


Simulated solar panels create altered microhabitats in desert landforms

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Abstract. Solar energy development is a significant driver of land-use change worldwide, and desert ecosystems are particularly well suited to energy production because of their high insolation rates. Deserts are also characterized by uncertain rainfall, high species endemism, and distinct landforms that vary in geophysical properties. Weather and physical features that differ across landforms interact with shade and water runoff regimes imposed by solar panels, creating novel microhabitats that influence biotic communities. Endemic species may be particularly affected because they often have limited distributions, narrow climatic envelopes, or specialized life histories. We used experimental panels to simulate the effects of solar development on microhabitats and annual plant communities present on gravelly bajada and caliche pan habitat, two common habitat types in California's Mojave Desert. We evaluated soils and microclimatic conditions and measured community response under panels and in the open for seven years (2012–2018). We found that differences in site characteristics and weather affected the ecological impact of panels on the annual plant community. Panel shade tended to increase species richness on the more stressful caliche pan habitat, and this effect was strongest in dry years. Shade effects on diversity and abundance also tended to be positive or neutral on caliche pan habitat. On gravelly bajada habitat, panel shade did not significantly affect richness or diversity and tended to decrease plant abundance. Panel runoff rarely affected richness or diversity on either habitat type, but effects on abundance tended to be negative—suggesting that panel rain shadows were more important than runoff from low-volume rain events. These results demonstrate that the ecological consequences of solar development can vary over space and time, and suggest that a nuanced approach will be needed to predict impacts across desert landforms differing in physical characteristics.

Key words: annual plant community; aridland ecosystems; desert landform; microhabitat; Mojave Desert; renewable energy; solar panel.

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INTRODUCTION

Renewable energy development is accelerating globally to meet the rising demand for

sustainable energy, and solar will outpace all other alternative energy sources by 2050 (EIA 2019). While clearly providing environmental benefits through reduced carbon emissions,

renewable power generation can also incur steep ecological costs (Harte and Jassby 1978, Abbasi and Abbasi 2000, Stoms et al. 2013, Hernandez et al. 2014). Large-scale, ground-mounted projects require land conversion to accommodate solar arrays, roads, and transmission corridors—features that change surface runoff patterns, affect habitat connectivity, and facilitate the movement of exotic species (Gelbard and Belnap 2003, Abella 2010, Lovich and Ennen 2011). Solar development impacts on regional land-use and vegetation cover have been quantified on at least three continents to date (Fluri 2009, De Marco et al. 2014, Hernandez et al. 2015*b*, Parker et al. 2018). In some cases, innovative facility designs incorporate agriculture or grazing underneath panels to promote co-benefits (Hoffacker et al. 2017, Hernandez et al. 2019), or retain native vegetation to reduce impacts on local communities (e.g., ISEGS in Ivanpah Valley, California).

Development pressure is particularly strong in deserts because the harsh conditions that have historically limited economic productivity in these systems make them ideal for solar energy. Insolation rates are high, land is inexpensive, and human density is low, reducing barriers to energy development. Approximately 157,000 hectares of public land have been made available for development in California's Mojave Desert, with another 162,000 hectares potentially available in the future (California Energy Commission 2016; California S. B. 100 2018). Deserts are also iconic landscapes with unusual and striking landforms such as bajadas, dunes, playas, desert pavements, and volcanic fields. Rainfall regimes interact with landform soil, aspect, and elevation to create habitats where growing conditions are variable but often difficult, driving evolution of desert-adapted life-history strategies and high species endemism (Mulroy and Rundel 1977, Hernández et al. 2001). During this period of rapid energy transition, the need to anticipate and minimize negative effects of energy development on natural assets and sensitive species is recognized.

Ecosystems inside energy facilities are a matrix of microhabitats affected by solar infrastructure. Soils and organisms below panel and mirror arrays are subjected to variable light gradients that shift with the movement of the sun, potentially altering carbon cycling, soil water

retention, erosion, and ecosystem energy balances (Hernandez et al. 2014, Armstrong et al. 2014). Arrays also intercept and divert rainfall to their downslope edge, creating a gradient in soil moisture moving from the open to the panel edge and into the shade underneath. Shifts in rainfall can have greater ecological impact than shifts in temperature (Thorne et al. 2015), and meta-analysis of experiments manipulating precipitation has shown stronger response to water addition than removal (Wu et al. 2011). Shade and moisture gradients imposed by panels are likely to interact with natural gradients that are features of underlying landforms, such as soil texture or microtopography. To date, there has been little empirical research to quantify the microhabitat impacts of solar arrays (but see Smith et al. 1987, Armstrong et al. 2016, Suuronen et al. 2017), and no studies comparing panel effects on ecological processes and communities across habitat types.

