

# A tale of ENSO, PDO, and increasing aridity impacts on drought-deciduous shrubs in the Death Valley region

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## Abstract

Germination, establishment, phenology, and death among three drought-deciduous shrubs were influenced by ENSO/PDO and precipitation, based on 37 years of annual surveys. *Encelia farinosa* forms near monospecific stands on slopes, whereas *E. frutescens* and *Ambrosia salsola* dominate wash habitats. All shrubs exhibited phenological coherence. While germination, establishment, and mortality patterns were similar among wash species, these dynamics contrasted with *E. farinosa* on slopes. Germination was associated with El Niño years. Slope plant establishment was dependent on precipitation in the subsequent year, but not evidently so in wash species. Major mortality events were episodic, with *Encelia* mortality just as likely to occur in years with below or above average precipitation. In both *Encelia* species, mortality was associated with transitions to a cold PDO phase. In *E. frutescens* this response was more rapid, whereas in *E. farinosa* mortality lagged 1 year, resulting in contrasting slope-wash mortality patterns. 50% of newly established shrubs died within 5, 5, and 18 years for *E. frutescens*, *E. farinosa*, and *A. salsola*, respectively. The 90% mortality ages were 26 years for *E. frutescens*, 24 years for *E. farinosa*, and 51 years for *A. salsola*. While maximum life expectancies are unknown, estimated maximum life expectancies were 56, 66, and 86 years for *E. frutescens*, *E. farinosa*, and *A. salsola*, respectively. Overall, as the climate has become more arid over the past four decades, the populations in both slope and wash habitats have exhibited similar responses: reduced shrub abundances and reduced total supportable leaf areas.

**Keywords** *Encelia* · *Ambrosia* · Life expectancy · Germination · Mojave Desert · Climate change

## Prolog

Hal Mooney believed that group projects within the lab complemented a student's thesis research and were essential elements to broaden a student's training. It was in such spirit that this project began. Each March, members of the Ehleringer Lab (students, postdocs, technicians, and significant others) would escape winter in Salt Lake City and venture to Death Valley. At first, group projects were largely eco-physiological (e.g., Forseth et al. 1984; Werk and Ehleringer

1983; Werk et al. 1983), but in 1981 we began to census *Encelia farinosa*, *E. frutescens*, and *Ambrosia salsola* populations. The expectation was of a 20-year study since these shrubs were thought to live less than two decades. More than three decades later, 2% of the initial *E. farinosa* and 40% of the *A. salsola* populations still persist. Only the initial *E. frutescens* population has turned over completely during that time period. Along the way, we have begun to unravel some of the long-term trajectories and the climatic drivers influencing dynamics of these desert shrubs. Thanks Hal for the motivation.

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## Introduction

It is generally accepted that the distributions of Mojave and Sonoran Desert plants are controlled by climatic conditions (Livingston and Shreve 1921; Shreve 1922; Shreve and Wiggins 1964; Smith et al. 1997), with moisture availability thought to be a primary factor and temperature (particularly

freezing temperatures) of secondary importance. Given a changing climate today and its global impacts on plant distributions tomorrow (Diffenbaugh and Field 2013), it is relevant to ask how will the distributions of desert shrubs change in the future. On one hand, many desert plant species are thought to have adaptive features that allow them to persist through extended dry periods and so a change in water availability might not have an easily detected impact on plant distributions. There are differences in opinion as to whether recent climate changes are already having or have had impacts on the distributions of desert plants, given the difficulties in distinguishing between shifts in plant abundances and distributions versus the episodic nature of both plant establishment and mortality. Several decadal-scale census studies have suggested elevational shifts in Mojave Desert shrub distributions over the past three decades (Guida and Abella 2014; Kelly and Goulden 2008). Here, the implication is an upward expansion of species distributions as climates warm, with an implied reduction in a species' abundances at lower elevational limits. At the same time, Tielbörger and Salguero-Gómez (2014) reviewed a number of published studies and suggested that the adaptive nature of desert plants resulted in a high resilience to changes, even when plants are subject to changes in precipitation. To explore ramifications of a changing Mojave Desert climate and its influence on plant distributions in the driest regions, there may be no better place to examine long-term plant population changes than in perennial shrubs from the Death Valley area, long regarded as one of the driest and hottest regions in North America.

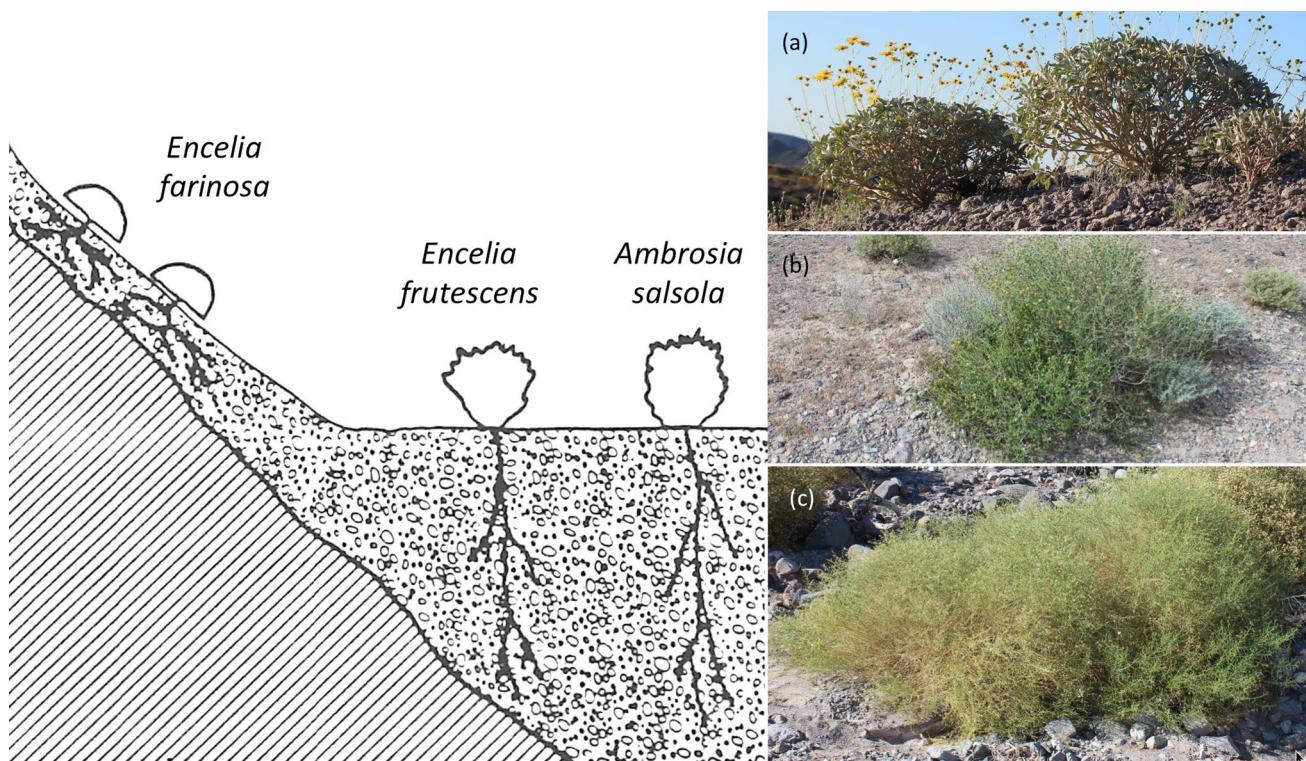
Across the Mojave Desert, shrubs are the dominant perennial life form (MacMahon 2000; MacMahon and Wagner 1985; Webb et al. 1988). Here, slope and wash landscapes are typically dominated by both evergreen-leaved and drought-deciduous perennial shrubs (Comstock and Ehleringer 1992; Ehleringer 1994; Hunt 1966; Shreve and Wiggins 1964). We selected three drought-deciduous-leaved shrub species for study, based on the concept that drought-deciduous shrubs have life expectancies that are far shorter than those of evergreen-leaved perennial shrubs (Goldberg and Turner 1986; Hastings and Turner 1980; Martin and Turner 1977; Turner and Karpiscak 1980; Webb 1996; Webb et al. 1987, 1988). The rationale for examining drought-deciduous shrubs for study was that, despite periodic establishment and mortality periods, it might be possible to detect trends in plant abundances over a multi-decadal period as the region's climate warmed. The three drought-deciduous shrubs selected for study were *Encelia farinosa*, *E. frutescens*, and *Ambrosia salsola* (formerly *Hymenoclea salsola*). Although there are differences in leaf size, shape, and spectral characteristics among the three species, all three are very common and widely distributed species that typify

low-stature shrubs across the Mojave and Sonoran Deserts (Hastings et al. 1972; Shreve and Wiggins 1964; Turner et al. 1995).

