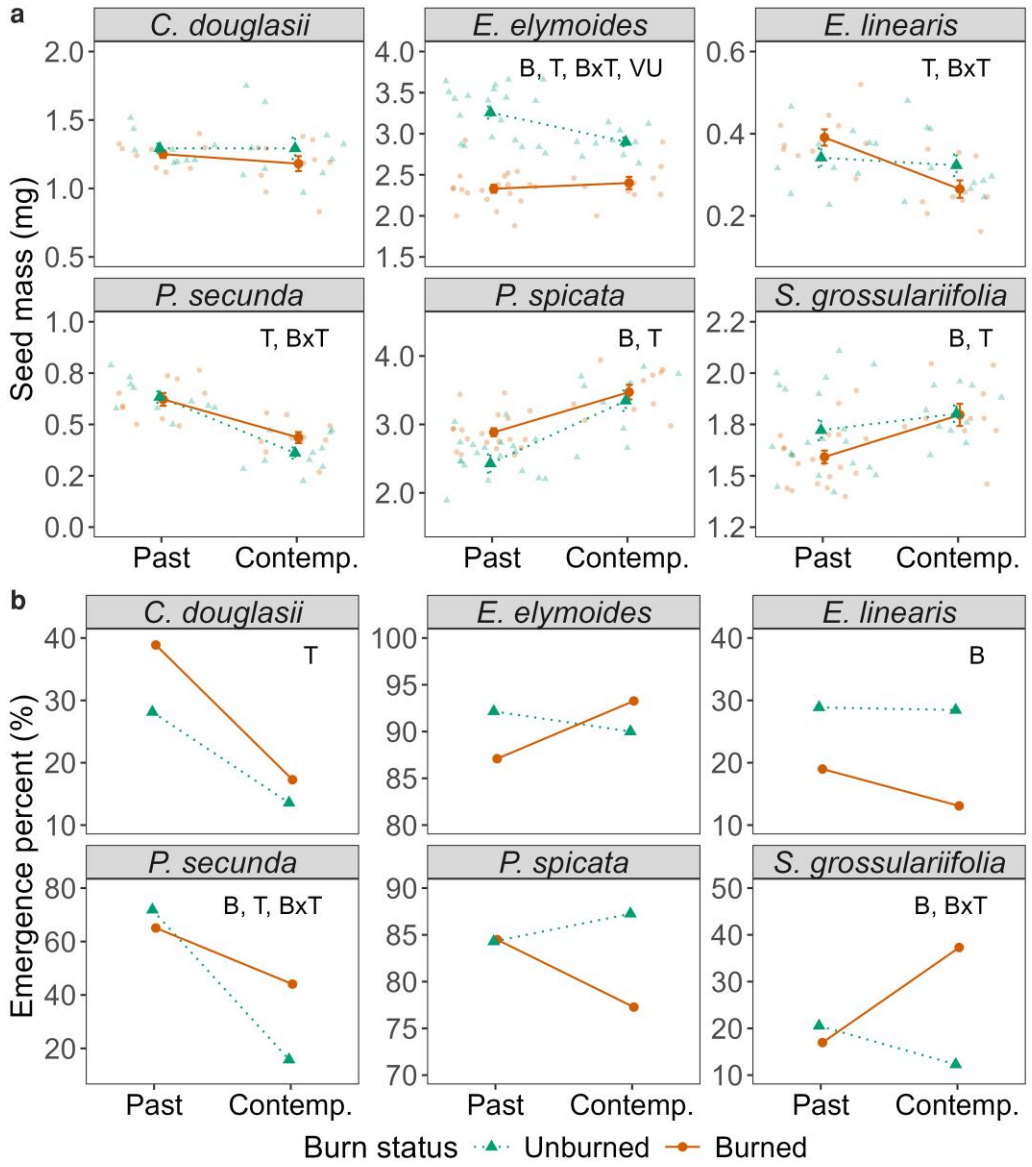

Figure 3 Trait change over time for burned and unburned populations of each species for seed and seedling traits: a: seed mass (of one seed) in milligrams and b: emergence per cent. The *x* axes represent time from past to contemporary (contemp.) populations and the *y* axes represent trait values. The y axes differ among species to clearly visualize within-species change over time. Burned populations are represented by red circles and solid lines while unburned populations are represented by blue triangles and dashed lines. Error bars represent standard error and are not included in the plots for emergence per cent as points represent exact values. Letters within each graph represent significant mean trait value change over time (T), time by burn interactions (BxT), and trait variance change over time in the burned (VB) or unburned (VU) population. Table 2.