Experimental arrays have been widely used to test the effects of habitat modification on species and ecosystems under controlled conditions. For example, free-air CO₂ enrichment (FACE) arrays have been used to examine effects of elevated CO₂ (Ainsworth and Long 2005, Smith et al. 2014), warming arrays test effects of temperature change (Panetta et al. 2018), and rainout shelters simulate reduced rainfall on microhabitats and communities (Tielbörger et al. 2014). We used arrays of experimental panels in the Mojave Desert to explore how photovoltaic arrays alter biophysical conditions on two different landforms and examine whether resulting novel microhabitats differ in effects on annual plant communities present. We focus on annuals because these communities are key components of desert ecosystems, providing resources for wildlife and spectacular superblooms with high aesthetic value (Brown et al. 1979, Venable et al. 1993, Chávez et al. 2019). Long-lived seeds of annuals may also persist within or disperse into developed sites, and annuals provide a tractable experimental system for assessing solar impacts because of their short generation times. Desert annuals are also well recognized for their sensitivity to moisture thresholds (Tevis 1958, Beatley 1974), providing an ideal system for testing the effects of increased or reduced rainfall.

Experimental arrays were established on two landforms commonly targeted for solar energy development. The gravelly bajada array was situated on coarse soil in relatively dense creosote scrub, and the caliche pan array was installed at an exposed location with fine soils high in sodium and boron. Each landform supported a largely distinct annual plant community, including two rare endemic species at the caliche pan site. Our study addressed the following questions: (1) Do solar panels generate differences in microhabitat conditions that are biologically relevant to annual plants? (2) Do the microhabitats imposed by solar panels differ across two sites with different physical characteristics? (3) Do conditions imposed by solar panels drive change in annual plant communities, and are these changes consistent across two desert landforms with different soil types?

METHODS

Study sites

We installed arrays in the western Mojave Desert, where ~60 km² of land has already been converted to solar energy use (Parker et al. 2018). Gaining access to operational energy facilities is difficult, and differences in technology and sub-technology employed across sites (e.g., solar concentrating power versus photovoltaic panels, or fixed-tilt vs. dual-axis) may contribute to variability in infrastructure effects. Many existing facilities are also installed on graded sites, although there is a trend toward designs meant to preserve and support native vegetation onsite. Our decision to use experimental panels resolved site access difficulties, imposed identical treatments across sites, and afforded the opportunity to track panel microhabitat effects on undisturbed plant communities. We chose site locations with low elevation, topography, and slope, consistent with siting practices for ground-mounted photovoltaic installations (Hernandez et al. 2015a). Selected sites had < 20% cover by creosote scrub and flourishing annual plant communities in good rainfall years (annual communities persist belowground as dormant seeds when conditions are unfavorable). We focused on species-rich winter annual communities, defining October–March as the relevant rainfall

period for these plants (Beatley 1974), and using hydrologic year naming conventions (e.g., the period October 2012–March 2013 is the 2013 hydrologic year). Community composition was dissimilar across sites—out of sixty-three total plant species observed across landforms, only five natives and two exotics occurred at both locations (Appendix S1: Table S1). No species of special concern were found on gravelly bajada habitat, but the caliche pan habitat supported two rare, narrowly distributed endemics. Physical characteristics (e.g., soil texture, water-holding capacity) with the potential to influence plant performance also differed across sites as described below.

Caliche pan site.—The caliche pan array was installed ~18 km outside Boron, California, USA (Fig. 1). Habitat loss to renewable energy development is a concern for two rare plants present at this site (*Chorizanthe spinosa* and *Eriophyllum mohavense*, California Native Plant Society Rare Plant Program 2020), which is less than 10 km from multiple solar plants (Solar Energy Generating Facility [SEGS] III–VII, Mojave Solar, and SEGS VIII–IX). Experimental panels were installed on low, south-facing knolls of alluvium exposed through weathering. These sparsely vegetated edaphic islands have a hardpan calcium carbonate layer (“caliche”) near the surface that appears to exclude perennial species (ERT 1988, McAuliffe 1994). Soil samples collected to a depth of 10 cm in shrub interspaces were classified as sandy clay loam, with pH = 7.7, high sodium and boron content, and estimated water-holding capacity of 30% (A & L Western Agricultural Laboratories, Modesto, California, USA; see Appendix S1: Table S2 for more details and laboratory protocols).