There has been long history of interest in the ecology and ecophysiology of *Encelia* (Smith et al. 1997). Pioneering studies by Edith and Forest Shreve at the Carnegie Institution's Desert Research Laboratory focused on controls over transpiration by *E. farinosa* under hot, arid conditions (Shreve 1915, 1923, 1924). Subsequent studies with *E. farinosa* explored the importance of variations in trichome-based leaf reflectance changes on altering energy balance and its influence on leaf temperature, especially during hot, summer months (Cunningham and Strain 1969; Ehleringer et al. 1976; Ehleringer and Mooney 1978). Here, very high *E. farinosa* leaf reflectances resulted in greatly reduced leaf energy balances and temperatures that were several degrees below air temperatures. The reduced leaf temperatures and reduced transpiration rates are thought to be key factors favoring the survival and widespread distribution of these shrubs across rocky slopes in both Mojave and Sonoran Desert sites. In support of this, mutant *E. farinosa* lacking trichomes exhibited higher leaf temperatures, higher transpiration rates, and a much shorter leaf persistence into drought periods (Ehleringer 1983). In contrast, *E. frutescens* co-habits many of the same landscapes and has low leaf reflectance, glabrous green leaves which exhibit higher transpiration rates under field conditions (Comstock and Ehleringer 1984, 1986; Ehleringer and Cook 1988).

Differences in slope versus wash microhabitat distributions of *E. farinosa* and *E. frutescens* provide an explanation for persistence of the contrast in leaf energy balance features. While *E. farinosa* shrubs are largely found on dry slopes with shallow rocky soils, *E. frutescens* shrubs occur only in deep gravelly washes where the capacity for soil water retention is higher (Fig. 1). *Ambrosia salsola* is also commonly only found in desert washes. In fact, *A. salsola* is the dominant drought-deciduous shrub in many desert wash sites across the Mojave Desert, although in the Death Valley region *A. salsola* can be codominant with *E. frutescens* (Fig. 1) (Hastings et al. 1972; Shreve and Wiggins 1964; Turner et al. 1995; Webb et al. 1988).

Less is known about the ecophysiology of *A. salsola* than *Encelia* species. In contrast to *E. frutescens*, *A. salsola* has photosynthetic stems which persist longer into drought periods than its long, narrow leaves (Comstock et al. 1988; Comstock and Ehleringer 1988). Yet all three species possess drought-deciduous leaves with similar ecophysiological tolerances to soil water deficits as measured through decreases in plant water potential (Comstock and Ehleringer 1984, 1986; Comstock and Mencuccini 1998; Comstock 2000; Ehleringer and Cook 1984; Mencuccini and Comstock 1997; Sandquist and Ehleringer 1998). Each shrub species exhibits suffrutescent canopy architecture with



**Fig. 1** *Encelia farinosa* (plate a) commonly dominates dry rocky slopes in both the Mojave and Sonoran Deserts. In contrast, *E. frutescens* (plate b) and *Ambrosia salsola* (plate c) are found in wash habitats

multiple stems emerging from a common base, dieback of some basal stems would be expected as an initial response to multi-year droughts, with mortality thought to occur under only the more protracted droughts.

The initial field study was designed to examine how phenology, plant establishment, plant size, and mortality among shrub species were influenced by interannual variations in precipitation (water availability). Data would be collected to explore three hypotheses:

**Hypothesis 1** As most of the annual precipitation occurs during winter–spring storm events, all three species are predicted to exhibit similar year-to-year phenologies despite differences in soil water capacities of slope versus wash habitats.

**Hypothesis 2** Germination and new plant establishment will be driven by absolute precipitation amounts and thus similar patterns are expected for all three species.

**Hypothesis 3** Extended multi-year drought periods are predicted to have non-equivalent impacts on plants in slope versus wash habitats. Given similar drought tolerances among all three species, we hypothesize that periodic and extended drought periods during the study period will result in similar mortality impacts on *E. frutescens* and *A. salsola*.

in wash habitats, but have a greater impact on *E. farinosa* shrubs since they occur on drier slope habitats. Specifically, we expect that population sizes on slope habitats should decrease more during multi-year drought periods than populations in wash habitats.

Climate syntheses reveal increased drought conditions in arid regions over the last several decades, which likely have broad impacts on perennial plant populations. Other studies spanning the period of this study reveal that this has been a period of greater drought across many parts of the western United States (Ficklin et al. 2015; Weiss et al. 2009). Ficklin et al. (2015) found that droughts across the western United States were associated with both decreased precipitation amounts as well as elevated temperatures. Thus metrics, such as the Palmer Drought Severity Index (PDSI), which combines the impacts of changes in precipitation and humidity into a single index, have increased during this period. Seager and Hoerling (2014) attributed these droughts to changes in sea surface temperatures (SST) across the Pacific Ocean, creating a potential teleconnection between broad oceanic temperature conditions and precipitation amounts at our study sites in the Death Valley region. Wang and Kumar (2015) attribute droughts in the southwestern United States between 1948 and 2014 to variations in the El Niño Southern Oscillation

(ENSO), with both Cook et al. (2015) and Udall and Overpeck (2017) predicting that drier conditions in arid lands will continue into the future.

## Materials and methods

### Site descriptions

A near monospecific population of *E. farinosa* occupying a south-facing slope was selected in the Death Valley National Park, some 21 km west southwest of Shoshone, California (although the site was on Bureau of Land Management lands at the time the study was launched). The perennial vegetation at this site has remained greater than 95% *E. farinosa* throughout the monitoring period 1981–2017, with a few *Larrea tridentata* also occupying the site. The area selected for population monitoring is 480 m<sup>2</sup> and dominated by rocky hill-slope soils as is typical of the area (Hunt 1966; Hunt and Mabey 1966).

*Encelia frutescens* and *A. salsola* populations have been monitored in a broad wash site on Bureau of Land Management lands, some 22 km south southwest of Shoshone, California. The perennial vegetation at this site has remained greater than 80% *E. frutescens* and *A. salsola* throughout the monitoring period 1981–2017, with a few *Bebbia juncea*, *Ferocactus acanthoides*, *Larrea tridentata*, and *Peucephalium schotii* also occupying the site. The area selected for population monitoring is 3286 m<sup>2</sup> of active wash, dominated by rocky to sandy soils, and subject to flashfloods which occasionally modify the surface geomorphology (Hunt 1966; Hunt and Mabey 1966).

### Census measurements

Within the population plots, censuses have occurred annually during the last 2 weeks of March. A team consisting of undergraduate students, graduate students, postdocs, technicians, and significant others from both the University of Utah and California State University Fullerton have assisted in the data collections each year. Team composition varied from year to year. Since 1981, more than 100 individuals assisted in this sampling. As initially described by Will Pockman (now on the faculty at the University of New Mexico), the census team is known as the DEPRAVED Team (Desert Ecological Population Research Analyzing Variations associated with Environmental Determinants). Field assistants were trained prior to censusing each year. Attention was given to measurement details to ensure interannual measurement consistency and also to ensure that seedlings and shrubs were not damaged during data collection. While there are no high-resolution aerial photographic comparisons to show that annual censuses did not have an impact, there have

been no visual indications of human impacts on the populations. However, the wash habitat of the *E. frutescens* and *A. salsola* populations experienced periodic flashfloods, which impact surface structure and occasionally uprooted shrubs or partially cover them with rocks and fluvial debris.

Individual plants were tagged with numbered aluminum tags near their stem base. The location of each individual was recorded on x–y plot coordinates with a precision of 10 cm. For each individual plant, size, and phenology metrics were recorded annually. These measurements include (a) projected shrub width at maximum and perpendicular widths (cm), (b) shrub height for uppermost leaves (cm), (c) estimated leaf cover (scale of 0–4), (d) presence or absence of dieback from the previous year, (e) presence or absence of parasites such as dodder (*Cuscuta* sp.), and (f) the presence or absence of flowers. The leaf cover scale of 0–4 correlated with estimated leaf cover in percentages of 0% leafless, but appeared to be alive, 0–25%, 26–50%, 51–75%, and 76–100%. A sample of 5–10 sun leaves were collected for biochemical analyses (carbon isotope ratio, nitrogen isotope ratio, nitrogen content, and C/N ratio), although none of these results are presented here. Remaining leaf tissues are archived for future analyses.

Plants that appeared to be dead at the time of the census were listed as “looks dead” and monitored for two successive years to determine whether or not they were actually dead or happened to be drought deciduous at the time of the census. On the third year, if a plant still appeared to be dead, its tag was removed and the year of death recorded as the first year in which a plant looked dead. Seedling counts were recorded, but the location of each seedling was not recorded until a seedling survived the summer drought period and became established as a yearling (i.e., its second year of life).

