Microhabitats associated with solar energy development alter demography of two desert annuals

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Abstract. Political and economic initiatives intended to increase energy production while reducing carbon emissions are driving demand for solar energy. Consequently, desert regions are now targeted for development of large-scale photovoltaic solar energy facilities. Where vegetation communities are left intact or restored within facilities, ground-mounted infrastructure may have negative impacts on desert-adapted plants because it creates novel rainfall runoff and shade conditions. We used experimental solar arrays in the Mojave Desert to test how these altered conditions affect population dynamics for a closely related pair of native annual plants: rare *Eriophyllum mohavense* and common *E. wallacei*. We estimated aboveground demographic rates (seedling emergence, survivorship, and fecundity) over 7 yr and used seed bank survival rates from a concurrent study to build matrix models of population growth in three experimental microhabitats. In drier years, shade tended to reduce survival of the common species, but increase survival of the rare species. In a wet year, runoff from panels tended to increase seed output for both species. Population growth projections from microhabitat-specific matrix models showed stronger effects of microhabitat under wetter conditions, and relatively little effect under dry conditions (lack of rainfall was an overwhelming constraint). Performance patterns across microhabitats in the wettest year differed between rare and common species. Projected growth of *E. mohavense* was substantially reduced in shade, mediated by negative effects on aboveground demographic rates. Hence, the rare species were more susceptible to negative effects of panel infrastructure in wet years that are critical to seed bank replenishment. Our results suggest that altered shade and water runoff regimes associated with energy infrastructure will have differential effects on demographic transitions across annual species and drive population-level processes that determine local abundance, resilience, and persistence.

Key words: annual plants; aridland ecosystems; California; demography; matrix model; Mojave Desert; population dynamics; rare species; renewable energy; seed bank; solar panel.

Introduction

Plant distribution, abundance, and species diversity are affected by complex physical gradients and variable climatic patterns at the landscape scale (Gleason 1917, Went 1948, Tevis 1958, Vazquez and Givnish 1998). Yet, microhabitat differences can mitigate effects of these drivers on plant performance locally (Kadmon 1993, Gómez-Aparicio et al. 2005, Stephens et al. 2014). Human impacts are layered over these sources of natural variation, often mediated through land type conversion and climate change, further altering species and population performance (Lovich and Bainbridge 1999, Easterling et al. 2000, Fischer and Lindenmayer 2007, Selwood et al. 2015). Recently, political and economic initiatives have triggered a renewable energy development boom in the southwestern United States, driving extensive land-cover change in previously unfragmented desert landscapes (Cameron et al. 2012, Hernandez et al. 2014, California Energy Commission et al. 2016, Parker et al. 2018). Photovoltaic (PV) panels create novel shade and

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moisture gradients that overlay natural microhabitats created by topographic variation (Smith et al. 1987, Tanner et al. 2020). Solar energy facility designs that retain ecological functions have been recommended as a means to increase the sustainability of solar energy development (Moore-O'Leary et al. 2017, Hernandez et al. 2019), and plant communities have been retained or restored under panels in some locations (Beatty et al. 2017, Walston et al. 2018, Choi et al. 2020). To develop best management practices that mitigate adverse solar energy development impacts, as mandated by state and federal policies, we need to understand how plant vital rates and population trajectories are affected by PV solar energy infrastructure.

Desert annual plant species may be especially sensitive to altered microhabitats associated with energy infrastructure due to the finely tuned demographic processes that allow them to persist in highly variable environments. Annuals rely on temperature and precipitation triggers to stimulate germination and favor emergence (Beatley 1974, Freas and Kemp 1983), and seed dormancy enables persistence of populations through unfavorable periods: in any given year, only a fraction of seeds germinate, spreading germination risk over time (Philippi 1993, Adondakis and Venable 2004). Microsite conditions following seed dispersal affect rates of seed survival and mortality, driven by the effects of physical stress (heat, pressure, cold) on seed coats and microhabitat favorability to seed pathogens (Parker et al. 1989, Schafer and Kotanen 2003, Mordecai 2012, Li et al. 2019). Although seed demography is a critical driver of annual plant population performance (Schmidt and Lawlor 1983, Brown and Venable 1986, Salguero-Gómez et al. 2012), we lack detailed understanding of how microsite variation affects desert annual seed demography, making it difficult to forecast how novel microhabitats created by energy infrastructure may influence native plant populations. Furthermore, even when microsites are suitable for seed survival and seedling emergence, individuals may still fail to reproduce if conditions change or microhabitat conditions do not favor later life stages (Went 1948, Tevis 1958, Beatley 1967, Pavlik 2008). For this reason, surveys documenting annual species presence or abundance alone, particularly in a single year, may not indicate long-term species response to novel or altered habitat conditions.

Population growth models integrate species performance across the life cycle and predict population-level consequences (Caswell 2001, Salguero-Gómez et al. 2012), providing an effective tool to compare species responses to the novel microhabitats generated by energy infrastructure. For annual plants, population growth models can also be used to explore effects of microhabitat variation on belowground vs. aboveground life stages, yielding a more comprehensive assessment of the mechanisms underlying species resilience or vulnerability. At present, there is little empirical work testing energy infrastructure impacts on plant performance (but see Smith et al. 1987, Armstrong et al. 2016, Suuronen et al. 2017, Tanner et al. 2020) and to our knowledge, no studies have examined novel microhabitat effects at the population level.

The impacts of novel microhabitats are likely to vary among species, and may depend in part on whether plants occupy a generalist or specialist niche. Rare species often occupy narrow or uncommon niches, which may make them more sensitive to shifts in abiotic conditions and lead to disproportionate impacts from landscape-level changes (Rabinowitz et al. 1986, Markham 2014, Wamelink et al. 2014). Land conversion (e.g., agriculture, livestock grazing, urban development) is a major driver of rare plant extinctions (Lavergne et al. 2005), but logistical or regulatory barriers can make direct study of rare species impacts very challenging. In some cases, the study of carefully chosen common species that share a life history strategy or ecological niche may provide the opportunity to test effects of experimental treatments or conservation actions (Caro et al. 2005). Such use of "surrogate species" has been challenged on numerous grounds (Andelman and Fagan 2000, Murphy et al. 2011) and there is a need to test whether designated surrogates fulfill their heuristic function (Caro et al. 2005).

Recently, experimental panels have been used to simulate the distinct microhabitats created under photovoltaic arrays in the western Mojave Desert (Tanner et al. 2020), an area disproportionately impacted by solar energy development (Parker et al. 2018). Microsites under experimental panels had lower soil moisture compared to the open, with strong reductions in soil temperature and photosynthetically active radiation in panel shade (Tanner et al. 2020). Assay of the plant community demonstrated that the effect of altered abiotic conditions varied by habitat type and rainfall year, with a tendency for higher species richness and abundance in shade on stressful caliche pan habitat compared to gravelly bajada habitat (Tanner et al. 2020). Here, we link demographic responses of two focal species, partitioned into belowground and aboveground components, to observed microhabitat variation in order to predict the population trajectories and sensitivities of these annual plants to novel microhabitats.

We evaluated the demographic response of two Mojave Desert annuals, *Eriophyllum mohavense* (rare) and *E. wallacei* (common), to runoff and shade conditions created by experimental panels that simulate solar installations. We applied belowground seed survival rates obtained in a concurrent experiment (Hernandez et al. 2020), measured rates at which seeds germinated and emerged as seedlings, and tracked seedlings through reproductive maturity over a seven-year period. We used these data to parameterize matrix models (Caswell 2001) to analyze population growth and sensitivity to varying life cycle transitions under contrasting microhabitat conditions. Model projections represent the cumulative demographic impact of each microhabitat across life

stages, manifesting as relative population growth. We hypothesized that the rare species would be more responsive to both natural and manipulated environmental variation than the common species.

We address three questions: (1) How do microhabitats created by simulated solar panels affect population numbers and demographic rates (seedling emergence, survival to adulthood, fecundity) in the context of year-to-year variation in rainfall? (2) Are there differences in the effects of microhabitats on demographic transition rates between a rare and common species? (3) How do experimental microhabitats affect the projected population growth rate of each species?

METHODS

Rare–common species pair

Our focal taxa are two plant species with similar morphology and life history strategies, both associated with low-elevation creosote scrub typical of the Mojave Desert (Appendix S1: Fig. S1). *Eriophyllum mohavense* ((I.M. Johnst.) Jeps., Asteraceae) is a rare California endemic species of conservation concern (California Energy Commission et al. 2016), bearing the California Rare Plant Rank 1B.2 (California Native Plant Society 2020). It is found in small, isolated occurrences, restricted to edaphic islands in the western Mojave Desert (ERT 1988, California Native Plant Society 2020). *E. wallacei* (A. Gray) A. Gray is a common, self-incompatible forb (Mooring 2002) that is widely distributed across the American southwest, although not found in the special edaphic conditions that support *E. mohavense*. Both species are diminutive winter annuals found in shrub interspaces. Seeds germinate in fall or winter and plants set achenes (hereafter called seed) in late spring (Jepson Flora Project 2020).