Total emergence

Emergence was higher for grass species (*E. elymoides*: 91%, *P. secunda*: 44%, *P. spicata*: 83%) than for forbs (*C. douglasii*: 23%, *E. linearis*: 22%, *S. grossulariifolia*: 22%). For three of six species, emergence changed significantly over time, with a significant main effect of time (*C. douglasii*: $\chi^2_1 = 10.70$, $P < .01$), a significant burn by time interaction (*S. grossulariifolia*: $\chi^2_1 = 11.99$, $P < .001$), or both (*P. secunda* time: $\chi^2_1 = 26.35$, $P < 0.0001$; burn by time: $\chi^2_1 = 11.10$, $P < .001$, Table 2, Supplementary Table S6). The direction of change was not consistent across species or by burn status, though generally the past collections had higher emergence than contemporary (Fig. 3b). Contemporary *C. douglassii* seeds had lower emergence than past seeds, regardless of burn status (20 percentage points lower, Fig. 3b). For *P. secunda*, contemporary emergence was also lower than past emergence, and this difference was greater in the unburned population (56 percentage points lower) than the burned (21 percentage points lower, Fig. 3b). For *S. grossulariifolia*, emergence increased over time in the burned population (20 percentage points greater), while the unburned population had similar past and contemporary emergence (Fig. 3b).

Emergence timing

Emergence timing differed significantly between past and contemporary sources for four of five species, with a significant effect of