For the calculation of mean and maximum shrub longevity, three different approaches had to be used to determine individual plant longevity. First, for plants that germinated and subsequently died within the observation period, longevity was calculated as the difference between birth and death years. For shrubs that germinated during the study period and that were still alive in 2017, longevity was calculated as the difference between 2017 and the birth year. We recognize that this approach underestimates shrub longevity. For shrubs alive at the time of the initial observations, we calculated each shrub’s birth year based on regressions between shrub size and age, using all plants born during the study period as our regression set. For *E. farinosa*, the dependence of shrub size (projected area in cm<sup>2</sup>) on age was  $y = -142 + 226x$ ,  $r^2 = 0.539$ ,  $p < 0.0001$ . For *E. frutescens*, the dependence of shrub size (projected area in cm<sup>2</sup>) on age was  $y = -117 + 383x$ ,  $r^2 = 0.506$ ,  $p < 0.0001$ . For *A. salsola*, the dependence of shrub size (plant width in cm) on age was  $y = 24 + 5.1x$ ,  $r^2 = 0.465$ ,  $p < 0.0001$ .

All data are stored in a relational database (FileMaker), which now contains in excess of 20,000 individual annual plant observations, with each observation containing 5–10 measurements (canopy size, leaf and flowering phenology, carbon and nitrogen stable isotopes, C and N concentrations, and C/N ratios). The database is updated following each annual census. Stable isotope, carbon concentration, and nitrogen concentration data were analyzed at SIRFER (<http://sirfer.utah.edu>) and will be presented in a future publication. Data for analyses were exported and analyzed using Microsoft Excel, StatPlus, Prism, or KaleidaGraph software. Colleagues or collaborators wishing to access the database should contact the authors. Once an initial round of analyses has been published, the entire database will be made available for public access.

Precipitation and temperature data used in analyses were derived from PRISM (<http://prism.oregonstate.edu>) for the Shoshone, California location (data accessed September 1, 2017). Each of the two site locations is within 22 km of Shoshone.

Since larger scale weather phenomenon could impact plant phenology and population dynamics patterns, El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) metrics were used to further assess phenology and population patterns. As the Oceanic Niño Index (ONI) for the December–January–February period is commonly used as an indicator of El Niño years (<https://data.noaa.gov/dataset/climate-prediction-center-cpcceanic-nino-index>), this parameter was used in data analyses (data downloaded September 1, 2017). An ONI value equal to or greater than 1 was used to indicate an El Niño year, which, in this region may or may not indicate above average precipitation. ONI values of less than 1 indicate a neutral or La Niña (dry) year. Over the study period, the winter–spring precipitation amounts were significantly related to ONI values ( $y = 21.75x + 142$ ,  $r^2 = 0.468$ ,  $n = 35$ ,  $p = 0.00006$ ). Yet because the regression of ONI versus winter–spring precipitation explained less than half of the variation, precipitation amounts were below average during nearly 40% of the El Niño years. Conversely, precipitation amounts were above average during more than 20% of the non-El Niño years. This distinction becomes relevant during subsequent analyses when vegetation patterns were significantly related to El Niño events but not necessarily to precipitation amounts and vice versa. PDO data were derived from <http://research.jisao.washington.edu/pdo/> (data downloaded September 1, 2017). PDO analyses were categorized as either “warm” phase ( $\text{PDO} > 0$ ) or “cold” phase ( $\text{PDO} < 0$ ).

Trend data were analyzed using linear regressions between vegetation response variables and single explanatory climate variables. Categorical comparison data

analyses were conducted using a contingency table analysis with significance based on Chi-square tests.

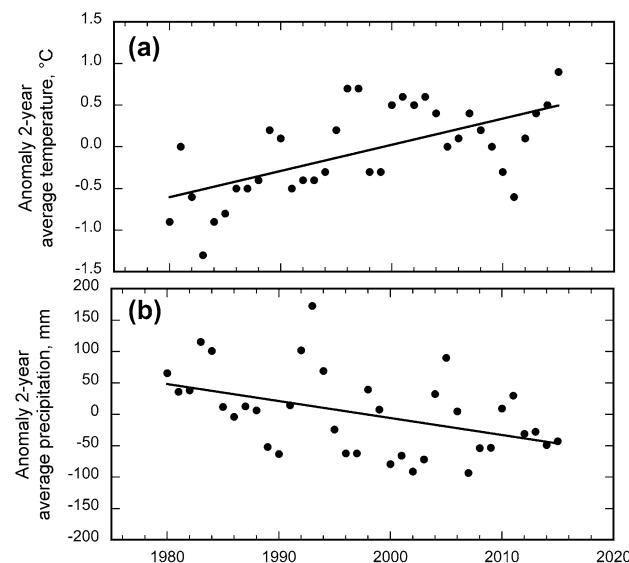
## Results

### Climate trends of the past four decades

Over the past four decades, there are indications of climate shifts in the Death Valley region. Both mean annual temperature and mean winter–spring precipitation changed in a systematic manner, consistent with the region becoming more arid.

A single mean temperature value for the Death Valley region where these three shrub species were monitored might convey a measure of the warmth of the region, but it hides the temperature trends of the past four decades. Figure 2 (upper plate) shows the anomaly 2-year average annual temperature from 1980 to 2015 versus the mean value for all years of this study (the baseline value). The trend of increasing annual temperatures is highly significant ( $r^2 = 0.65$ ,  $n = 36$ ,  $p < 0.000001$ ). Over the 37-year period of this study, mean annual temperatures have increased by 1.2 °C.

Between 1980 and 2015, the long-term average precipitation during the winter–spring months exhibited a statistically significant downward trend (Fig. 2, lower plate),



**Fig. 2** Plate **a**. Anomalies in the 2-year average temperatures for Shoshone, California between 1980 and 2015 ( $r^2 = 0.65$ ,  $n = 36$ ,  $p < 0.000001$ ). Plate **b**. Anomalies in the 2-year average winter–spring precipitation for Shoshone, California between 1980 and 2015 ( $r^2 = 0.184$ ,  $n = 36$ ,  $p = 0.009$ ). Anomalies are based on deviations from the long-term average conditions between 1980 and 2015

contributing to increasing aridity in the region ( $r^2=0.184$ ,  $n=36$ ,  $p=0.009$ ).

### Phenological coherence across species and habitats

A typical response when traveling through the Mojave Desert in the spring is the visible distinction between a “good year” versus a “bad year”, by which colleagues and visitors are usually referring to the abundance of or absence of flowering across the landscape. One remarkable feature from our long-term observations is the coherence among all three species in spring time leaf cover and of flowering phenology.

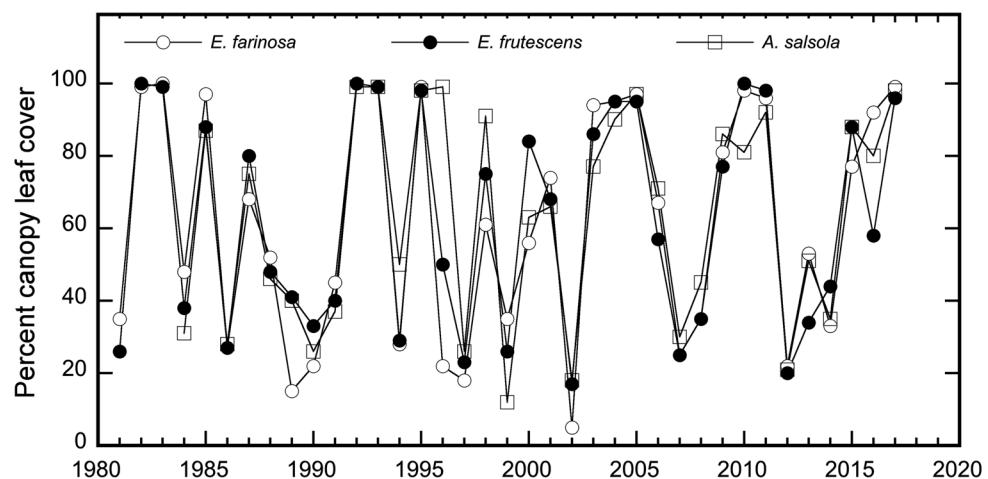
Leaf cover at the canopy scale is a semi-subjective measure by paired individuals of the census team and varies between 0% (leafless) and 100% (fully leafed canopy). Sampling occurred at a time when plants were likely to have their greatest leaf areas, following winter–spring rains. Data presented represent the average canopy leaf area of all plants within the same species. Over the 37-year observation period, there have been 10 periods where canopy leaf areas were high in these populations and 10 periods of low canopy leaf area (Fig. 3). For all three species, there have been large variations in the extent of canopy leaf cover across years, varying from a low population-level value of 5% during the 2002 drought to 100% during wettest periods. Coherence in the extent of leaf canopy development was expected for *E. frutescens* and *A. salsola*, since both populations occur in the same wash habitat. Here, the correlation of paired canopy leaf cover in *E. frutescens* versus *A. salsola* across years was highly significant ( $r=0.894$ ,  $n=34$ ,  $p<0.000001$ ). These data also support Hypothesis 1, where we expected coherence of canopy leaf cover between wash and slope habitats given similar regional climates (*E. frutescens* versus *E. farinosa*, respectively;  $r=0.904$ ,  $n=37$ ,  $p<0.000001$ ). This latter

observation was anticipated despite the contrasting nature of potential water availability between wash and slope habitats, because the driver for variations in canopy leaf cover is winter–spring soil moisture availability. Statistically, the regression of percent canopy leaf cover against total winter–spring precipitation combining observations of all three species was highly significant ( $y=0.2143 \ln(x)+0.49$ ,  $r^2=0.539$ ,  $p<0.00001$ ) as are the regressions of leaf cover and winter–spring precipitation for each of the species (Table 1).