Study sites

Arrays of experimental panels (Fig. 1a) were used to measure species response to solar infrastructure, circumventing difficulties in securing facility access. This strategy also ensured identical experimental treatments across sites (operational arrays often differ in details, e.g., fixed vs. tracking arrays), and allowed a test of panel effects on intact plant communities absent from nearby graded sites. Because the industry is moving toward designs that retain native vegetation understories (e.g., Ivanpah Solar Energy Generating System, California, USA), this approach is highly relevant for understanding site impacts.

As expected given their distinct edaphic niches, we could not find a location with both *Eriophyllum* species, so we had to select two separate sites for the two species. The sites are separated by ~55 km and by definition differ in physical attributes that may affect plant performance. The "Caliche-*mohavense*" experimental array

was installed on a series of south-facing knolls east of Boron, California, USA, at an elevation of 721 m. This array is sandwiched between the Solar Energy Generating Facility (SEGS) III–VII at Kramer Junction, and SEGS VIII–IX and Mojave Solar at Harper Dry Lake to the east. Here *E. mohavense* occurs on edaphic "islands" with a subsurface caliche layer and soils high in boron (ERT 1988). The "Gravelly-*wallacei*" array was installed on a gently sloping bajada at an elevation of 925 m. The nearest operational solar facility is Longboat Solar outside Barstow, California, USA, ~25 km to the northwest, and the decommissioned Solar One/Solar Two site is ~8 km to the northeast.

Plots

The distribution and density of both focal species is very patchy at scales under 1 m^2, so we chose plots nonrandomly in spring 2011 to contain a threshold number of individuals (see Appendix S1: Experimental plots), thus increasing the probability of natural seed banks within plots. Twenty plots were randomly assigned to control or experimental treatment at each site. At treatment plots we installed experimental panels to create "Shade" and "Runoff" microhabitats (Fig. 1b) that simulate conditions under photovoltaic panels (Tanner et al. 2020). Panels consisted of a metal frame holding a ~61 × 61 cm wood insert at a 30° angle (Appendix S1: Fig. S2). Despite the smaller size of experimental panels, reductions in photosynthetically active radiation underneath were commensurate with measurements under a full-scale panel near solar noon (Tanner et al. 2020). However, more early morning and late afternoon sunlight can penetrate under experimental panels compared to full-size operational arrays, where rows of contiguous panels also have the potential to divert more rainfall to their downslope edge. Thus, we consider experimental panel effects to be a conservative estimate of commercial panel array impacts.

Aboveground population numbers

We counted the total number of *Eriophyllum* individuals present across microhabitats at each plot on peak season surveys (late March–early April) from 2012 to 2018.

Fates of seeds

To track emergence, seeds were attached to toothpicks with water-soluble glue (see Appendix S1: Seedling emergence, Table S1) and sown into Control, Runoff, and Shade microhabitats. This allowed us to estimate the proportion of individuals successfully transitioning from seed to seedling (Baack et al. 2006) for each microhabitat.

Results from concurrent seed bank studies (Hernandez et al. 2020) at the same experimental arrays were
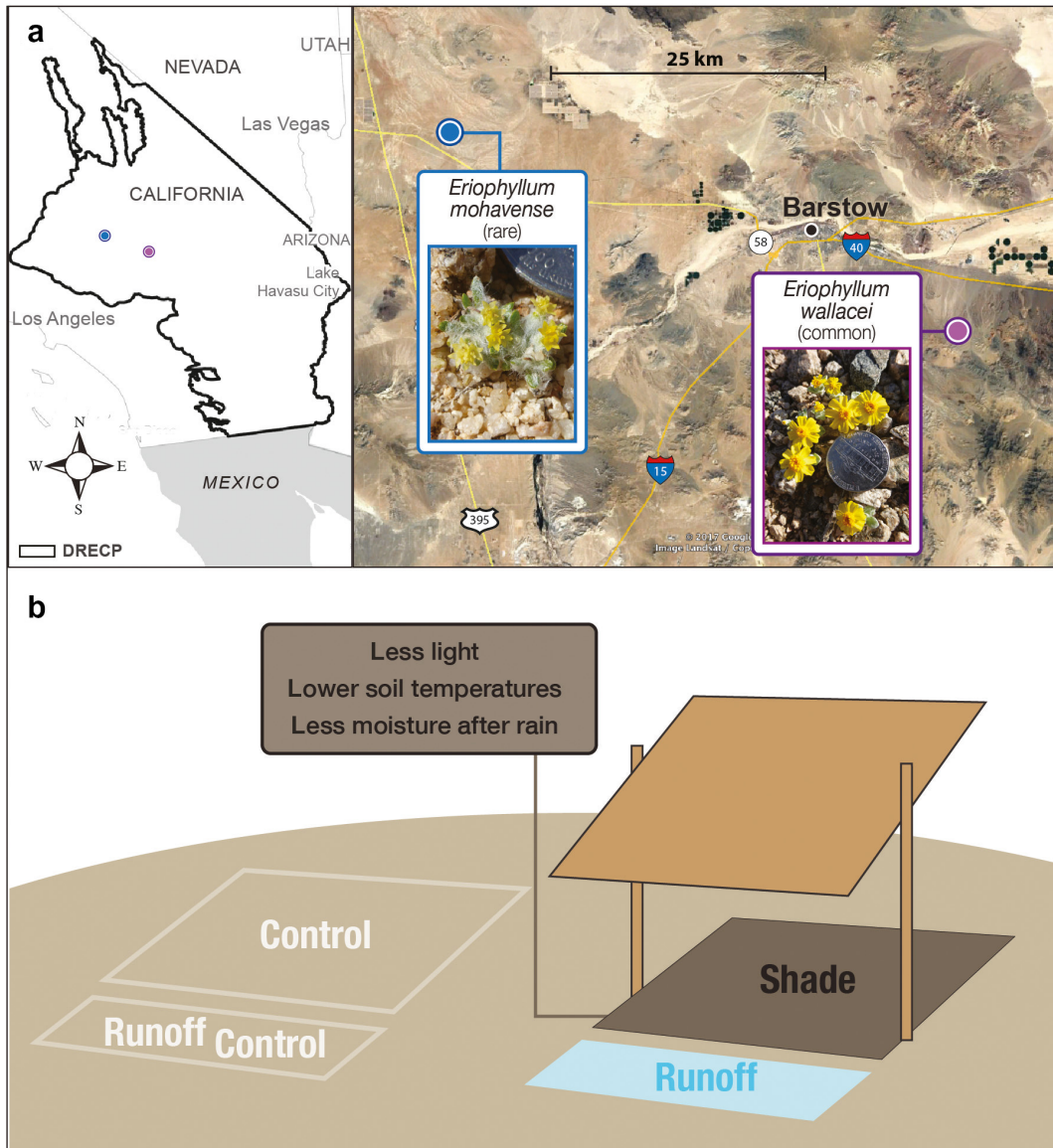
Fig. 1. (a) Locations of the Caliche-*mohavense* and Gravelly-*wallacei* experimental arrays, and focal species at each array and (b) plot experimental treatment design. Each plot consisted of a pair of microhabitats: either Control and Runoff Control, or Shade and Runoff. Experimental panels created the Shade and Runoff microhabitats, where light, water input, and temperature differed from ambient conditions (Tanner et al. 2020). The heavy outline on the map in panel a shows the Desert Renewable Energy Conservation Plan Area. Satellite imagery was acquired using Google Earth Pro 7.3.2.5776 (4 September 2015). Mojave Desert, California, USA.

used to parameterize seed bank survival rates for each species. In that study, seeds were sewn into fabric packets in summer 2016, distributed among the Control, Runoff, and Shade microhabitats in fall 2016, and retrieved in March of 2017 or 2018 to allow estimation of the percentage of seed remaining intact in the seed bank (the "retained seed pool") through one or two growing seasons. Seed produced in 2016 was limited and had to be supplemented with 2015 seed; we tracked 2015 and 2016 seed cohorts separately. In addition, we subjected a subset of recovered intact seed to a tetrazolium staining assay to test viability (Hernandez et al. 2020). In the

modeling work reported here, the percentage of retained, intact seed (determined from visual inspection) is considered to be a "generous" estimate of survival in the seed bank. Multiplying the "generous" estimates by the percentage of seed assessed viable in tetrazolium assays provides a more "conservative" estimate of seed bank survival (Appendix S1: Table S2).