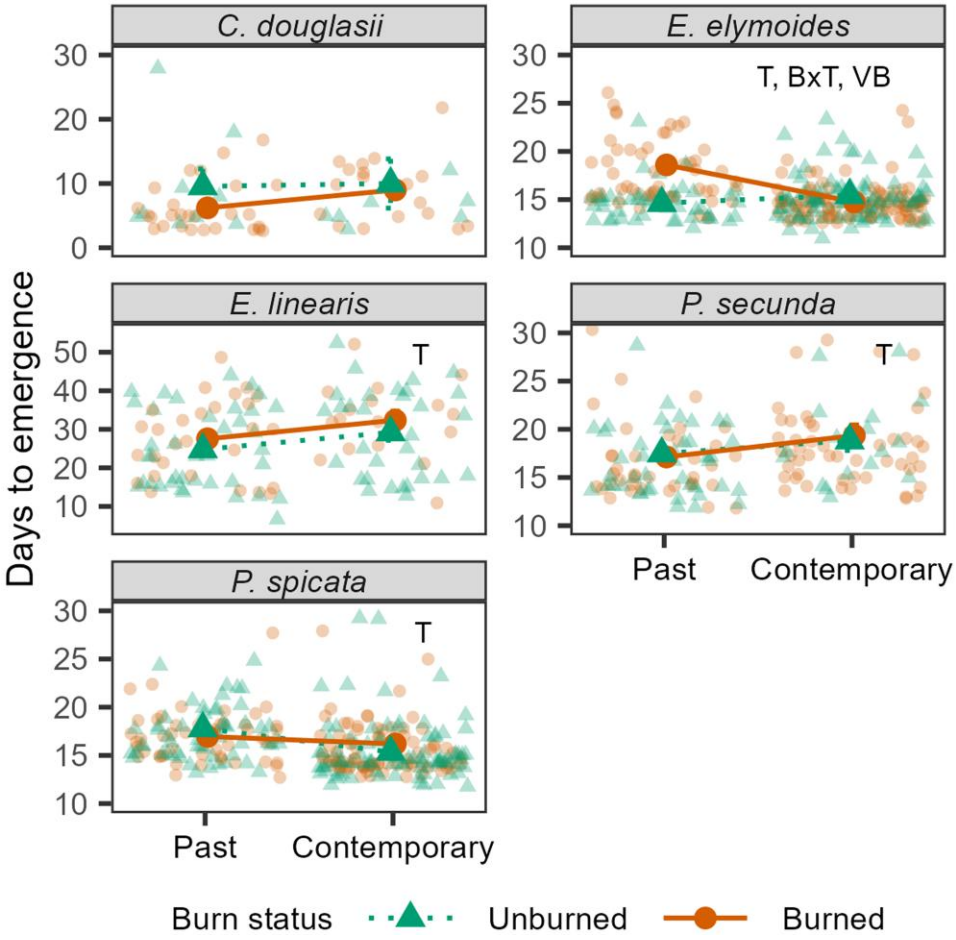

Figure 4 Trait change over time for burned and unburned populations of each species for emergence timing (days to emergence). The x axes represent time from past to contemporary populations and the y axes represent trait values. The y axes differ among species to clearly visualize within-species change over time. Burned populations are represented by red circles and solid lines while unburned populations are represented by blue triangles and dashed lines. Error bars represent standard error. Letters within each graph represent significant mean trait value change over time (T), time by burn interactions (BxT), and trait variance change over time in the burned (VB) or unburned (VU) population. Table 2.

time (*E. elymoides*: $\chi^2_1 = 11.06$, $P < .001$, *E. linearis*: $\chi^2_1 = 4.64$, $P < .05$, *P. secunda*: $\chi^2_1 = 3.94$, $P < .05$, and *P. spicata*: $\chi^2_1 = 11.28$, $P < .001$), and for *E. elymoides*, a significant burn by time interaction ($\chi^2_1 = 21.27$, $P < .0001$, Table 2, Supplementary Table S6). The direction of change was not consistent among species or by burn status (Fig. 4). For the *E. elymoides* burned population, contemporary seeds emerged 3.8 ± 0.2 days earlier with significantly lower variance (±0.4 days less, $F_{1,147} = 27.65$, $P < .0001$) than the past seeds, while the unburned population changed little over time (Fig. 4, Supplementary Table S7). For *E. linearis* and *P. secunda*, contemporary seeds emerged later than past seeds (*E. linearis*: 4.4 ± 0.3 days later; *P. secunda*: 1.9 ± 0.3 days later), while *P. spicata* contemporary seeds emerged earlier than past seeds, regardless of burn status (1.7 ± 0.1 days earlier, Fig. 4).

Mortality

In general, forb species had higher mortality than grasses, and annual/biennial *C. douglasii* had the highest mortality (Fig. 5a). For three of six species, mortality after emergence significantly differed among past and contemporary sources, with a significant time effect (*E. linearis*: $\chi^2_1 = 4.52$, $P < .05$, *S. grossulariifolia*: $\chi^2_1 = 4.37$, $P < 0.05$) or significant burn by time interaction (*P. secunda*: $\chi^2_1 = 4.06$, $P < .05$, Table 2, Supplementary Table S6), though the direction of change was not consistent across species or by burn status (Fig. 5a). Regardless of burn status, mortality was lower for contemporary sources of *E. linearis* (17 percentage points lower) and *S. grossulariifolia* (24 percentage points lower, Fig. 5a). For *P. secunda*, mortality was lower for contemporary sources from the unburned population (8 percentage points lower) while mortality was higher for contemporary sources in the burned population (15 percentage points greater, Fig. 5a).

Height

For three of six species, height differed significantly among past and contemporary sources, with significant time (*E. elymoides*: $\chi^2_1 = 6.20$, $P < .05$) or burn by time interactions (*P. secunda*: $\chi^2_1 = 6.46$, $P < .05$; *S. grossulariifolia*: $\chi^2_1 = 5.07$, $P < .05$, Table 2, Supplementary Table S6). The direction of change over time was not consistent across species or by burn status (Fig. 5b). Contemporary *E. elymoides* plants were shorter than past plants, and this trend was stronger in the burned population (15.08 ± 1.61 cm shorter) than in the unburned (2.63 ± 1.19 cm shorter) with a nearly significant time by burn interaction

($\chi^2_1 = 3.28$, $P = .0700$, Fig. 5b). For the burned *P. secunda* population, contemporary plants were shorter than past plants (12.94 ± 0.56 cm shorter) while in the unburned population, contemporary plants were taller than past plants (13.03 ± 4.70 cm taller, Fig. 5b). The opposite was true for *S. grossulariifolia*, as contemporary burned plants were taller than past burned plants (0.43 ± 0.03 cm taller) while contemporary unburned plants were shorter than past unburned plants (0.37 ± 0.01 cm shorter, Fig. 5b).