Flowering typically occurs in spring for these shrubs, although flowering can also occur in autumn in those rare years with extensive summer monsoon precipitation. Over the last 37 years, we observed 19 years with extensive flowering in these populations and 18 years during which little or no flowering occurred (Fig. 4). Extensive flowering in one year did not preclude flowering in a subsequent year, suggesting that the driving factor for flowering was winter–spring precipitation amounts influencing carbon gain and that nutrient limitations did not impose an obvious constraint on flowering (Table 1). Again, as with canopy leaf cover, there was highly significant within year coherence in flowering percentages. For the wash habitat, as might be expected, in years when *E. frutescens* flowered, a similar flowering pattern occurred in *A. salsola* shrubs ( $r=0.874$ ,  $n=34$ ,  $p<0.000001$ ). An equivalent coherence of population-scale flowering occurred in the slope species, *E. farinosa*, 22 km away (*E. farinosa* versus *E. frutescens*,  $r=0.828$ ,  $n=37$ ,  $p<0.000001$ ).

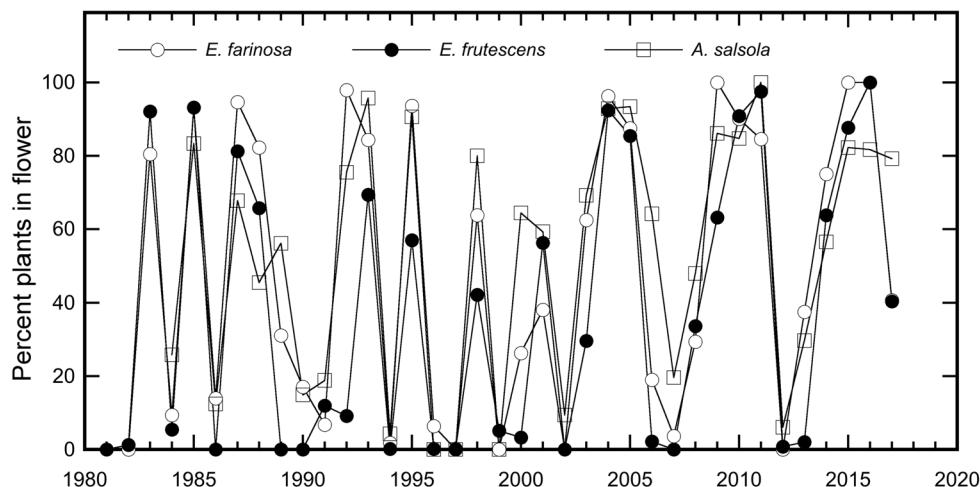
The population-level flowering (that typically brings spectacular color to the Mojave Desert in spring) was significantly related to total winter–spring precipitation for each of the three species (Table 1). At the same time, flowering was also significantly related to larger scale climate conditions. If we classify a high-flowering year as any year in which 20% or more of each population flowered, then 19 of the 37 years were high-flowering years (51%).

**Fig. 3** Variations in the annual percentage leaf cover for *Encelia farinosa* (open circles), *E. frutescens* (filled circles), and *Ambrosia salsola* (open squares) populations in spring between 1981 and 2017. *E. farinosa* occur on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other



**Table 1** Linear regressions of the relationships between population and climate parameters for *Encelia farinosa*, *E. frutescens*, and *Ambrosia salsola*

Population parameter	Climate parameter	<i>Encelia farinosa</i>	<i>Encelia frutescens</i>	<i>Ambrosia salsola</i>
Leaf cover	Total winter–spring precipitation	$y=0.1072x+0.34$ $R^2=0.515$	$y=0.1018x+0.35$ $R^2=0.543$	$y=0.2143 \ln(x)+0.49$ $R^2=0.539$
Flowering	Total winter–spring precipitation	$y=0.1796 \ln(x)+0.2665$ $R^2=0.212$ $p=0.002$	$y=0.219 \ln(x)+0.334$ $R^2=0.311$ $p=0.00002$	$y=0.2146 \ln(x)+0.404$ $R^2=0.413$ $p=0.00001$
Seed germination	Total winter–spring precipitation	— $R^2=0.161$ $p=0.028$	— $R^2=0.083$ $p=0.180$	— $R^2=0.013$ $p=0.955$
Yearling establishment	Total winter–spring precipitation	$Y=35.83x-40.2$ $R^2=0.218$ $p=0.019$	— $R^2=0.002$ $p=0.841$	— $R^2=0.024$ $p=0.480$
Yearling establishment	ONI (in the current year)	— $R^2=0.071$ $p=0.232$	— $R^2=0.071$ $p=0.182$	— $R^2=0.0001$ $p=0.99$
Yearling establishment	ONI (in the previous year)	— $R^2=0.02$ $p=0.283$	— $R^2=0.017$ $p=0.258$	— $R^2=0.099$ $p=0.294$
Mortality rates	Total winter–spring precipitation	— $R^2=0.081$ $p=0.091$	— $R^2=0.087$ $p=0.153$	—

**Fig. 4** Variations in the annual percentage of plants in flower for *Encelia farinosa* (open circles), *E. frutescens* (filled circles), and *Ambrosia salsola* (open squares) populations in spring between 1981 and 2017. *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other

Flowering was more likely during El Niño years than non-El Niño years (Table 2).

### Seed germination and subsequent new plant establishment occurs in pulses

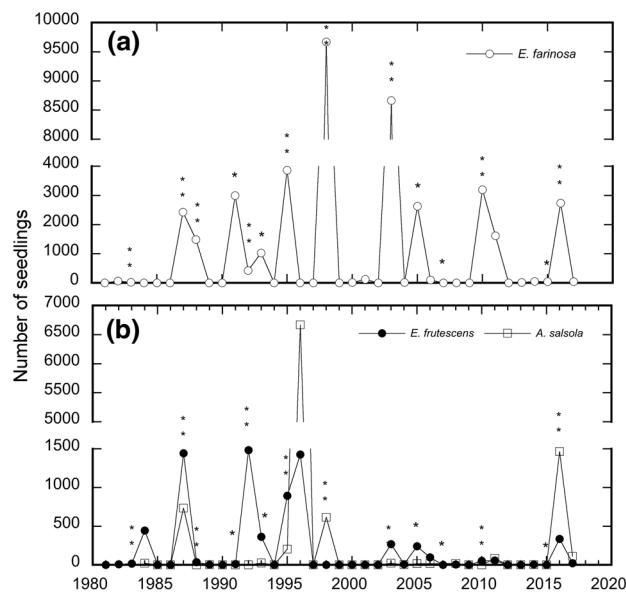
Despite high seed production when populations did flower, germination did not occur every year for any of the species. In fact, germination of 25+ seedlings per site in a given year happened only 18 years for *E. farinosa*, 13 years for *E. frutescens*, and 8 years for *A. salsola* (Fig. 5). During the 37-year observation period, high germination rate

years, when 500+ seeds germinated per plot, occurred 11 years for *E. farinosa*, 4 years for *E. frutescens*, and 4 years for *A. salsola*.

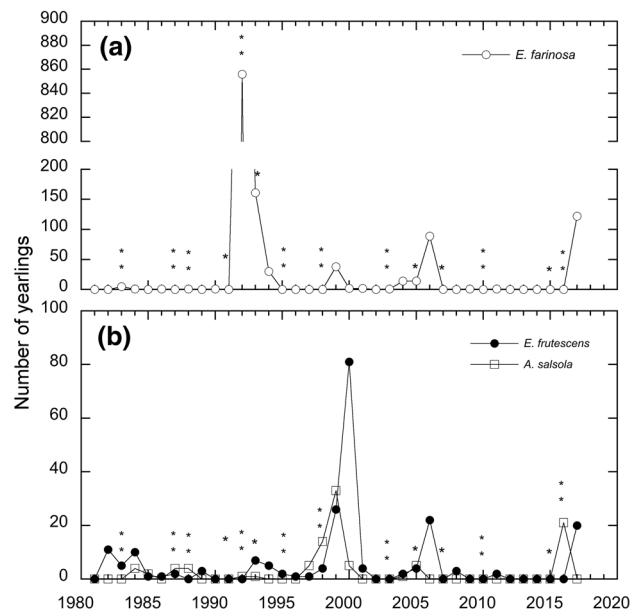
As might be anticipated, germination of new seedlings was significantly dependent on winter–spring precipitation amounts for the slope species *E. farinosa*, but not for the wash species *E. frutescens* and *A. salsola* (Table 1). A good year for seed germination for one species was not necessarily a good year for all species. However, a strong predictor of seedling germination rates was the occurrence of an El Niño year, irrespective of cumulative winter–spring precipitation amounts. When categorizing

**Table 2** Chi-square analyses of the relationships between population and climate parameters for *Encelia farinosa*, *E. frutescens*, and *Ambrosia salsola*