Seedling survivorship

Between late January and early February in six years (2012–2014 and 2016–2018), we randomly selected

seedlings with two whorls of true leaves or fewer ("juveniles") and marked them with colored toothpicks. These plants were followed through the growing season, and final state was assigned as "non-reproductive" or "reproductive" (Appendix S1: Fig. S1) based on observations between late March and early April. We assumed that plants in bud or flower would successfully complete the life cycle.

Mean seeds per plant

A subset of marked, reproductive individuals was randomly selected for collection to estimate number of seeds produced per plant across microhabitats in each year. When sample sizes of mature, marked plants in a given microhabitat were low, we collected additional mature, unmarked plants from the same location where possible. When this was not possible, we supplemented collections with additional mature plants from the appropriate microhabitat at other plots. Collected plants were stored individually in paper coin envelopes until capitula could be dissected under a stereoscope at University of California. Only apparently viable, mature seeds (black and firm) were included in seed counts.

Rainfall

The rainfall season for winter annual plants begins in fall and extends through spring, so we define the growing season as October through March and use hydrologic year naming conventions (e.g., 1 October 2011 to 31 March 2012 is the 2012 hydrologic year; see Appendix S1: Rain window modeling for more details). We acquired historic rainfall data for each site from nearby weather stations as described in Tanner et al. (2020). We calculated cumulative rainfall for rain windows of interest, and used data from 1945 to 2018 to calculate 5th through 95th rainfall percentiles for each site.

Data analyses

Aboveground population numbers.—Plant density was calculated at the plot level for each microhabitat in all years where data were available. To accommodate the patchy distribution of plants at scales under 1 m^2, we focused on contrasts between microhabitats with the same dimensions (i.e., Control vs. Shade, and Runoff Control vs. Runoff). We broke data into the appropriate subsets and used a square-root transformation to reduce heteroscedasticity. The influence of total rainfall, early rainfall, and late rainfall on density was tested by building sets of linear models using cumulative precipitation from five different "rain windows" as predictors (see Appendix S1: Rain window modeling). The early rain window had most influence on plant density, in agreement with earlier work on desert winter annuals (Beatley 1974). Final regression models of density response to weather included early rainfall, microhabitat, and the interaction between microhabitat and rainfall. We then compared patterns in model predictor significance to a model substituting a categorical year predictor for rainfall (the year predictor implicitly captured rainfall as well as additional sources of environmental variability across years). Diagnostic plots showed some deviation from linear assumptions for both model variants (in particular, heteroscedasticity could not be entirely eliminated in the year model). We also found that the patterns in model predictor significance shifted between the rainfall and year model variants; we present results for the latter here because environmental cues other than rainfall are known to affect emergence (e.g., temperature during or following rainfall; Went and Westergaard 1949, Adondakis and Venable 2004, Levine et al. 2008). We used the car package to extract Type III P values from models (Fox and Weisberg 2011), and we conducted post hoc comparisons of density between microhabitats using the emmeans package (Lenth 2019) to generate adjusted marginal means for unequal sample sizes. Significant differences are reported at the $P \leq 0.05$ level and marginally significant differences are reported at the $P \leq 0.10$ level throughout.

Demographic rates

Seedling emergence rate.—Seedling emergence rate was calculated by dividing the total number of seedlings observed on toothpicks by the total seed present in toothpick arrays. Because emergence rates were low across all years and seed cohorts, a single emergence rate was calculated for the 2011 cohort and the combined 2015/2016 cohorts in each microhabitat and year (see Appendix S1: Seedling emergence for more details). Fisher's exact tests were used to compare emergence across microhabitats in all years with non-zero emergence.

Seed bank survival rates.—We extracted the percentage of intact, retained seed recovered from packets buried for one growing season and two growing seasons from Hernandez et al. (2020). Although we found differences between the 2015 and 2016 seed cohorts, which may be related to differences in seed quality, maternal effects, or other causes (Hernandez et al. 2020), we found no strong evidence of seed deterioration associated with storage, as would be demonstrated by consistently lower retained seed pools in the older (2015) cohort. We believe variability is an important feature of seed bank behavior in this system. We therefore chose to include as much data as possible and combine cohort datasets for bootstrapping "generous" seed bank survival rates (Appendix S1: Table S2), thus incorporating variability in seed performance captured by the two cohorts. We then generated "conservative" seed bank survival rates by multiplying the bootstrapped "generous" values by the percentage of seed that stained in tetrazolium assays carried out by Hernandez et al. (2020). In the rare species, neither microhabitat nor seed cohort had an effect on the

percentage of seed that stained (indicating viability). In the common species, microhabitat also had no effect on the percentage of seed that stained, but we observed a lower staining rate for the 2015 cohort after the first year of burial. This pattern would be consistent with a loss of viability in storage, but it could also reflect other biological or methodological factors (see Hernandez et al. 2020 for more details), and the absence of a similar pattern in the "generous" seed bank survival rates suggests the latter. Given our goal to model *Eriophyllum* performance using the best possible demographic rates, we chose to accommodate uncertainty of the viability estimates by averaging the staining rate across cohorts as well as microhabitats for each species.

Survivorship and fecundity.—Plant survivorship and mean seed output were calculated at the plot level for each microhabitat in all years where aboveground data were available. Before calculating survivorship and seed output on this basis, we combined data from Control and Runoff Control microhabitats (where growing conditions were identical for any given year). We tested the influence of total rainfall, early rainfall, and late rainfall on survivorship and seed output by building sets of linear models (ANCOVAs) with cumulative precipitation from five different "rain windows" as a predictor (see Appendix S1: Rain window modeling). Full models included microhabitat, rainfall, and microhabitat × rainfall as fixed effects; we removed non-significant interactions involving the rainfall covariate to avoid compromising the calculation of Type III sum of squares, reporting results using the reduced model where appropriate. Seed count data were square-root transformed to help control spread of model residuals at higher fitted values. Comparisons of model AIC values were used to identify the rain window with greatest explanatory power for survivorship and seed output of each species (Appendix S1: Table S3). We used lmList in the lme4 package (Bates et al. 2015) to obtain linear equations for response variables in each microhabitat from the models of best fit, and conducted post hoc tests of marginal means across microhabitats at all levels of rainfall using the emmeans package (Lenth 2019).

Demographic modeling

Matrix models (Caswell 2001) were built for the target species using rates obtained in the Control, Runoff, and Shade microhabitats over the seven-year period 2012–2018. Separate experiments for each life stage were used to estimate belowground and aboveground demographic rates needed to parameterize models, avoiding seed bank disturbance otherwise needed to obtain seed survival and germination estimates. Because our models incorporate aboveground and belowground transition rates from different individuals obtained over unequal time periods (seven years for aboveground estimates vs. two years for belowground estimates), our demographic analyses do not fully capture covariance structure that may exist among rates. We therefore assume that associations between above and belowground transition rates are not primary drivers of variation in population performance (Kalisz and McPeek 1992). We used time-invariant, linear models taking the form $n_{(t+1)} = A \times n_{(t)}$, where A is an age-structured 3×3 matrix of fecundity and survival probabilities for seed aged 1 to 3+ yr (see Appendix S1: Models and parameters, Fig. S3). For convenience we reduced the life stages to seed age classes (Schmidt and Lawlor 1983), and we chose a 3×3 matrix because we observed rapid change in seed survival once seed entered the soil seed bank for both species (Hernandez et al. 2020). Models therefore included age-specific seed survival in the seed bank with the simplifying assumption that seed age does not affect survivorship or fecundity once individuals germinate and emerge aboveground (Schmidt and Lawlor 1983). We used a starting vector (**n**) of 1,000 1-yr-old seeds, and a projection interval from September of year X to August of year $X + 1$, consistent with a winter annual life cycle (no individuals survive aboveground from one interval to the next).

In years with sufficient aboveground data (transition rates estimated from at least seven marked plants, Appendix S1: Table S4), bootstrapping techniques were used to estimate seedling survivorship to maturity and seed output. From data sets for each microhabitat and year, we randomly drew individuals with replacement to generate bootstrapped data sets of equal size (Kalisz and McPeek 1992). In years (or microhabitats) where plants exhibited no or minimal aboveground activity (transition rates derived from less than seven marked plants), λ was calculated using only belowground matrix elements (Appendix S1: Table S4, Fig. S3), allowing microhabitat effects to operate on seed bank survival in the absence of aboveground activity. For seed survival through year 1 and through year 2, we used both generous and conservative seed bank survival estimates as described in *Demographic rates* above. For seed aged 3 yr or older, we used the year 2 seed bank survival rate. Population growth estimates using the generous vs. conservative seed bank survival rates were compared to examine model sensitivity to differences in these belowground estimates.