Leaf number and aboveground biomass

There were no significant time effects or burn by time interactions for any species for leaf number or aboveground biomass (means), though there was a significant increase in aboveground biomass variation in the unburned *S. grossulariifolia* population (±1.29 mg more, $F_{1,17} = 5.83$, $P < .05$, Table 2, Supplementary Tables S6 and S7).

Discussion

Through a resurrection study, we assessed change over time in native plants collected through the SOS programme, comparing seed and seedling traits in populations collected before and after wildfire. We found evidence of temporal change across all species and nearly all traits. The most change was observed in seed and emergence traits, which often predict survival and performance in the invaded Great Basin (Leger et al. 2021). However, our hypothesis that wildfire would lead to larger changes and shift traits towards potentially adaptive means with decreased trait variance was not widely supported. Instead, trait change occurred in both burned and unburned populations, and change occurred in a diversity of directions per trait, rather than the consistent shifts and decreases in trait variance that we hypothesized. These results are consistent with global patterns across resurrection studies, as we observed temporal changes that differed across species and traits, supporting the notion that trait evolution differs among species, populations, and by environmental context (Pennington et al. 2026). While trait shifts could be driven by rapid evolutionary change, either through adaptive natural selection or random processes such as genetic drift and gene flow, they could also be influenced by differences in past and contemporary seed collection methods, storage effects, or maternal effects. While we cannot determine the precise agent(s) of trait change, our characterization of *ex situ* seed collections for six species from the Great Basin suggests that we should expect seed and seedling traits to vary across collection years.

Our hypothesis that traits would shift in potentially adaptive directions with decreased variance, consistent with rapid evolution via natural selection, was supported for only one species, *E. elymoides*. Emergence timing shifted almost 4 days earlier with lower variance in the burned *E. elymoides* population, while the unburned population changed little over time. Emergence phenology can predict adult plant traits and success (Donohue et al. 2010), and early emergence can increase competitive ability with *B. tectorum* (Goergen et al. 2011, Barak et al. 2015, Leger et al. 2019, 2021). Plants from the burned, highly invaded *E. elymoides* site may have experienced directional selection for earlier emergence, consistent with rapid evolution towards earlier emergence of *E. elymoides* or congener *E. multisetus* from invaded sites in other studies (Goergen et al. 2011, Kulpa and Leger 2013, Leger et al. 2019, Agneray et al. 2022). We also observed temporal shifts towards smaller plant size (height) in the *E. elymoides* burned population, and the *P. secunda* burned population, though variance did not change over time for either species. Smaller plant size may be adaptive in the Great Basin for *E. elymoides* and *E. multisetus*, as studies associate smaller plant size with enhanced *B. tectorum* competition and restoration success for these species (Rowe and Leger 2011, Kulpa and Leger 2013, Ferguson et al. 2015, Leger and Baughman 2015).

Beyond this well-studied species, we found little evidence for broad or consistent trait change in response to fire. It is possible that changes associated with fire are not a strong driver of evolution in the Great Basin (at least for these species and populations), or that the single fire events studied here did not have a large enough effect on site conditions to induce change. Alternatively, differences between burned and unburned sites may have masked or overpowered any evolutionary influence of fire, as our pairs diverged in characteristics other than fire history. Even if fire exerted selection pressures, adaptive evolution requires sufficient genetic diversity underlying heritable traits (Strauss et al. 2006, Leger and Espeland 2010). If fire reduced populations through non-selective mortality, associated genetic diversity loss could limit their ability to adapt to post-fire changes, leaving populations susceptible to further diversity loss via genetic drift (Leger and Espeland 2010). However, changes in population size did not appear driven by fire for any perennial species, and we saw no declines in trait variance without trait mean change that could indicate genetic drift via a population bottleneck or stabilizing selection (Franks et al. 2018).