Population parameter	Climate parameter	<i>Encelia farinosa</i>	<i>Encelia frutescens</i>	<i>Ambrosia salsola</i>
Flowering	El Niño years versus non-El Niño years	$\chi^2=6.79$ $p=0.009$	$\chi^2=5.31$ $p=0.021$	$\chi^2=4.57$ $p=0.033$
Seed germination	El Niño years versus non-El Niño years	$\chi^2=14.59$ $p=0.0001$	$\chi^2=8.40$ $p=0.004$	$\chi^2=4.51$ $p=0.034$
Mortality rates	Wet versus dry years (in the current year)	$\chi^2=0.09$ $p=0.764$	$\chi^2=0.0$ $p=1$	—
Mortality rates	Wet versus dry years (in the previous year)	$\chi^2=2.25$ $p=0.134$	$\chi^2=7.20$ $p=0.066$	—
Mortality rates	El Niño years versus non-El Niño years	$\chi^2=1.41$ $p=0.221$	$\chi^2=0.15$ $p=0.700$	—
Mortality rates	El Niño years versus non-El Niño years (in the previous year)	$\chi^2=0.33$ $p=0.568$	$\chi^2=0.002$ $p=0.968$	—
Mortality rates	PDO (warm versus cold phase)	$\chi^2=0.71$ $p=0.400$	$\chi^2=4.21$ $p=0.04$	—
Mortality rates	PDO (warm versus cold phase) (in the previous year)	$\chi^2=6.22$ $p=0.013$	$\chi^2=5.6$ $p=0.180$	—

**Fig. 5** Variations in the annual total number of seedlings for *Encelia farinosa* (plate a, open circles), *E. frutescens* (plate b, filled circles), and *Ambrosia salsola* (plate b, open squares) populations in spring between 1981 and 2017. *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other. Asterisks indicates a weak (\*, ONI = 1) or strong (\*\*, ONI > 1) El Niño year

germination rates for species, we classified a “germination year” as one in which 25 + seeds per plot germinated. For these years, germination rates were highly correlated with ENSO events. Seeds were more likely to germinate during an El Niño year than during a non-El Niño year (Table 2).

**Fig. 6** Variations in the annual total number of yearlings for *Encelia farinosa* (plate a, open circles), *E. frutescens* (plate b, filled circles), and *Ambrosia salsola* (plate b, open squares) populations in spring between 1981 and 2017. *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other. Asterisks indicates a weak (\*, ONI = 1) or strong (\*\*, ONI > 1) El Niño year

While germination rates were positively associated with El Niño years, the subsequent transition of seedlings into yearlings was not ENSO driven (Fig. 6). The number of yearlings, defined by seedlings persisting through a first year and then tagged in the following spring, were not significantly

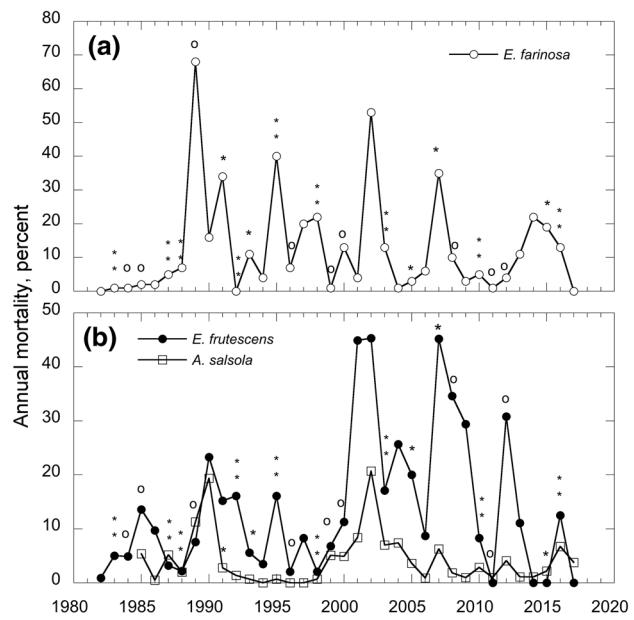
related to ENSO conditions, as evaluated by ONI values for any of these three species (Table 1). Whether evaluating the impact of ENSO conditions in the year of yearling establishment or in the prior year (i.e., El Niño year triggering germination), there were no significant relationships between new plant establishments and ENSO conditions. However, for *E. farinosa*, the slope species, the amount of rainfall in the year following germination did influence the likelihood that a seedling would establish as a yearling. The number of *E. farinosa* seedlings establishing into yearlings was significantly related to the establishment year's cumulative winter–spring precipitation (Table 1). That is, an El Niño event triggers *E. farinosa* seed germination and adequate winter–spring precipitation in the subsequent year increases the likelihood of new plant establishment. In contrast, for the two wash species, there were no significant relationships between yearling establishment and cumulative precipitation amounts (Table 1). The factors facilitating *E. frutescens* and *A. salsola* establishment are unclear at this time. One challenge to identifying patterns related to new plant establishment is that recruitment of new plants into these populations occurred only sporadically over last 37-year study period (Fig. 6).

Yearling establishment occurred 18 times for *E. farinosa*, 22 times for *E. frutescens*, and 13 times for *A. salsola* (Fig. 6) And in most cases, only a few plants established during an establishment year. Appreciable new plant establishment of 20+ plants in a given year occurred only 6 times for *E. farinosa*, 4 times for *E. frutescens*, and twice for *A. salsola*.

### Death and decreases in population size are episodic

Death of established plants for each of the three species was episodic, with each species experiencing 5–6 major mortality periods during the 37-year observation period (Fig. 7). While there was coherence in the shrub mortality patterns for the wash species *E. frutescens* and *A. salsola*, these mortality event periods were not always the same as those observed for established *E. farinosa* shrubs. Factors explored as potential contributors to shrub mortality included total winter–spring precipitation amounts, the presence or absence of an El Niño year, and the warm versus cold phases of the Pacific Decadal Oscillation (PDO).

For analyses, cumulative winter–spring precipitation were categorized as either “wet” years, with precipitation amount 30% above the long-term average (130% of long-term average, ~25% of the years), or “not wet” (i.e., dry or average) years, with precipitation amounts less than 130% of the long-term average (~75% of the years). The rationale for this wet–dry division is that annual precipitation patterns in arid regions follow a gamma distribution where high-precipitation years skew the mean above the median (Wilks 1990;



**Fig. 7** Variations in the percentages of deaths of established plants within populations for *Encelia farinosa* (plate **a**, open circles), *E. frutescens* (plate **b**, filled circles), and *Ambrosia salsola* (plate **b**, open squares) between 1981 and 2017. *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other. Asterisks indicates a weak (\*, ONI=1) or strong (\*\*, ONI>1) El Niño year. “o” indicates a strong La Niña year (ONI<-1)

Wu et al. 2007). For the Shoshone winter–spring precipitation data, the median total value (132 mm) was lower than the mean precipitation over this period (143 mm). Mortality was classified into high-mortality years, in which 10% or more of the population perished or low mortality years in which less than 10% of the population perished. The 10% categorization was based on previous literature estimate for *E. farinosa* life expectancies.

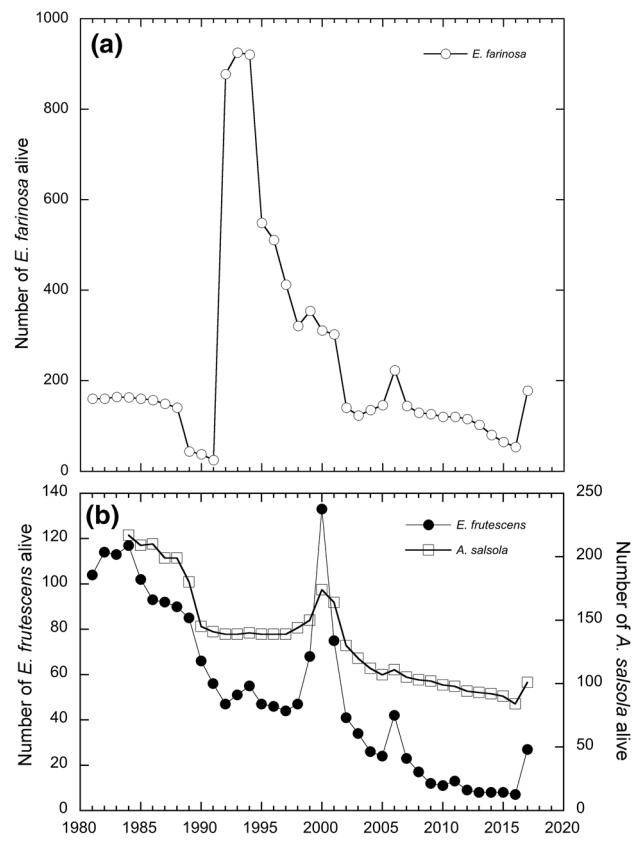
Surprisingly, *Encelia* high shrub mortality rates were not influenced by a simple categorization of high-mortality-rate years into “wet” versus “dry” years. For *E. farinosa*, occurring on shallow-soil slopes, shrubs were not more likely to experience high mortality rates during “dry” years than during “wet” years (Table 2). A similar pattern was repeated with the wash species, *E. frutescens* (Table 2). Even when precipitation conditions in the year preceding death were considered, there were still no significant patterns between mortality rates and “wet” versus “dry” years: *E. farinosa* and *E. frutescens* (Table 2). A statistical analysis was not possible with *A. salsola*, since a mortality rate of 10% or higher only occurred twice in the entire 37-year period. However, it is worth noting that the two high-mortality years for *A. salsola* shrubs occurred during “dry” years.