In some cases, alternative values were substituted for missing or unrealistic transition rates in matrices, when these were clearly artifacts of stochasticity and small sample size (Appendix S1: Table S4). For example, the experimental seedling emergence rate from seeds on toothpicks never exceeded 5.6%, and was zero in some years and microhabitats when natural emergence was relatively common. In such cases, including an emergence rate of zero in aboveground matrix elements effectively ignores microhabitat effects on survivorship and fecundity, an outcome we wished to avoid in years with obvious aboveground activity. To allow modeling of aboveground as well as belowground performance in these situations, we substituted Control emergence rates for missing rates within year. If no non-zero rates were

available for a given year, we took a conservative approach and substituted the lowest rate observed across years. In addition, logistical constraints prevented us from marking young plants in 2015, so we lack estimates of survivorship in this year. To fill this gap, we calculated mean survivorship for each microhabitat across two years bracketing 2015 in terms of late rainfall percentile (2014 and 2016 for *E. mohavense*, and 2013 and 2017 for *E. wallacei*; Fig. 2).

We bootstrapped matrices ($N = 1,000$) for each year and microhabitat (Control, Runoff, Shade) to estimate deterministic λ, as well as elasticity values for each transition rate. The parameter λ indicates species-specific performance (Caswell 2001) in each microhabitat given annual weather conditions, with 95% confidence intervals calculated from bootstrapped data sets for each species to evaluate microhabitat differences. The elasticity of λ to change in different demographic transition rates can reveal the influence of those rates on population growth for each species. Elasticity values across the set of transition rates for a given microhabitat and year always sum to 1, so the relative influence of aboveground vs. belowground matrix elements on λ can be assessed (de Kroon et al. 1986). We also tested the influence of individual demographic transitions incorporated in aboveground matrix elements (Franco and Silvertown 2004) in our highest rainfall year, applying constant values for seedling emergence, survivorship, and seed output in turn when bootstrapping λ for both species. All projections were generated and analyzed using the popbio package (Stubben and Milligan 2007) in R version 3.6.3 (R Development Team 2020).

RESULTS

Weather

Total October–March rainfall was below the historic median in most years of our study (Fig. 2). Rainfall was below the 25th percentile in 5 yr at the
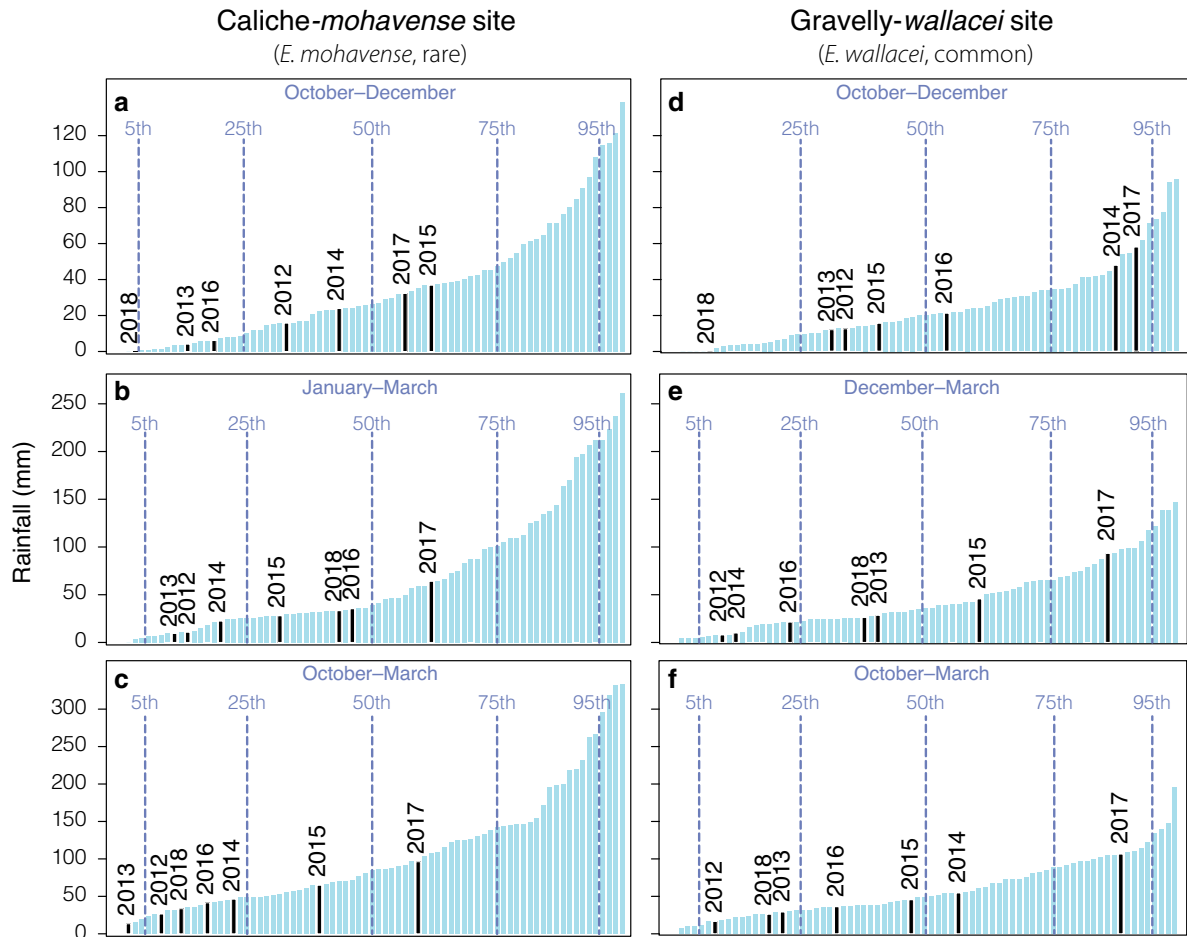

FIG. 2. Rainfall (mm) accumulation from 1945–2018 at permanent weather stations (a, b, c) KEDW, ~40 km southwest of the Caliche-*mohavense* site, and (d, e, f) KDAG, ~8 km northeast of the Gravelly-*wallacei* site. Three different rain windows are shown for each hydrologic year: early rain (a, d), late rain (b, e), and total rain (c, f). Each blue bar represents a single year, with years sorted by increasing rainfall within each rain window. Black bars indicate hydrologic years included in our study period. Dashed lines show the 5th, 25th, 50th, 75th, and 95th rainfall percentile for each rain window over the period 1945–2018.

Caliche-*mohavense* site (Fig. 2c), and 3 yr at the Gravelly-*wallacei* site (Fig. 2f). In 2017, total rainfall was in the 89th percentile at the Gravelly-*wallacei* site, but closer to the median at the Caliche-*mohavense* site. The latter therefore experienced a higher incidence of dry periods during our study. We observed high variation in precipitation within year at each site, with percentile rankings shifting depending on the rain window considered (compare 2014 rainfall windows at the Gravelly-*wallacei* site for a particularly dramatic example; Fig. 2d, e, f).

Aboveground population numbers

The year × microhabitat interaction had a significant effect on density across the Control vs. Shade microhabitats (Table 1a, c). Density of the rare *E. mohavense* was higher in Shade in two mediocre rainfall years, but did not differ from the Control in the driest and wettest years (Fig. 3a, b). The common *E. wallacei* showed a different pattern, with higher density in the Control in years where microhabitat effects mattered (Fig. 4a, b).

Only year affected density across the Runoff Control vs. Runoff microhabitats ($P < 0.001$ for both species, Table 1b, d).

Demographic transitions of seeds

In general, microhabitat did not affect the emergence of seedlings from seeds; the only difference observed was marginally higher emergence in the Control compared to Shade for *E. mohavense* in 2015 (Fisher's exact test, $P = 0.083$, Appendix S1: Table S5). Over all microhabitats, the proportion of seeds germinating and emerging as seedlings from toothpick cohorts ranged between 0 and 1.8% until 2017, the wettest year, when the average proportion across microhabitats increased to 4.7% for *E. mohavense* and 3.3% for *E. wallacei* (Appendix S1: Table S1). As described in Hernandez et al. (2020), microhabitat did not affect the seed staining rate for either species, or the percentage of intact seed recovered from packets buried for one growing season. However, more seed remained intact in the Shade microhabitat after two growing seasons.