We did, however, observe trait changes for all species and populations, including all five perennial species and populations with only 3–4 years between collections. Some changes align with observations from multi-species studies and reviews that found general shifts towards smaller seed size (Lenzo et al. 2025), earlier phenology (Pennington et al. 2026), and smaller plant size (Leger 2013) over time. We also observed changes in these traits, including seed mass (changes in five of six species), emergence phenology (changes in four of five species), and height (changes in three of six species). However, the direction and magnitude of change differed among species and populations, with only some populations shifting towards lower seed mass, earlier phenology, and smaller plant size; others surprisingly shifted in opposite directions. These inconsistent changes among species and sources suggest that populations are adapting to differing selection pressures, experiencing neutral genetic drift or gene flow, or that these changes are due to other, non-evolutionary factors, such as sampling differences, storage effects, or maternal effects.

Differences in past and contemporary seed collection methods may have influenced trait divergence by inadvertently sampling different genetic and trait diversity between past *ex situ* and contemporary *in situ* sources (Franks et al. 2018, Weis 2018, Pennington et al. 2026). All collections followed the SOS protocol, which aims to sample randomly across entire populations to capture genetic diversity (BLM 2023). However, sampling across the entire geographic extent of large populations and throughout the entire growing season for species that produce ripe seed over weeks or months is not always feasible. Collections made during a single visit (8 of 12 past and 10 of 12 contemporary) could