Since high germination rates were associated with El Niño years (i.e., ONI>1), it is possible that high mortality

rates could be associated with neutral and La Niña years (i.e., non-El Niño years, ONI < 1). This could capture some precipitation effects, but are related more broadly to general atmospheric circulation characteristics. It is also possible that high mortality rates might be associated with non-El Niño conditions of the previous year, given that such dry conditions might have weakened the shrubs, resulting in partial dieback of the canopy structure and increased sensitivity to drought-induced mortality. However, as with precipitation analyses, ENSO-driven mortality patterns did not emerge from the census data. For neither *Encelia* species were shrub mortality rates more likely to be higher during non-El Niño years (neutral and La Niña years) than during El Niño years (Table 2). Likewise, if we consider the previous year's ONI conditions, shrub mortality was just as likely in neutral and La Niña years as in El Niño years: *E. farinosa* (Table 2). This was unexpected given that the two extremes in water availability (El Niño and La Niña) could have been significant contrasting drivers for germination versus mortality events.

Instead *Encelia* shrub mortality appeared to be sensitive to a shift from the warm phase (wetter, PDO > 0) to the cold phase (drier, PDO < 0) of the PDO. In the wash habitat, *E. frutescens* shrub mortality was more likely to occur during the transition year to a cold phase of the PDO (Table 1), suggesting an immediate impact to the PDO change. There were too few high-mortality events for *A. salsola* during this 37-year observation period to evaluate this species' response, but when *A. salsola* mortality rates exceeded 10% (only twice), they were during negative phases of the PDO. In contrast, for *E. farinosa* shrubs, the effect of the current year's PDO transition to a cold phase on increasing mortality was not significant, but instead the pattern was statistically significant when evaluated against the previous year's transition to cold phase of the PDO (Table 2). This may imply that *E. frutescens* mortality rates were more sensitive than those of *E. farinosa* to PDO transitions. Irrespective, the differences in PDO-related mortality triggering events resulted in contrasting patterns during which *E. farinosa* versus *E. frutescens* experience high mortality rates (Fig. 7). While mortality patterns in both *Encelia* species appeared to be influenced by transitions in sea surface temperature conditions in the northern Pacific (i.e., PDO), mortality drivers contrasted with germination patterns which were influenced by sea surface conditions in the equatorial Pacific (i.e., ENSO). The basis for these subtle different large-scale SST influences is not clear at this time, although it is known that PDO and ENSO events are often correlated with each other.

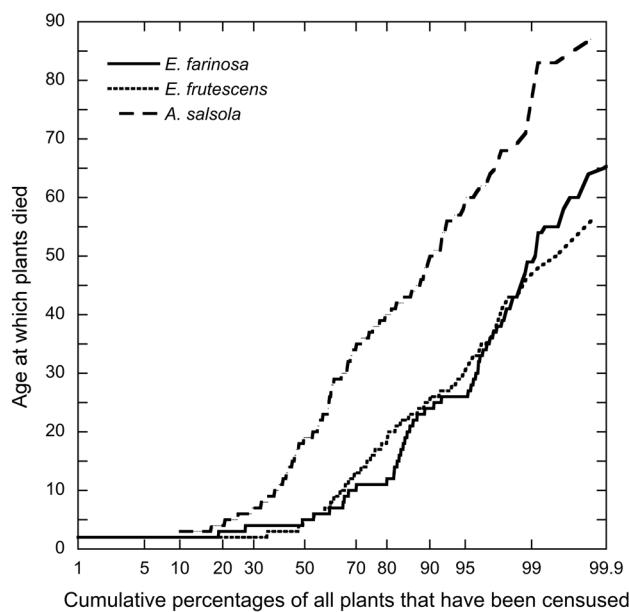
The consequence of episodic establishment and drought periods has been large fluctuations in the population sizes of *E. farinosa*, *E. frutescens*, and *A. salsola* (Fig. 8). Each of the three species has experienced but a single major and two minor establishment events during the 37-year observation



**Fig. 8** Variations in the annual total number of established plants for *Encelia farinosa* (plate a, open circles), *E. frutescens* (plate b, filled circles), and *Ambrosia salsola* (plate b, open squares) populations in spring between 1981 and 2017. *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other

period. The major establishment events occurred in different years for the slope versus wash species: 1992 for *E. farinosa* and 1999 for both *E. frutescens* and *A. salsola*, although all three species experienced an increase in the number of yearling plants in 2017. Over the last four decades, the long-term trend has been a decrease in total population numbers among all three species, with the decreased abundances most obvious for the two wash species: *E. frutescens* and *A. salsola*.

Our annual surveys allowed us to evaluate plant longevity in relation to the estimates that exist in the literature. Of the individual plant observations, 50% of the *E. farinosa* plants established as yearlings during this 37-year period were dead within 5 years (Fig. 9; 1378 plant observations). Mortality rates were higher in *E. frutescens* with 50% of established individuals dead within 5 years (299 observations). Longevity was longest in *A. salsola* shrubs, where 50% of established individuals persisted to 18 years (219 observations). Measurements of the 90% mortality rates provided a stronger indication of shrub life expectancies: 26 years for *E. frutescens*, 24 years for *E. farinosa*, and 51 years for *A. salsola*.



**Fig. 9** Variations in plant longevity for *Encelia farinosa* (solid line), *E. frutescens* (dotted line), and *Ambrosia salsola* (dashed line) versus the cumulative percentages of all plants that have been censused in these populations. *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other

(Fig. 9). Perhaps of greater interest is that of the individuals in the original *E. farinosa* population, 1.9% are still alive after 37 years and in many cases these were mature plants at the time the study began (based on flowering and plant sizes). None of the *E. frutescens* alive at the time the study began were still alive after 37 years of observations. Of the original *A. salsola* shrubs, 40% are still alive 35 years later. Using regression analyses to relate shrub age with plant size allowed an estimation of shrub ages for those present at the beginning of the study period. Based on this approach, the upper longevity estimates are 56, 66, and 86 years for *E. frutescens*, *E. farinosa*, and *A. salsola*, respectively.

We expect the shape of the shrub longevity curves to change slightly over time for two reasons. First, some plants in the original populations are still alive and maximum longevities may ultimately exceed the current estimates as episodic death events reshape these curves. Second, a legacy of establishment pulses can be seen in the data. These pulses appear as inflection points, indicating cohorts of plants that established very infrequently, but once established could persist for decades longer than the average plant longevity. A third possibility is that life expectancies may be changing as a result of episodic events of the last four decades or of changing climatic conditions.

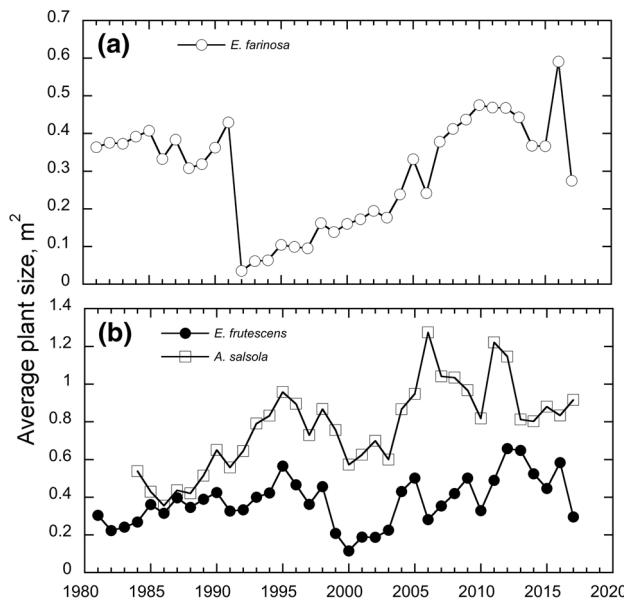
The age distributions over time differ among slope and wash species. For *E. farinosa*, the median and mean averages of plants have changed from 14.0 to 16.6 years, respectively,

in 1981, to 25.0 and 25.2 years, respectively, in 2015. However, the 75th percentile ages had changed little over the four decades, increasing from 22 to 25 years. This implies that the shifts in the *E. farinosa* population structure are occurring in the younger age classes. For *A. salsola*, the median and mean averages of plants have changed from 6.0 to 9.8 years, respectively, in 1984, to 40.0 and 40.6 years, respectively, in 2015. Coincident with the aging of the *A. salsola* population, the 75th percentile ages had changed appreciably over the four decades, increasing from 12.5 to 49.0 years. While the oldest *A. salsola* shrubs in the population were estimated to be 54 years in 1984, that upper age has increased to 85 years in 2015. The *A. salsola* population is persisting as the climate becomes more arid, but is aging with limited recruitment over the last four decades. The *E. frutescens* population had been nearly decimated by 2015, with only 8 plants alive compared to 104 in 1981. For those *E. frutescens* shrubs, the median and mean averages of plants have changed from 5.0 to 8.2 years, respectively, in 1981 to 15.5 and 13.9 years, respectively, in 2015. The 75th percentile ages had increased over the four decades, from 10 to 16 years. Thus, the trend is for aging populations in both slope and wash habitats, but with the largest differences apparent for the wash habitat shrubs.