TABLE 1. Results from linear regressions modeling the effects of rainfall year and experimental panel microhabitat on plant density.

Predictor	SS	df	F	P
E. mohavense (rare) density				
a) Control vs. Shade				
Intercept	8945.12	1	506.64	**<0.001**
Year	6729.94	6	63.53	**<0.001**
Microhabitat	60.81	1	3.44	*0.066*
Year × microhabitat	303.64	6	2.87	**0.012**
Residuals	2224.64	126		
b) Runoff Control vs. Runoff				
Intercept	3067.28	1	123.10	**<0.001**
Year	2069.43	6	13.84	**<0.001**
Microhabitat	33.14	1	1.33	0.252
Year × microhabitat	175.27	6	1.17	0.330
Residuals	1968.42	79		
E. wallacei (common) density				
c) Control vs. Shade				
Intercept	6496.25	1	380.70	**<0.001**
Year	4775.58	6	46.64	**<0.001**
Microhabitat	251.53	1	14.74	**<0.001**
Year × microhabitat	331.99	6	3.24	**0.005**
Residuals	2150.04	126		
d) Runoff Control vs. Runoff				
Intercept	8028.82	1	162.44	**<0.001**
Year	4806.86	6	16.21	**<0.001**
Microhabitat	2.38	1	0.05	0.827
Year × microhabitat	100.92	6	0.34	0.914
Residuals	6227.68	126		

Notes: Effects on the rare *Eriophyllum mohavense* on caliche soil are shown (a) for the Control and Shade microhabitats and (b) for the Runoff Control and Runoff microhabitats. Effects on the common *E. wallacei* on gravelly soil are shown (c) for the Control and Shade microhabitats and (d) for the Runoff Control and Runoff microhabitats. Analysis of variance table includes Type III *P* values generated using the car package (Fox and Weisberg 2011). Boldface text indicates significant effects at the $P \leq 0.05$ level and italic text indicates marginally significant effects at the $P \leq 0.10$ level.
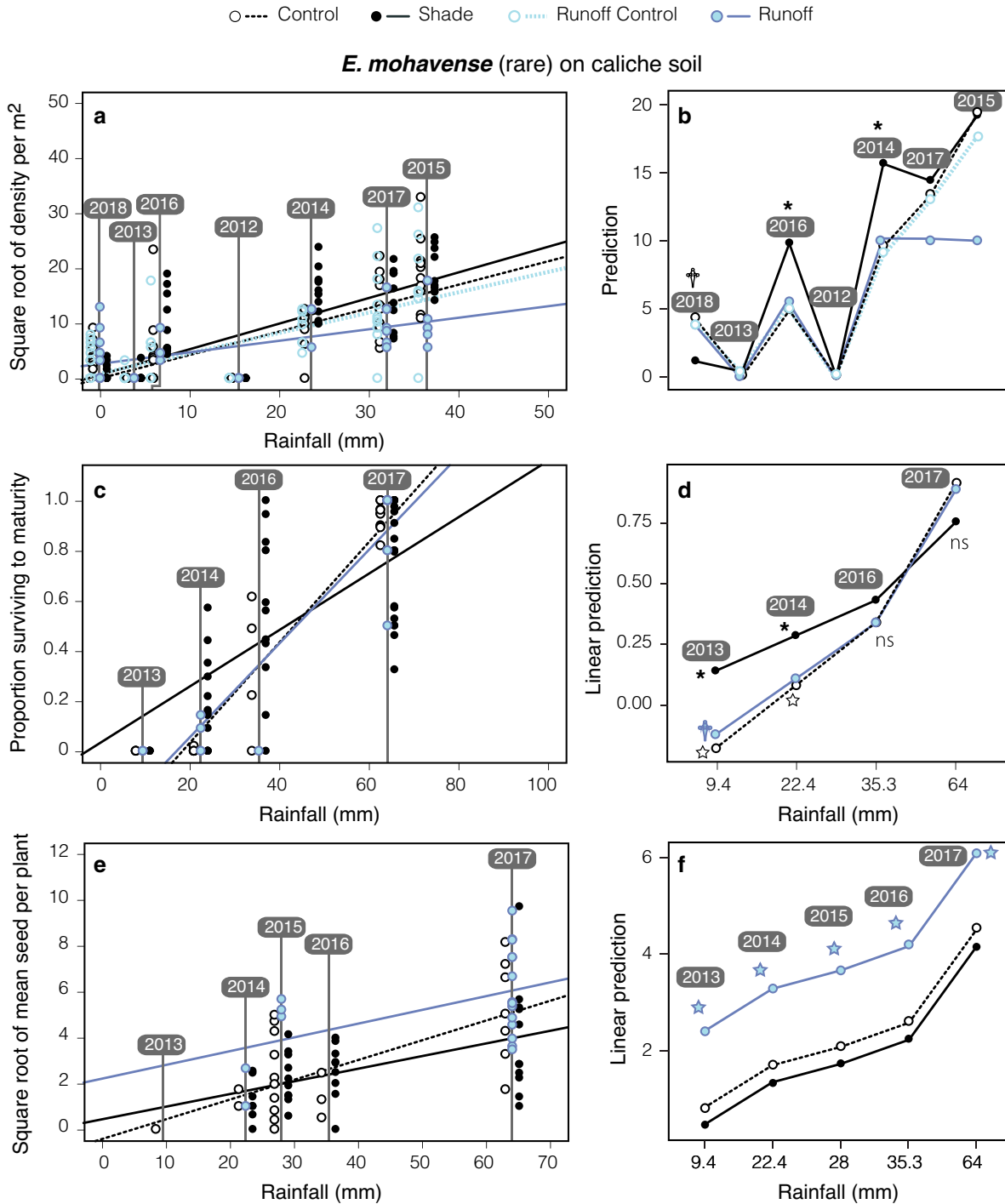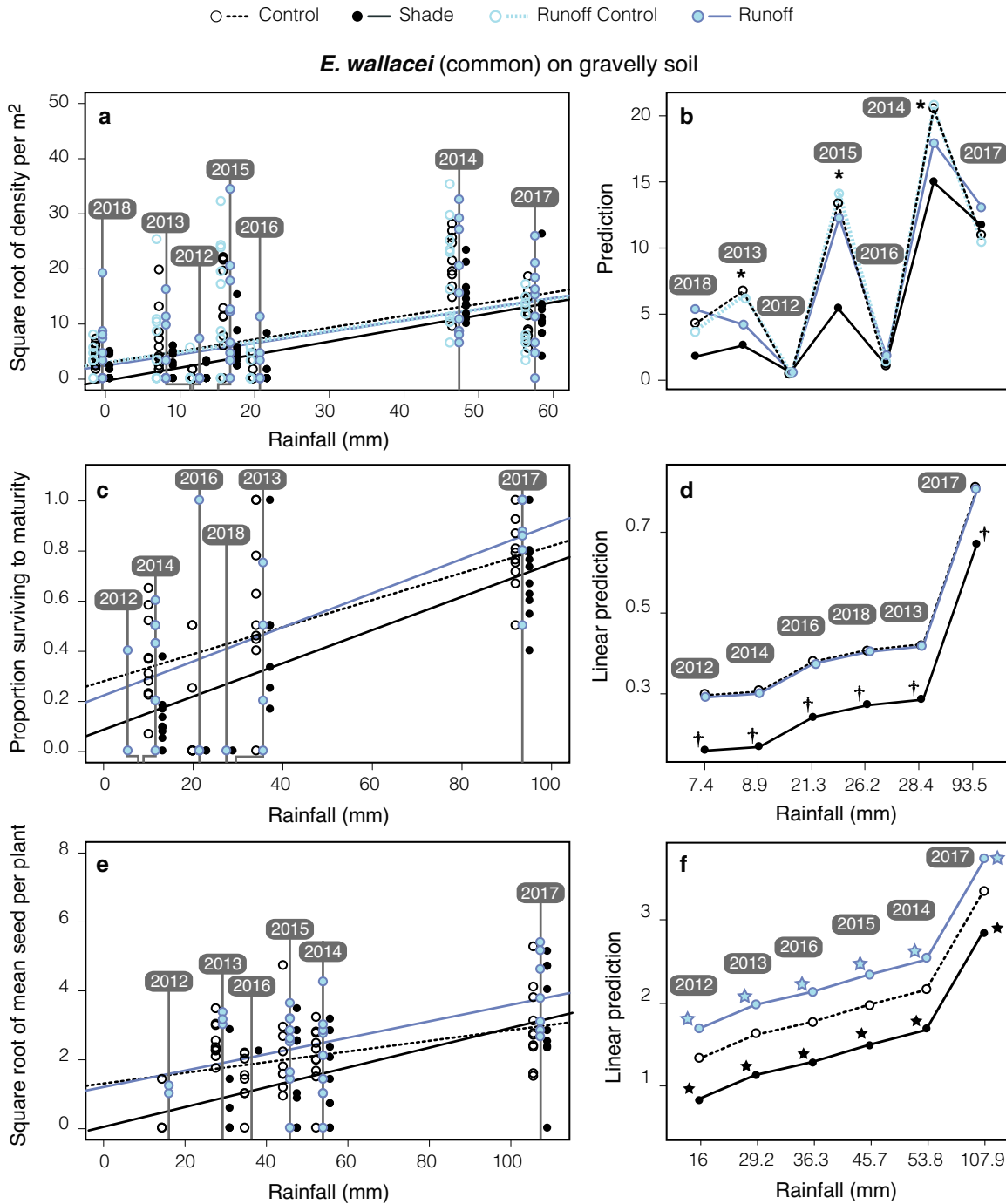
FIG. 3.   (a, b) Year and microhabitat effects on *Eriophyllum mohavense* density on caliche soil; (c, d) rainfall and microhabitat effects on survivorship; and (e, f) rainfall and microhabitat effects on seed output. Empirical data are shown on the left (a, c, e), and estimated marginal means from models are shown on the right (b, d, f). Density estimates using a categorical year predictor in (b) are arranged in order of increasing rainfall. Stars indicate significant differences ($P \leq 0.05$) among microhabitats, and daggers indicate marginally significant differences ($P \leq 0.10$); Tukey adjustments were applied to microhabitat comparisons within each rainfall level for survivorship and seed output. Stars and daggers are color coded to indicate which microhabitats differ.