Rainfall 2012–2018 was often low at the caliche pan site, remaining below the historic 25th percentile in five of seven years (Fig. 2a; see Appendix S1: Weather for more details). Rainfall reached the historic 59th percentile during 2017 (96.3 mm) but remained far below the maximum recorded (332.5 mm). Monthly mean peak wind speeds ranged between 31.5 and 47.3 km/h, increasing from January to March, the primary period for aboveground growth and maturation of winter annuals. Between January and March, the number of days with wind over 35 km/h more than doubled at this site, and the number

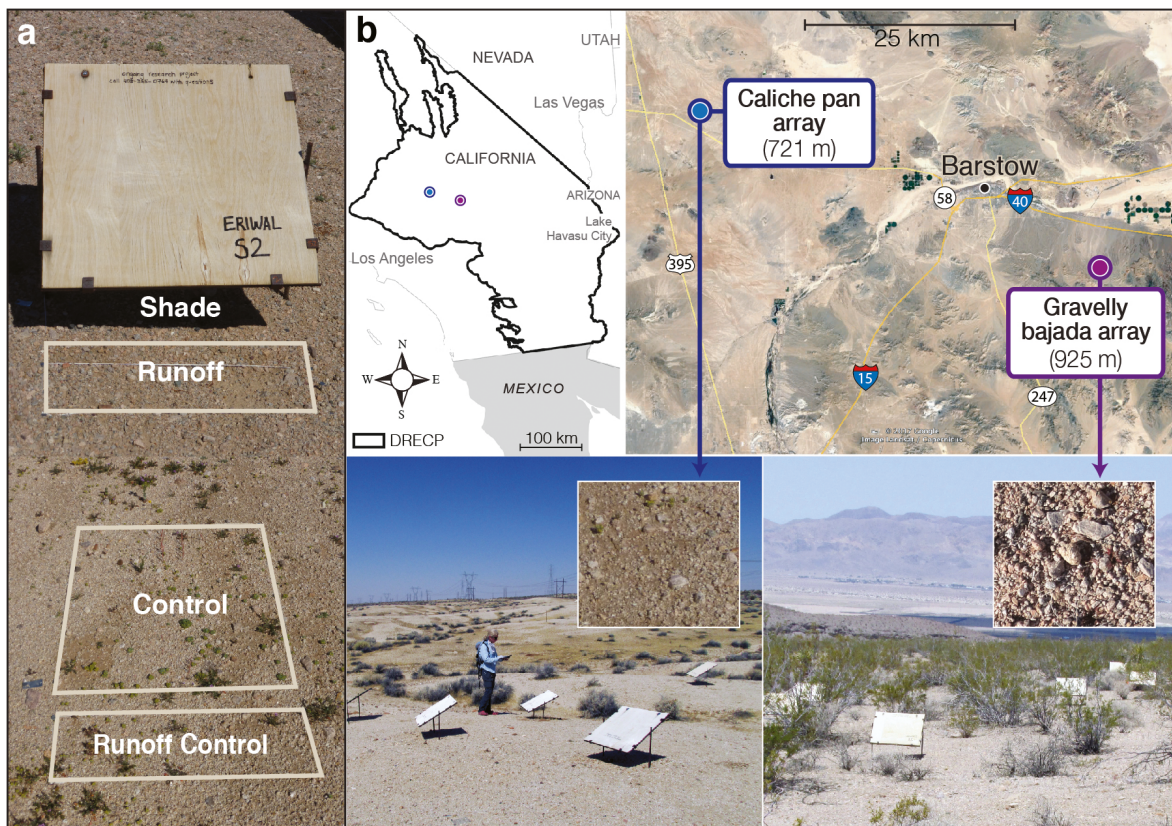


Fig. 1. Experimental sites and treatments; (a) layout of microhabitats for the shade + runoff and control + runoff control treatments, and (b) panel array locations on caliche pan and gravelly bajada habitat inside the Desert Renewable Energy Conservation Plan Area (DRECP). Footprints of the shade and control microhabitats in (a) were defined by the $\sim 60 \times 62$ cm shadow cast under panels at solar noon, and the $\sim 16 \times 60$ cm runoff and runoff control locations were established just to the south of panels. The areas surveyed were therefore 0.372 m^2 for the shade and control microhabitats and 0.096 m^2 for the runoff and runoff control microhabitats. Plant community metrics (plant abundance, species richness, and diversity) are presented on the basis of actual area for each microhabitat; see Appendix S1: Plot sampling schemes for additional details and justification of this approach.

of days with wind $> 65 \text{ km/h}$ increased by 162% (Appendix S1: Table S3).