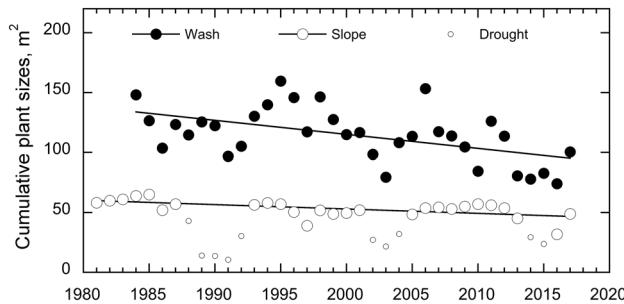
#### Average and total plant size changes imply competition for limited water on slopes

In an earlier study, Ehleringer (1993) established that *E. farinosa* shrubs compete for water and that once neighbors were removed plants rapidly increased in size. Our long-term observations confirm that the average *E. farinosa* plant sizes (ellipsoid projected plant area) increased, but only following decreases in population size (Fig. 10). Statistically, variation in the relationship of the interannual change in average *E. farinosa* plant size with a change in plant density is highly significant ( $y = -0.0004x - 0.0022$ ,  $r^2 = 0.477$ ,  $p = 0.000002$ ). While the lowest average plant sizes were observed when new plants were episodically added to the population, there was a persistent, subsequent long-term increase in average plant size to approximately  $0.4 \text{ m}^2$  as plants died. This was mostly associated mortality of young plants, but then subsequently by mortality of larger plants. There is an upper limit to *E. farinosa* plant size, with few plants ever achieving a size greater than  $1 \text{ m}^2$  projected surface area.

It is worth noting that if *E. farinosa* shrubs on shallow-soil slopes are indeed competing for a limited water supply, then we might expect to see a maximum supportable leaf area for the population. In Fig. 11, the sum of plant sizes for all *E. farinosa* in the near-monospecific population is plotted as a function of time. Note that the total projected plant surface area dipped three times over the last



**Fig. 10** Variations in the average plant size (projected ellipsoid,  $\text{m}^2$ ) within populations for *Encelia farinosa* (plate **a**, open circles), *E. frutescens* (plate **b**, filled circles), and *Ambrosia salsola* (plate **b**, open squares) populations in spring between 1981 and 2017. For *E. frutescens*, the relationship is  $y = 0.005x - 9.7$ ,  $r^2 = 0.176$ ,  $p = 0.005$ . For *Ambrosia salsola*, the relationship is  $y = 0.0163x - 31.8$ ,  $r^2 = 0.499$ ,  $p = 0.0001$ . *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other



**Fig. 11** Variations in the cumulative plant sizes (projected ellipsoid,  $\text{m}^2$ ) for slope species (*Encelia farinosa*, open circles) and wash species (*E. frutescens* and *Ambrosia salsola*, filled circles) in spring between 1981 and 2017. Small open circles represent years during which there was significant shrub death reducing projected plant areas. For wash species, the relationship is  $y = -1.264x + 22,650.7$ ;  $r^2 = 0.320$ ,  $p = 0.001$ . For slope species, the relationship is  $y = 0.363x + 777.1$ ,  $r^2 = 0.334$ ,  $p = 0.0008$ . *E. farinosa* occurs on slopes, whereas *E. frutescens* and *A. salsola* occur in washes; the slope and wash sites are approximately 22 km distant from each other

37 years. These short-term decreases in population-scale plant area were associated with events causing massive mortality (Fig. 7). For all remaining sample periods, the total plant sizes across the plot remained at a maximum of ~50–60 m<sup>2</sup>. This upper limit likely reflects a maximum

supportable shrub leaf area (transpiring surface), given interplant competition for a limited water resource in these slope habitats. However, the observed upper limits of supportable leaf area within the *E. farinosa* population significantly decreased between 1981 and 2017:  $y = 0.363x + 777.1$ ,  $r^2 = 0.334$ ,  $p = 0.0008$ . This 20.3% decrease in regressed upper-limit canopy leaf area reflects the trend of increased aridity as shown in Fig. 2.

In contrast, *E. frutescens* and *A. salsola* occupy a wash microhabitat, where competition for water is likely to be less because of large interplant distances (2–10 m), decreased shrub densities, and greater soil depth and water storage capacities relative to slope habitats. However, over the 37-year observational period, there has been a significant decrease in the numbers of *E. frutescens* and *A. salsola* shrubs (Fig. 8). Coincident with long-term decreases in plant density, there has also been a large and significant decrease in the cumulative shrub sizes (Fig. 11:  $y = -1.264x + 22,650.7$ ;  $r^2 = 0.320$ ,  $p = 0.001$ ). Although not quantified, there were no visible changes in overall wash-community species composition or in the total plant numbers of other wash species (mostly *Larrea tridentata*, a long-lived evergreen shrub) during the study period.

The decreases in wash shrub densities could be attributed to two possible factors: a decrease in moisture availability or an increase in destructive flashfloods. Our observations have not distinguished between these two possibilities, although increased flashfloods are less likely given an overall decrease in precipitation over time (Fig. 2). This long-term decrease in precipitation is likely having an impact on water availability or water storage at depth in the wash. Establishment of new wash shrubs over time has been low, especially when compared to more frequent establishment events for *E. farinosa*, the slope shrub species (Fig. 6). Since both wash and slope shrubs live in a similar precipitation-temperature climate regime, regional climate differences are not likely a factor contributing to differential mortality patterns. While the average cumulative sizes of all *E. frutescens* and *A. salsola* shrubs within the wash have decreased from 134 m<sup>2</sup> in 1984 to 95 m<sup>2</sup> in 2017 (42%) (Fig. 11), average individual shrub sizes have increased from 0.24 m<sup>2</sup> to 0.41 m<sup>2</sup> (68%) for *E. frutescens* and from 0.49 m<sup>2</sup> to 1.08 m<sup>2</sup> (120%) for *A. salsola* (Fig. 10). These time-trend relationships of increasing average plant size are statistically significant: *E. frutescens* ( $y = 0.005x - 9.7$ ,  $r^2 = 0.176$ ,  $p = 0.005$ ) and *A. salsola* ( $y = 0.0163x - 31.8$ ,  $r^2 = 0.499$ ,  $p = 0.0001$ ). In short, there are fewer plants in this wash landscape today, and those plants persisting are on average larger.

While the decreases in cumulative wash and shrub habitat plant sizes may not be immediately visible to the casual observer, the decadal decline rates in total projected plant

sizes of 11.7 and 3.6 m<sup>2</sup> per decade are substantial and will soon be evident to the casual desert visitor.

## Discussion

### Median and maximum life expectancies

A traditional theme in desert ecological research is that changes in structure occur slowly, especially changes in perennial plants populations (Vasek 1980; Wells 1961). For example, Cody (2000) estimated median life expectancies of 166–288 years for evergreen-leaf shrubs and 18–106 years for drought-deciduous shrubs in the Mojave Desert, based on population censuses in the 1980's. Bowers (2005a) provided similar average maximum longevity estimates of 184–330 years and 16–53 years for evergreen and drought-deciduous shrubs in the northern Sonoran Desert, respectively. On the other hand, repeat photography reveals occasional abrupt changes over time (Turner et al. 2003) and it is widely accepted that episodic drought and precipitation shifts have major impacts on mortality and in restructuring aridland communities (Bowers and Turner 2002; Breshears et al. 2005; Brown et al. 1997; Swetnam and Betancourt 1997; Turner 1990). Such patterns should also apply to the species in this study, but reported longevity observations are only available for *E. farinosa*.

Life expectancy estimates of *E. farinosa* in the Mojave and Sonoran Deserts have been based on multiple approaches: periodic plot observations and repeat photography. Reported *E. farinosa* life spans vary, likely in part because of the nature of the repeated observations to capture individual plants from a scene and possibly because different drought events may have occurred within each study. Based on permanent plots on Tumamoc Hill in southern Arizona, Shreve and Hinckley (1937) estimated an upper life span of 22 years for *E. farinosa*. Subsequently, repeated observations of these plots by Goldberg and Turner (1986), spanning multiple drought periods, revised these earlier estimates upward to 32 years. Bowers (2005a) provided an updated analysis of *E. farinosa* longevity on Tumamoc Hill and reported *E. farinosa* life spans ranging 6–32 years with an average life span of 16 years. A 2004 study by Bowers et al. (2004) estimated *E. farinosa* shrub life expectancy to be ~30 years. In contrast, Bowers et al. (1995) used repeat photography to estimate that *E. farinosa* shrubs could live for 70 years or longer at sites farther north in the Grand Canyon area. While these estimates clearly place *E. farinosa* life spans among those desert shrubs living less than a century, it is not clear as to the extent to which various estimates reflect different drought conditions, geographical factors, or constraints of different methodological approaches. Thus, it is not too surprising that we anticipated complete turnover

in plant population within three decades of initiating this study. However, there appear to be large differences between median longevity and maximum longevity.