FIG. 4. (a, b) Year and microhabitat effects on *E. wallacei* density on gravelly soil; (c, d) rainfall and microhabitat effects on survivorship; and (e, f) rainfall and microhabitat effects on seed output. Empirical data are shown on the left (a, c, e), and estimated marginal means from models are shown on the right (b, d, f). Density estimates using a categorical year predictor in (b) are arranged in order of increasing rainfall. Stars indicate significant differences ($P \leq 0.05$) among microhabitats, and daggers indicate marginally significant differences ($P \leq 0.10$); Tukey adjustments were applied to microhabitat comparisons within each rainfall level for survivorship and seed output. Stars and daggers are color coded to indicate which microhabitats differ.

Demographic transitions of aboveground plants

The late rain window held most explanatory power for seedling survivorship of both species (Appendix S1:

Table S3a, c). During our 7-yr study, cumulative late rain was below the 50th percentile in at least 5 yr at both sites, with three of those years below the 25th percentile (Fig. 2b, e). Microhabitat and rainfall interacted to

TABLE 2. Results from ANCOVAs modeling rainfall year and experimental microhabitat effects on survivorship and mean seed per plant for (a, b) the rare *E. mohavense* on caliche soil, and (c, d) the common *E. wallacei* on gravelly soil.

Predictor	SS	df	F	P
E. mohavense (rare)				
a) Survivorship				
Intercept	0.61	1	14.69	**<0.001**
Rainfall (late)	8.27	1	200.50	**<0.001**
Microhabitat	0.56	2	6.75	**0.002**
Rainfall × microhabitat	0.51	2	6.14	**0.004**
Residuals	2.85	69		
b) Mean seed per plant				
Intercept	6.08	1	2.00	0.161
Rainfall (late)	98.22	1	32.37	**<0.001**
Microhabitat	40.14	2	6.61	**0.002**
Residuals	227.58	75		
E. wallacei (common)				
c) Survivorship				
Intercept	1.63	1	27.35	**<0.001**
Rainfall (late)	4.56	1	76.47	**<0.001**
Microhabitat	0.39	2	3.27	**0.043**
Residuals	5.36	90		
d) Mean seed per plant				
Intercept	19.84	1	14.81	**<0.001**
Rainfall (total)	44.16	1	32.96	**<0.001**
Microhabitat	11.23	2	4.19	**0.018**
Residuals	146.05	109		

Notes: Statistics shown are from models using the rain window with greatest predictive power; non-significant interactions involving the Rainfall covariate were dropped (see *Methods: Data analyses, survivorship, and fecundity* for details), and Type III *P* values were generated using the car package (Fox and Weisberg 2011). See Appendix S1: Table S3 for model AIC values using each rain window, associated R^2 values, and equations for lines of best fit. Boldface text indicates a significant effect at the $P \leq 0.05$ level.

regulate *E. mohavense* seedling survival (Table 2a). When late rainfall was low, *E. mohavense* survival was higher in Shade than in the Control microhabitat (Fig. 3c, d). Rainfall had a strong effect on *E. wallacei* survivorship, and microhabitat also had a significant effect (Table 2c), with slightly higher survivorship in the Control and Runoff microhabitats across observed rainfall levels (Fig. 4c, d).

For seed output, late or total rainfall was the best predictor, depending on species (Appendix S1: Table S3b, d). Microhabitat had a significant effect on mean seed output in both species, with the most seed produced by plants in Runoff (Table 2b, d; Figs. 3e, f, 4e, f). For *E. mohavense*, Runoff plants produced significantly more seed than those in either the Shade or Control microhabitats. For *E. wallacei*, Runoff plants produced significantly more seed than Shade plants, but there was no difference between Runoff and Control plants.

Collectively, microhabitat and rainfall explained more of the variability in survivorship and seed output for *E. mohavense* than *E. wallacei,* suggesting the rare species was more sensitive to environmental variation from natural or experimental sources. Microhabitat and rainfall explained 74% of the variability in survivorship and 45% of the variability in seed output for the rare species, compared to 46% and 25% for the common species (Appendix S1: Table S3, a–d).

Population growth projections

Estimates of annual population growth in all microhabitats were below the replacement rate ($\lambda = 1$) in all years except 2017 (Fig. 5a, b). In this single boom year, both species showed important responses to microhabitat variation generated by the experimental arrays. For the rare *E. mohavense,* population growth was positive across all microhabitats in 2017. In this prime season, there was a strong negative effect of Shade on λ, which was substantially lower in Shade compared to the Control and Runoff. In contrast, positive growth of the common species in the same year was restricted to the Runoff microhabitat. These contrasting results demonstrate clear differences in the responsiveness of the two species to environmental variation.