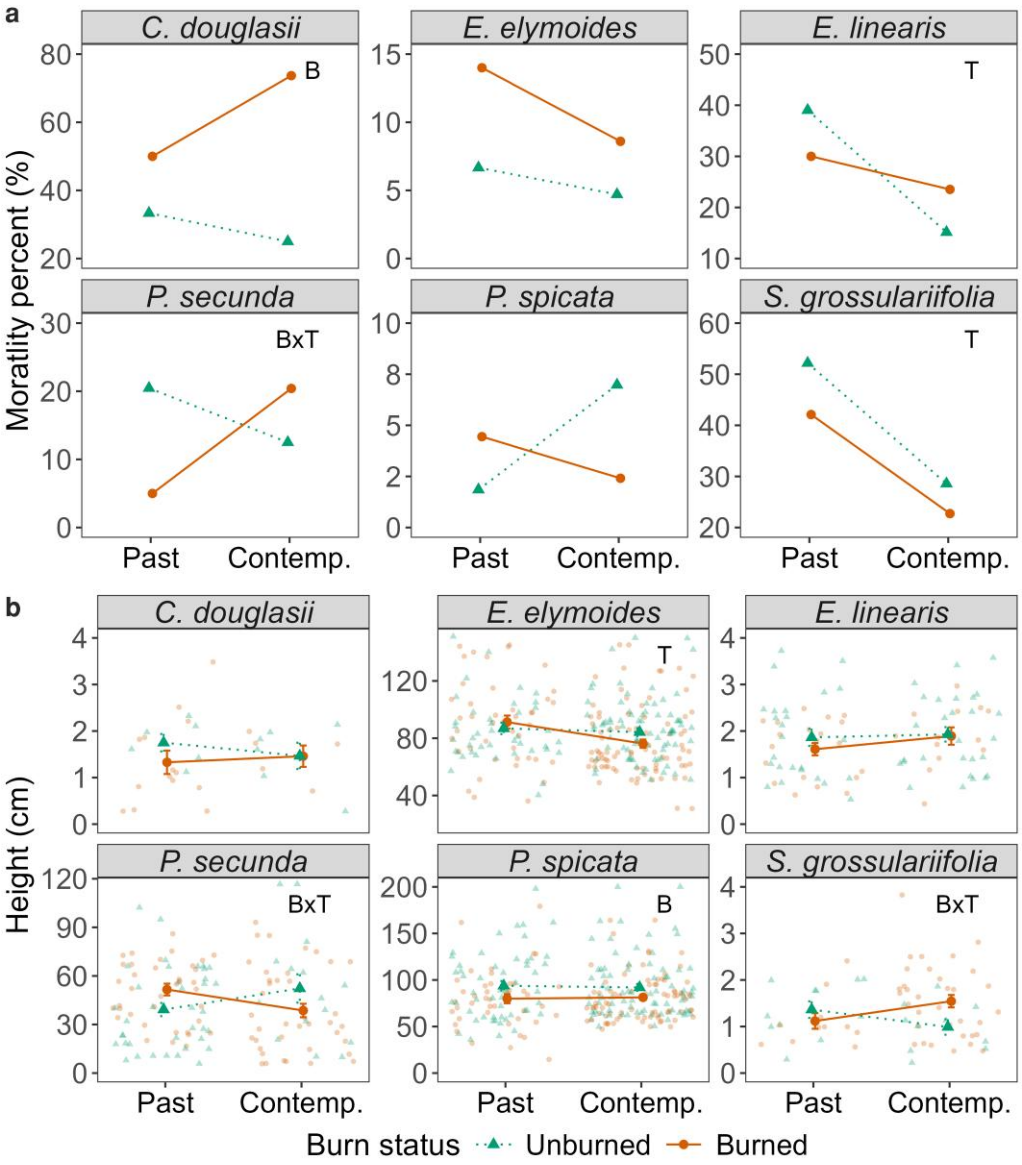

Figure 5 Trait change over time for burned and unburned populations of each species for mortality and morphology traits: (a) per cent mortality after emergence and (b) plant height (cm). The x axes represent time from past to contemporary (contemp.) populations and the *y* axes represent trait values. The *y* axes differ among species to clearly visualize within-species change over time. Burned populations are represented by red circles and solid lines while unburned populations are represented by blue triangles and dashed lines. Error bars represent standard error. Letters within each graph represent significant mean trait value difference between burned and unburned populations (B), change over time (T), and time by burn interactions (BxT). Table 2.

have missed early, mid, or late season seed, potentially affecting results. Additionally, the SOS protocol focuses on collecting populations during one, not multiple, years (BLM 2023). While this method protects populations from overharvesting, it could lead to incomplete capture of genetic and phenotypic diversity if only certain individuals emerge or produce viable seed during a given year (Franks et al. 2018). The SOS programme is essential to conservation, restoration, and provides valuable resources for research, but these potential sampling inconsistencies highlight the benefits of seed banking programmes like Project Baseline that are designed to study evolution via a resurrection approach (Etterson et al. 2016, Franks et al. 2018).

Storage and seed ageing effects could also influence *ex situ* and *in situ* trait divergence, as our past seed collections were stored for 3–11 years while contemporary collections were grown within a year of collection. Past seeds were stored under optimal conditions, but we were unable to grow a refresher generation to further reduce storage effects (Weis 2018, Pennington et al. 2026). Even under optimal conditions, non-random mortality during storage can lead to differential trait expression, also known as the 'invisible fraction' bias (Franks et al. 2018, Weis 2018, Pennington et al. 2026). When emergence percentages are high in both past and contemporary populations, the invisible fraction bias is trivial (Weis 2018), and this was the case with *E. elymoides* and *P. spicata*. For *E. linearis*, past and contemporary sources had similar (low) per cent emergence, and *C. douglasii* and *P. secunda* contemporary sources had higher emergence than the past. Although high germination is often

associated with plant success, reduced germination is not necessarily a sign of maladaptation; these populations could be exhibiting increased dormancy (which occurs for these species, Gucker and Shaw 2019, Gucker and Shaw 2024a, Gucker and Shaw 2024b, Chen et al. 2022, Kildisheva et al. 2019), possibly as a bet-hedging response to climate change or increased climatic variability (Venable and Brown 1988, Pausas et al. 2022). Even with lower contemporary emergence, we cannot rule out the possibility that storage affected emergence, and potentially associated traits. Storage and seed ageing did seem to affect some *S. grossulariifolia* traits, as past seeds generally had lower seed mass, lower emergence, and higher post-emergence mortality. Seed mass and viability can decline in storage and with age as seeds metabolize stored resources (Franks et al. 2018, De Vitis et al. 2020), which could explain these differences, as we weighed seeds from initial collections (rather than from a refresher generation). Only the *S. grossulariifolia* burned population had higher contemporary emergence, and was collected 2 years before the unburned, possibly increasing seed ageing and non-random mortality during storage. The *E. lienaris* past sources also had higher post-emergence mortality than contemporary, but unlike *S. grossulariifolia*, this was not accompanied by lower past seed mass nor lower emergence.