Gravelly bajada site.—The gravelly bajada array was established on the flank of the Newberry Mountains east of Barstow, California, USA, on a gentle east-facing slope in the Nebona–Mirage–Joshua–Cajon soil unit (USDA Soil Survey Staff 2019). Shrub cover was relatively dense (see Appendix S1: Fig. S1 for more details), and experimental panels were installed in open areas between shrubs. Longboat Solar and Solar One/Solar Two (now decommissioned) are $< 26 \text{ km}$ to the northwest and northeast, respectively. Soil

samples collected to a depth of 10 cm in shrub interspaces were classified as loamy sand with $\text{pH} = 7.9$ and had less than one-third of the water-holding capacity of caliche pan soil. Cation exchange capacity was also 50% lower here, and sodium and boron were present at 1% and 10% of the concentrations observed on caliche soil, respectively (Appendix S1: Table S2).

Although total rainfall 2012–2018 was similar across sites (Fig. 2), rainfall at the gravelly bajada site was below the historic 25th percentile in only three years, and 2017 rainfall was in the 89th percentile. Mean monthly wind speeds were slower

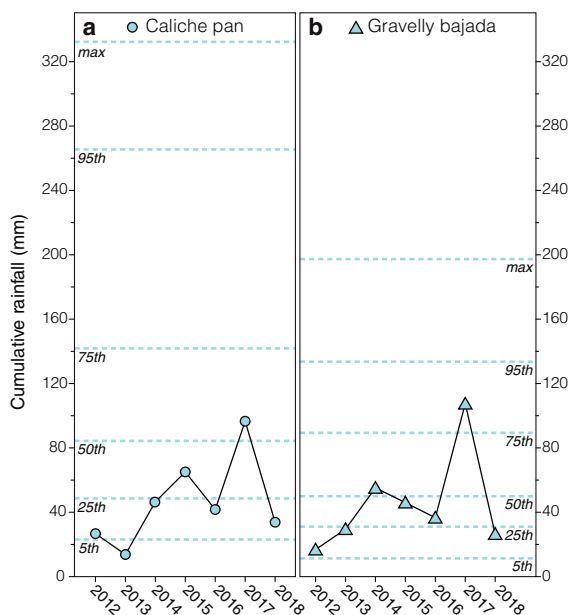


Fig. 2. Rainfall (mm) accumulation for the hydrologic years 2012–2018 at permanent weather stations near (a) the caliche pan site (circles) and (b) the gravelly bajada site (triangles). By convention hydrologic years run October–September; for example, the 2012 hydrologic year runs from 1 October 2011–30 September 2012 (U.S. Geological Survey). Maximum volume and rainfall percentiles calculated from the historic period of record (1945–2018) at each station are indicated with blue dashed lines and italic labels.

and less variable at this site, and winds > 35 km/h were much less common (Appendix S1: Table S3).

Experimental panels

Plot selection.—The distribution of annual species is patchy at small spatial scales, so we used the presence of plentiful native species at each site (*Eriophyllum mohavense* on caliche pan habitat and *Eriophyllum wallacei* on gravelly bajada habitat) to choose plot locations non-randomly. Because these two taxa tended to co-occur with many other annuals representative of shrub interspace communities, this approach increased the likelihood of strong annual community seed banks in our plots. We chose plots ($n = 52$ total) with similar substrate and slope on each landform in spring 2011, randomly assigning plots to

abiotic monitoring efforts ($n = 12$) or plant community monitoring efforts ($n = 40$). Within each monitoring group, plots were assigned to control or panel treatments randomly (see Appendix S1: Plot sampling schemes for more details). In summer 2016, we installed additional panels ($n = 4$ per site) to facilitate soil moisture sampling in 2017 (disturbance from 2013 collections precluded reuse of existing plots).