The average life expectancies (50% survival) of all *E. farinosa* individuals in this study was 5 years, similar to previous Tumamoc Hill longevity results, and mortality rates among all *E. farinosa* were greatest during intermittent drought periods. However, when consideration is given to estimated ages of the 160 *E. farinosa* in the initial population, the suggested maximum life expectancies are 60+ years. The contrast between median and average life expectancies versus maximum longevity based on estimated age distributions in 1981 versus 2015 reveal that focusing on the former may underestimate the value of longer lived individuals in contributing seedlings to future establishment events.

An important aspect of plant longevity in desert systems is water-use physiology. Intrinsic water-use efficiencies are known to be genetically based and may contribute to variations in individual plant productivity and drought survival (Ehleringer et al. 1990; Farquhar et al. 1989; White et al. 1990; Zacharisen et al. 1999), with strong evidence that intrinsic water-use efficiency differences occur in *E. farinosa* (Sandquist et al. 1993; Schuster et al. 1992, 1994). In a study of competition and drought survival in monospecific *E. farinosa* in the northern Sonoran Desert, Ehleringer (1984) found that individual shrubs were more likely to persist through a drought if they had higher intrinsic water-use efficiencies. It may be that longer lived individuals persisting for multiple decades may have higher intrinsic water-use efficiencies than the average in the population, increasing the likelihood of persistence through an extended drought period.

We estimated that the two wash species had significantly different life expectancies, with *E. frutescens* shrubs attaining a maximum age of 56 years, while *A. salsola* achieves a maximum age of 85 years. Yet the persistence of these wash shrubs is more likely to be dependent on a climatic shift to wetter conditions than the region has experienced over the last four decades. The aging of *A. salsola* shrubs from an average of 6 years in 1981 to 40 years in 2015 highlights the lack of new plant establishment during these arid decades, but also highlights the resilience of this shrub species to persist through long-term drought. By contrast, the maximum life expectancy of *E. frutescens* shrubs is lower, and when combined with limited recruitment of new individuals over the last four decades has resulted in population sizes low enough that local populations are at risk of becoming extinct.

## Episodic mortality of desert perennials

While it is likely that individual shrubs will die each year, two patterns emerge: high mortality rates are not necessarily associated with year-to-year drier climate conditions and younger plants are more likely to die than older individuals. That high mortality rates are episodic is not surprising and has been noted for both *Encelia* and other Mojave and Sonoran Desert shrubs (Miriti 2007; Miriti et al. 1998; Webb et al. 2003; Webb et al. 1987, 1988). What is perhaps surprising is that high mortality rates did not occur more often during dry years than wet years, but instead occurred disproportionately during periods when there is a shift from the warmer to colder phase of the PDO cycle. The impacts of precipitation shifts that occur with changes in PDO on desert ecosystems are not well understood at the moment, but Hereford et al. (2006) have suggested a broad pattern. The results of this study confirm a precipitation-independent and PDO-related pattern of higher shrub mortality rates for both slope and wash *Encelia* species. Studies forecasting mortality patterns into the future recognize that water limitations will play an ever increasing role on productivity and plant distributions in the arid Southwest (Bunting et al. 2017; Munson et al. 2011). Understanding the impacts of PDO on desert vegetation may be an important part of such predictions in the future.

Koepke et al. (2010) and Lloret et al. (2012) reviewed morphological features thought to be beneficial for surviving extreme mortality events, which included reduced leaf areas and dieback. Over the 37-year period, episodic mortality was uncommon, occurring only about once every 6 years for both slope and wash species, and typically not in the same years. We had predicted that mortality rates in the slope species would be more sensitive to drought than wash species, because of lower soil moisture availability. However, the data did not support this hypothesis (Hypothesis 3), as wash species were more likely to die in years when the PDO cycle shifted from warm to cold, whereas the mortality impact on the slope species was not evident for 2 years following the PDO shift. Counter to a pattern of good years and bad years for the widespread growth of annuals in southwestern deserts (Ehleringer 1985; Forseth et al. 1984; Fox 1990), mortality was not clearly aligned with drought.

## Cross-habitat coherence in phenology

We found strong and consistent data to support Hypothesis 1. There are similar year-to-year phenological patterns for slope and wash species, despite these shrubs occurring in microhabitats with different soil moisture dynamics and availability. As shown in Figs. 3 and 4, these three drought-deciduous perennials exhibited remarkable year-to-year

phenological coherence. Leaf areas across habitats were driven by variations in winter–spring precipitation, suggesting that precipitation was the key driver in the development of canopy leaf cover. Similar to the notion of good years versus bad years for desert annuals and blooms (Bowers 2005b), flowering in these three shrubs varied appreciably from year to year. Yet there was again a remarkable coherence in flowering intensities for all three shrub species.

## ENSO drives germination, but what drives establishment?

Although it is commonly assumed that El Niño years produce a desert landscape that is alive with spring annuals, that has not been the case when examined in detail across the Mojave and Sonoran Deserts (Bowers 2005b). Germination and productivity among spring desert annuals are more significantly related to above normal precipitation amounts (Beatley 1974), forming the basis predictions of Hypothesis 2. However, while precipitation amounts explained approximately 8–16% of the germination numbers for *E. farinosa* and *E. frutescens* seedlings, germination rates of *A. salsola* seeds were not significantly related to precipitation amounts. Instead, El Niño was the common event triggering extensive germination. Seeds of all three species were more likely to germinate during an El Niño year than during a non-El Niño year.

Bowers et al. (2004) documented the importance of continued soil moisture inputs to the establishment of perennial shrubs. Consistent with this earlier observation, we found that in *E. farinosa*, the slope species, rainfall amounts in the year following germination mattered and seedling establishment was significantly related to the establishment year's cumulative winter–spring precipitation. That is, while an El Niño event triggered seed germination, adequate winter–spring precipitation in the subsequent year increased the likelihood of new *E. farinosa* establishment. However, there were no significant relationships between yearling establishment and cumulative precipitation amounts in the wash species and the factors facilitating *E. frutescens* and *A. salsola* establishment are unclear at this time.

## Long-term trajectories with increased drought over the past four decades

Projections into the future forecast increasing aridity for southwestern desert landscapes. Both Hereford et al. (2006) and Cook et al. (2015) predict more arid landscapes in southwestern North America, with cascading impacts on desert vegetation. The effects of increasing aridity are already apparent as evidenced by decreasing shrub abundances in wash habitats, aging populations, and a trend for decreasing maximum supported leaf areas in both slope and

wash habitats. During the four decades of this study, the abundances of both wash species have declined, with only a single significant new plant establishment event during the entire observation period. Plant population sizes in 2017 were only one-third of the number at the time the censuses began. As shrub number decreased and recruitment was limited, the average shrub sizes effectively doubled. Yet because the net population loss was not balanced by higher shrub growth rates, the total projected shrub areas decreased. In effect, the total transpiring surface at the landscape level decreased over time, and more so in wash habitats than on the slopes. The long-term trajectory is for continued decreases in shrub abundances and decreased transpiring surface areas as the region becomes more arid. Given the decadal total projected plant area decline rates of  $11.7 \text{ m}^2$  per decade in the wash habitat, we should expect to see *E. frutescens* disappear from the wash in the coming decade unless there is a long-term shift toward the warmer phase of the PDO in the near future. The long-term trajectories for *A. salsola* are also for continued decreased in population size, yet because of this species greater longevity, the diminishment of this population will take a substantially longer time.

The results of this study also forecast longer term decreases in shrub abundances for *E. farinosa* on slopes. Despite the recruitment of new *E. farinosa* individuals in 2017, the trend since 1981 and certainly the trend since the major 1992–1994 establishment period has been one of decreasing population size. Given that these shrubs occur in such close proximity to each other on shallow soils in which competition for water is likely to be high (Ehleringer 1984), the mortality of any individual opens new belowground space to be exploited by neighbors. If interplant root interactions among neighbors constraining belowground acquisition of water (Mahall and Callaway 1991, 1992), then it is expected that these shrubs will be increasingly competing for a decreasing water supply. Based on forecast by Munson et al. (2011), we can expect that the trends toward increasing regional aridity will exacerbate competitive interactions and limit population size for the foreseeable future.

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**Author contribution statement** JRE designed the study; JRE, DRS, and colleagues collected the data; JRE analyzed the data; and JRE and DRS wrote the manuscript.

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