Over the 7-yr study period, elasticity analyses showed that the population growth rate of both species was most responsive to variation in aboveground demographic rates in 2017, the boom year (Fig. 5c, d). However, microhabitat-specific λ's for *E. mohavense* and *E. wallacei* were not equally sensitive to different component rates included in aboveground matrix elements (Appendix S1: Fig. S4). Sensitivity analysis showed that λ in the Runoff was substantially limited by seedling emergence rate for *E. mohavense* (Appendix S1: Fig. S4, panel a vs. b), but not *E. wallacei* (Appendix S1: Fig. S4,
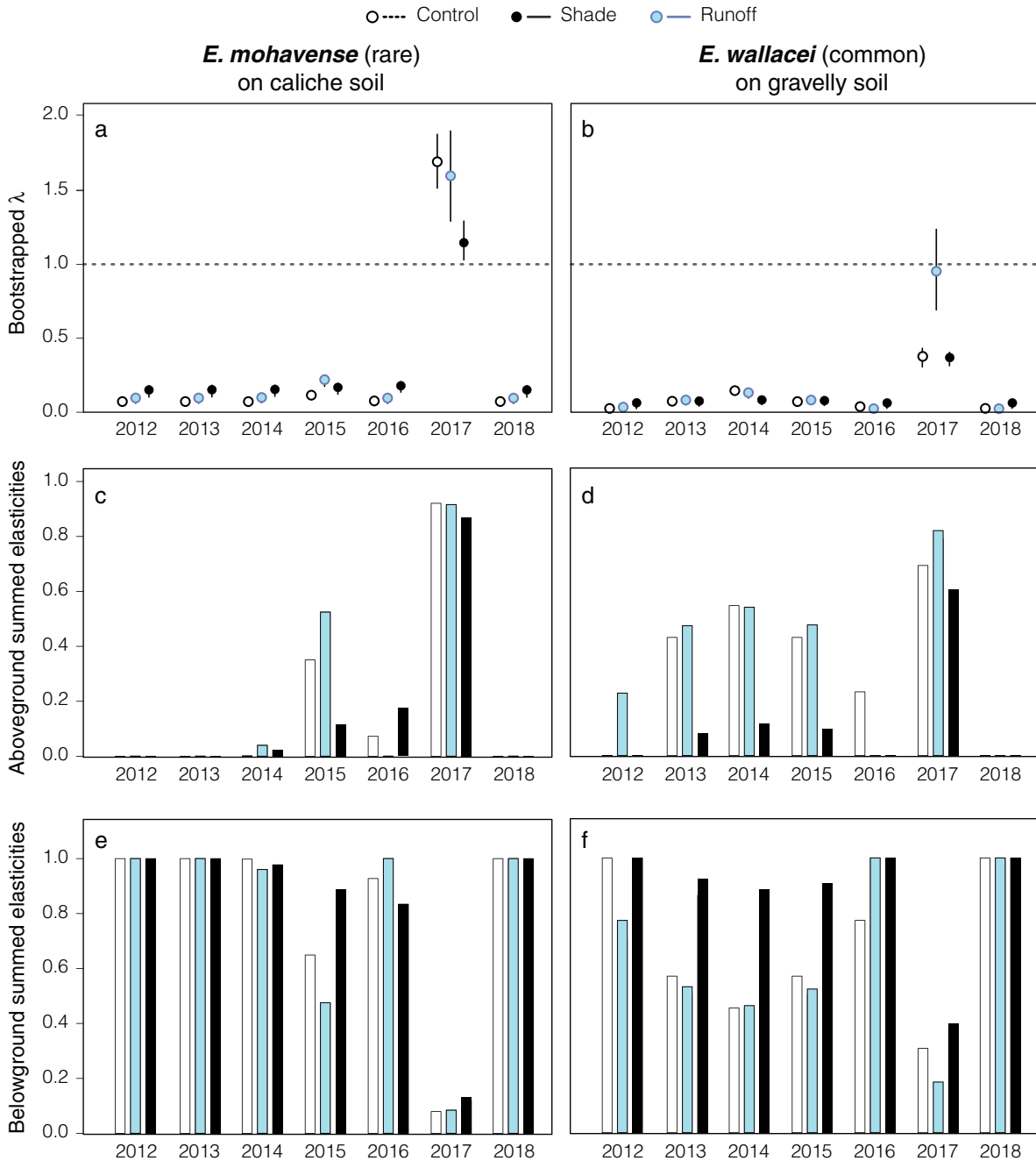
FIG. 5. Projections of deterministic λ using conservative seed bank survival rates in each year and microhabitat for (a) *E. mohavense* on caliche soil and (b) *E. wallacei* on gravelly soil; the dashed line indicates replacement rate (λ = 1), and error bars are 95% confidence intervals calculated from bootstrapped λ values. Partitioning of model elasticity between (c, d) aboveground and (e, f) belowground matrix elements is shown for each species; the maximum elasticity value is 1, and higher values indicate greater influence on modeled λ.

panel e vs. f). Similarly, λ was limited in Shade by survivorship (Appendix S1: Fig. S4, panel a vs. c) and seed output (Appendix S1: Fig. S4 panel a vs. d) for the rare species, but not the common species (Appendix S1: Fig. S4, panel e vs. g; and Fig. S4, panel e vs. h).

In drier "bust" years, seed bank dynamics were strong determinants of overall decline in λ for both rare and common populations. Aboveground rates had no influence on *E. mohavense* λ in 2012, 2013, or 2018 (Fig. 5c), reflecting either total aboveground absence or 0% survivorship across microhabitats (Appendix S1: Table S4); the same pattern occurred for *E. wallacei* in 2018 (Fig. 5d). Elasticity is, by definition, zero for transition rates that are not observed, and consequently, all of the

model elasticity resides in belowground rates for these years (Fig. 5e, f). For the remaining years, belowground elasticity tended to be greatest in the Shade microhabitat (Fig. 5e, f). Substituting generous seed bank survival rates for conservative rates increased λ somewhat across the board (Appendix S1: Fig. S5), but had a disproportionate effect on *E. wallacei* in Shade. *E. wallacei* also tended to show more elasticity to aboveground matrix elements across years, reflecting its greater ability to achieve some level of survivorship and fecundity across the study period, in keeping with a habitat generalist strategy (Fig. 5d, Appendix S1: Table S4b).

Discussion

Annual plants comprise 40–50% of desert floras, and provide critical resources for desert animals (Brown et al. 1979, Parker et al. 1989, Venable et al. 1993). It is therefore important to understand the potential impacts of renewable energy development on this foundational component of desert ecosystems. We found evidence that solar infrastructure may affect demographic processes of two desert annuals through alteration of key microsite habitat conditions. Our closely related focal species showed different demographic responses to microhabitats generated by experimental arrays as well as rainfall. Because our two species had different edaphic niches and did not co-occur across sites, we cannot isolate differences in inherent demographic response from effects of the local environment. However, the rare, narrowly distributed *E. mohavense* on caliche soil appeared to be more sensitive to environmental variation, whether imposed by experimental arrays or naturally occurring weather patterns. These findings are consistent with theory that this narrowly distributed endemic has a more constrained edaphic niche (Kruckeberg and Rabinowitz 1985, ERT 1988, Wamelink et al. 2014). For both species, performance tended to improve where plants received additional water from panel runoff, and in years of higher rainfall. Yet plant response to under-panel microhabitats differed between species and across rainfall years, providing evidence that impacts of solar infrastructure can vary across species and on the same species under different climatic conditions (Moore-O'Leary et al. 2017).

Both timing and total amount of precipitation drive strong fluctuations in desert annual performance (Went and Westergaard 1949, Beatley 1974, Fox 1989). Our study period captured a broad range of rainfall variability both across and within years, particularly at the Gravelly-*wallacei* site. Rainfall variation was well distributed across the early, late, and total rainfall windows having greatest influence on plant density, survival, and seed output, respectively. Our experiment encompassed weather conditions associated with mass germination events, which are triggered by early rain exceeding 25 mm (Beatley 1974). We observed a mass germination event in 2017, confirmed by on-site rain gauges. Rainfall

above 15 mm but below the critical 25 mm threshold results in "scattered emergence," often concentrated in favorable microhabitats (Beatley 1974). We observed scattered emergence in 2014 at both sites, and at the Caliche-*mohavense* site in 2015, when weather stations confirmed rainfall in the 15–25 mm range. Lastly, our study covered a historic drought period in California (Griffin and Anchukaitis 2014), when we observed low (or no) plant emergence. The wide breadth of rainfall conditions captured in our study give a robust sense of the possible response spectrum for both species.

Our work agrees with previous studies showing that early rainfall strongly regulates winter annual germination, and we found that the October–December rainfall window was the best predictor of *Eriophyllum* density. However, for each species, we found that within-season weather variation decoupled density and reproductive success in some years. Our life-stage transition results demonstrate that high density does not necessarily lead to demographic success, because survival and reproduction are contingent on persistence of favorable conditions throughout the growing season (Tevis 1958, Beatley 1967). For example, in 2014 nearly all *E. mohavense* individuals that were not shaded desiccated before flowering. In 2018 the first rains were delayed until January, and relatively high density was observed afterward, but very few individuals advanced to the juvenile stage and none appeared likely to flower.

Shade mediated the responses of both species to rainfall, the critical driver of germination for desert annuals (Juhren et al. 1956, Beatley 1974, Freas and Kemp 1983). In drier years, shade tended to improve microsite favorability for *E. mohavense,* as expressed by plant density, while reducing favorability for *E. wallacei*. Similar patterns emerged for the native community as a whole; in mediocre rainfall years, mean abundance tended to be higher in shade on caliche pan habitat, where *E. mohavense* occurs, and abundance tended to be higher in the open on gravelly bajada habitat, where *E. wallacei* occurs (Tanner et al. 2020). Interestingly, shade did not affect density of either species in the highest rainfall year. Moisture penetration under small-scale panels was likely greatest in this year, suggesting that moisture rather than other factors constrained *Eriophyllum* density in drier years. Desert annuals can perform well in shrub canopy shade, likely due to light saturation in the open at levels below maximum production efficiency (Mooney et al. 1976, Patten 1978, Werk et al. 1983). Slower moisture loss in the shade also means that stomata can remain open longer, reducing carbon limitation. However, two single-year studies have found that shade under full-size panels can limit biomass of desert annuals and grassland communities (Smith et al. 1987, Armstrong et al. 2016).