Another potential, and perhaps likely explanation for some of our observed trait divergence is maternal environmental effects. Maternal effects occur when the maternal environment affects the phenotype of the offspring in a process distinct from evolutionary change (Roach and Wulff 1987). Maternal effects can be difficult to differentiate from changes in gene frequencies (i.e. evolutionary changes), especially without a refresher generation (Bischoff and Müller-Schärer 2010). Even with a refresher generation, maternal effects can sometimes persist over multiple generations (i.e. transgenerational maternal effects), requiring multiple refresher generations to eliminate their influence (Roach and Wulff 1987, Bischoff and Müller-Schärer 2010, Franks et al. 2018). Maternal effects are well documented in early life stages, including seed mass and emergence traits (Bischoff and Müller-Schärer 2010). Given that we saw the most change in early seed and emergence traits, rather than later seedling mortality and morphology traits, maternal effects could have affected early traits, then decreased at later stages of plant development.

Our resurrection study revealed temporal trait shifts across several traits, species, and populations, but we cannot say with certainty how these changes arose. In addition to sampling differences, the impracticality of producing a refresher generation from perennial species with longer generation times can be a major challenge in resurrection studies, leading to potential biases from maternal effects, storage effects, and seed ageing (Franks et al. 2018, Weis 2018). This may be part of the reason many researchers use annual species in resurrection studies (Pennington et al. 2026). However, perennial species should not be overlooked, as they are common and important components of Great Basin ecosystems, where they may compete with invasive annual grasses (Svejcar et al. 2017, Johnson et al. 2022). Irrespective of cause, trait divergence between *ex situ* and *in situ* populations has important implications for seed banking, conservation, and restoration, as offspring from stored seeds used in restoration efforts could express phenotypes that are poorly suited to their environment, reducing fitness and restoration success. Repeat sampling over time, especially in areas of rapid or extreme environmental change, may be necessary to ensure that *ex situ* samples remain representative of their *in situ* counterparts, especially if they are used for restoring increasingly disturbed and degraded ecosystems.

Conclusions

We observed change over time in at least one trait for every species, regardless of burn status or degree of invasion. For *E. elymoides*, change was consistent with fire and subsequent invasion as the selective agent, as the earlier emergence and smaller size are likely adaptive in this well-studied species and genus (Rowe and Leger 2011, Kulpa and Leger 2013, Ferguson et al. 2015, Leger and Baughman 2015). Other species changed in opposite directions, and it is possible that these changes are also adaptive, but we lack the information needed to understand fitness strategies for seedlings of these plants. Whether observed changes were a result of evolutionary change or rooted in sampling differences, storage effects, or maternal effects, our observation that seed bank samples and contemporary collections often differ in potentially adaptive traits is relevant for using these seeds for restoration or research. Specifically, given the ubiquity of change observed here, one should expect that seed banked seeds are not a mirror image of contemporary populations, which can change while the seed bank gene pool remains relatively static. Our conclusions support the continued effort of programmes like SOS (Haidet and Olwell 2015) to collect wild seed for restoration and long-term storage. While current guidelines encourage visiting populations throughout the same season to capture genetic variation (BLM 2023), our results suggest that guidelines could include collecting from one population over multiple years to maximize genetic and trait diversity capture across dynamic wild plant populations.

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Author contributions

L.C.S., E.A.L., and S.C.B. developed the research questions and research design; L.C.S. and S.C.B. collected contemporary seed; L.C.S. performed the experiments and analysed the data; L.C.S.

and E.A.L. wrote the initial manuscript; L.C.S., E.A.L., and S.C.B. edited the final manuscript.

Supplementary material

Supplementary material is available at *AoB Plants* online.

Conflicts of interest

None declared.

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Data availability

Raw data and R code for this study are available at the U.S. Department of Agriculture U.S. Forest Service Research Data Archive: https://doi.org/10.2737/RDS-2025-0063

Ethics approval

The species sampled are not endangered or protected.

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