Differences in soil and site properties likely contributed to variable plant response in the under-panel microhabitat. In mediocre rainfall years, water diversion by panels may have had a stronger negative effect at the Gravelly-*wallacei* site because the coarse substrate had

lower water-holding capacity (Tanner et al. 2020). Rainfall diversion combined with well-drained soil could drive stronger water limitation under panels at this site (Noy-Meir 1973). Wet conditions in 2017 appeared to be favorable enough to eliminate this effect, and each species had similar density in the open and in under-panel microhabitats. Regardless of the specific mechanisms at play, this equivalent density in the control and shade microhabitats under wet conditions resulted from higher *E. wallacei* density under panels, but higher *E. mohavense* density in the open. When rainfall is more plentiful, *E. mohavense* appears to specialize more strongly on exposed habitat, perhaps because few other species colonize these locations at high density. It is worth noting that 2017 rainfall at the Gravelly-*wallacei* site was near the high end of the historic range, while our study did not capture any years of particularly high rainfall at the Caliche-*mohavense* site. *E. mohavense* density in the open may therefore outpace that in the shade as rainfall increases.

Effects on demographic rates

We found no significant effects of microhabitat on emergence of experimental seeds across years. This finding is consistent with the equivalent percentage of intact seed observed across microhabitats for packets buried through the 2017 growing season, but cannot help explain the larger number of intact seeds in shade packets buried through 2018 (Hernandez et al. 2020). Because 2018 was relatively dry, we speculate that stronger moisture limitation under panels may have reduced seed germination or seed decay rates, possibly mediated by shifts in soil microbial activity in shade (Schafer and Kotanen 2003, Mordecai 2012, Li et al. 2019). Interestingly, we found higher fungal infection rates on seed buried in caliche pan soil (Tanner 2020), perhaps related to its higher water-holding capacity (moisture can favor fungal activity). Although a fungicide treatment used in one of our seed bank studies had no effect on the percentage of intact seed retained in packets across microhabitats (Tanner 2020), we cannot rule out a role for pathogen activity. Our choice of fungicidal agents, the one-time nature of the treatment, and/or its timing before fall rains may have contributed to the lack of treatment effect.

We confirmed that emergent *Eriophyllum* seedlings in any single year represent a small fraction of the belowground population. For both species, experimental emergence rates were always less than 5%, often less than 1%, and frequently zero. Low and variable germination fractions have been documented for many desert annual species (Philippi 1993, Pake and Venable 1996, Clauss and Venable 2000), including 2% for *Eriophyllum lanosum* seed under conditions that should favor germination (Adondakis and Venable 2004).

These high dormancy rates, typical of desert annuals, limited our power to detect differences in emergence across microhabitats, even with our extensive toothpick planting effort. In our experimental arrays, we found that emergence rates were unaffected by microhabitat differences. This was in surprising contrast to observed patterns in plant abundance across microhabitats. Although emergence rates between microhabitats were only marginally different for *E. mohavense* and only in a single year, *E. mohavense* density differed in the open and shaded microhabitats in 2 yr, and *E. wallacei* density differed across these locations in 3 yr. This suggests that seed bank numbers in our plots were high, such that even very small differences in emergence rates resulted in detectable differences in aboveground plant numbers. It is worth noting that because plots were chosen to contain a threshold number of adult individuals, local seed banks at these locations may provide an artificially high estimate of overall seed bank size.

Shade affected survivorship of aboveground plants differently for each species. For the rare species, *E. mohavense*, response to shade depended on rainfall year: *E. mohavense* survivorship was higher in the shaded microhabitat in drier years, but lower in shade in the wettest year. This potentially signals a shift in the relative importance of desiccation risk for *E. mohavense* on stressful caliche pan habitat vs. other factors limiting growth. In the wettest year, 2017, lower *E. mohavense* shade survivorship coincided with the highest observed abundance of the native community and the second highest abundance of the exotic community at the Caliche-*mohavense* site (Tanner et al. 2020). In such years of higher productivity, greater competition may reduce survival (Inouye 1980, Kadmon and Shmida 1990, Goldberg and Novoplansky 1997), and *E. mohavense's* small size likely puts it at a competitive disadvantage. Survivorship of emergent seedlings across control and runoff microhabitats was roughly equivalent in both species, consistent with the similar soil moisture conditions observed in those locations (Tanner et al. 2020).

Effect of microhabitat on projections of population growth

We used population projections as aggregate measures of demographic performance across microhabitats and years to make comparisons of life stage effects within and between species (Caswell 2001). Our population growth models were parameterized with aboveground life stage transition rates observed at each site over seven years, implicitly capturing the influence of microhabitat, prevailing weather, and physical factors characterizing each site on emergent plants. Although we parameterized models using seed data measured in just two years, this timeframe captured the most dynamic period of change in soil seed bank survival rates (Hernandez et al. 2020). Relatively few seeds survived burial for two growing seasons, but the accumulation of such longer-term dormant seeds in the soil seed bank is deemed critical for long-term population persistence (Cohen 1966, Nelson and Chew 1977, Ooi 2012).

Dry years acted as demographic "bust years" for both species, with declining λ almost entirely driven by rates of seed survival and death. Within these years, the shaded microhabitat often exhibited the highest λ because the percentage of intact seed found in packets was greatest in shade after two growing seasons for both species (Hernandez et al. 2020). There were slightly different patterns among growth rates across microhabitats for *E. mohavense* in 2015 and *E. wallacei* in 2014, when aboveground performance improved somewhat with higher rainfall. However, emergent seedlings in drier years had relatively low survivorship and fecundity, largely depleting the seed bank without replenishing it. Elasticity patterns also reflected the dominant influence of seed bank dynamics in these years, with belowground rates having an important influence on λ in dry years, and shade generally exhibiting highest λ due to higher seed bank survival in that location over time (Hernandez et al. 2020).

The highest rainfall conditions observed (2017) offered an important opportunity for *E. mohavense* seed bank replenishment. In this year, population growth was positive in all microhabitats for *E. mohavense,* but λ was substantially reduced by shade in comparison to the open or runoff microhabitats. For the common *E. wallacei*, λ only became positive in the runoff microhabitat; population growth was equivalent in the open and shade, and remained in decline. These results demonstrate a mediating influence of rainfall on microhabitat effects, with impacts that became substantial under wetter conditions, and manifested primarily through aboveground performance (seedling emergence, survivorship, and fecundity). This shift in importance from belowground to aboveground transitions was also reflected in demographic elasticities. Theoretical models have previously demonstrated a greater sensitivity of λ to performance aboveground than belowground in stable populations (Schmidt and Lawlor 1983), and empirical work has shown that relative importance of demographic rates can shift with environmental conditions. For example, Kalisz and McPeek (1992) found that adult life stages had most influence on annual population growth in good years, but the seed bank emergence rate was a stronger driver of population growth in poor years. Our results agree with this general pattern.

Conclusions

Shade associated with panel infrastructure affected both above and belowground demographic rates for two annual plant congeners. Shade suppressed population growth of the rare annual *E. mohavense* in a good rainfall year via negative effects on aboveground demographic rates. In contrast, population growth of the common annual *E. wallacei* increased where plants received additional water from panel runoff and was unaffected by shade. Due to their relatively small size, experimental panels should provide a conservative estimate of full-scale panel impacts; if these effects are exacerbated at utility-scale arrays, then performance of the rare species could be further suppressed in shade during good rainfall years, while population growth of the common plant increases in response to larger volumes of water runoff. These results suggest that novel habitat types imposed by solar infrastructure may have population-level impacts, and demonstrate that these impacts are likely to differ among species (Moore-O'Leary et al. 2017). However, species responses may also be mediated by physical site characteristics such as soil chemistry and water retention (Tanner et al. 2020). Taken together, these findings should discourage the use of surrogate species to make management decisions when data on rare taxa are lacking, especially when rare and common populations are spatially disjunct.

There is a need to reconcile rare species conservation and green energy goals, and our work highlights some pitfalls that can hinder effective management of rare plant populations in the desert southwest. First, surveys intended to reveal whether rare plants are present at proposed development sites must take place under environmental conditions that are likely to stimulate activity in dormant individuals. When rainfall during a critical period for plant emergence is low, the chance of detecting rare taxa present may decline to zero. In 2012, we were unable to find a single *E. mohavense* individual where we observed thousands of plants the previous year (Tanner et al. 2014). Moreover, modeling work also revealed that effects on individual life stage transitions do not necessarily foreshadow impacts at the population level. Although *E. mohavense* survivorship and seed output rates in the shade and open did not differ significantly in 2017, modeled growth in shade was suppressed in this important rainfall year, highlighting the need for demographic approaches that integrate impacts across the full life cycle. Finally, species with a shared life history strategy and evolutionary history may nonetheless respond differently to changes imposed by solar infrastructure and physical and climatic differences across sites may interact to influence this response.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2349/full

OPEN RESEARCH

Data (Tanner et al. 2021) are available in the Dryad Digital Repository: https://doi.org/10.7291/D1ST01