Panel construction and installation.—We built experimental panels measuring 0.37 m², using rebar frames to mount them at a 30° angle ~ 0.2 m off the ground. In summer of 2016, we covered panels with clear plastic sheeting (4-mm Coroplast, Corrugated Plastics.net, Hillsborough, New Jersey, USA) to improve rainfall runoff. We spaced plots to minimize shadowing from nearby shrubs and installed panels to face south, creating shade and runoff microhabitats (Fig. 1a). Panels block sunlight in the shade microhabitat and shed water along their southern edge into the runoff microhabitat. Experimental panels are relatively small compared to full-scale panels, which may affect the strength of observed panel effects. Large commercial panels (often ~ 1.9 m²) divert more rainfall to their downslope edge, potentially driving stronger increases in moisture availability and benefitting species able to rapidly utilize this resource. Light gradients are also stronger where panels are arranged in contiguous arrays, and plants near the center of arrays are more likely to experience light limitation. Small-scale experimental panels therefore provide conservative estimates of the shade and moisture concentration effects from full-size panels—especially where panels are arranged in continuous arrays.

Abiotic metrics

Soil moisture.—Gravimetric soil moisture was measured across sites and microhabitats using 10-cm soil cores collected the day after storms in March 2013 ($n = 18$ cores from the caliche pan array, and $n = 15$ cores from the gravelly bajada array) and February 2017 ($n = 12$ cores per array).

Soil temperature.—We used Thermochron iButtons (model DS1921G; Maxim Integrated, San Jose, California, USA) to sample soil temperatures in open and shaded microhabitats at four

plots per site in 2018 ($n = 2$ units per plot, 1 per microhabitat; see Appendix S1: Soil temperature for more details). Differences in maximum temperature between microhabitats should affect evapotranspiration and plant desiccation rates, so we identified and extracted sampling times corresponding to maximum temperature difference in each month for analysis.

Light environment.—We used a light ceptometer (AccuPAR LP-80; Meter Group, Pullman, Washington, USA) to quantify photosynthetically active radiation (PAR) under panels, reasoning that a reduced light environment may alter plant physiological processes in ways that affect community composition or diversity. On a clear day in June 2011, we measured equivalent PAR reductions underneath an experimental panel and a mockup of a full-size panel at solar noon (readings were ~12% of PAR measured in full sun; see Appendix S1: Light environment for more details). In three additional years, we took measurements across the light gradient under experimental panels at each site ($n = 270$ per site), sampling at mid-morning, solar noon, and mid-afternoon on dates near the spring equinox.

Plant community

During late March or early April 2012–2018, we counted the number of species present in each plot and the total number of individuals per species; plant abundance data were not collected in 2014 due to logistical constraints. We restrict community comparisons to microhabitats of the same size and present community metrics on the basis of actual area surveyed in each microhabitat to avoid artifacts driven by the species-area curve (see Appendix S1: Fig. S2a for more details and justification of these decisions).

Data analyses

Arrays were installed on two habitat types with divergent soil characteristics and annual communities sharing only seven species in common. The extreme logistical challenges associated with performing experiments at these sites precluded doing more than one site for each habitat; therefore, caution is required in generalizing beyond the comparison between these specific locations. To test the hypothesis that differences in soil characteristics influence panel effects, we chose to treat site (caliche pan vs. gravelly

bajada) as a fixed effect in analyses of (1) microhabitat characteristics (soil moisture, soil temperature) and (2) composition of shared communities (seven species total). Results are interpreted appropriately given this caveat. In analyses of richness, diversity, and abundance of the unique assemblages present on each habitat type, we focused on panel microhabitat effects, which were well replicated within site (caliche pan or gravelly bajada).

Abiotic metrics.—Soil core moisture data were evaluated with linear mixed models using the packages lme4 and car (Bates et al. 2015, Fox and Weisberg 2011) in R version 3.4.2 (R Core Development Team 2017). Year, microhabitat, site (caliche pan vs. gravelly bajada), and the year \times microhabitat \times site interaction were included as fixed effects, with plot as a random blocking factor nested inside site (see Appendix S1: Fig. S2b for more details and justification of this approach). Model diagnostic plots suggested normality in error structure and showed no evidence of heteroscedasticity. We carried out post hoc tests on estimated marginal means across microhabitats within each site and year using the emmeans package (Lenth 2019). We used a non-parametric Kruskal-Wallis test to examine microhabitat effects on soil temperature because data across microhabitats were strongly bimodal. Welch's two-sample t -tests were used to compare PAR in shade to measurements taken in full sun (control conditions); data across years were combined by sampling time (mid-morning, solar noon, mid-afternoon) for each site. All significant differences are reported at the $P \leq 0.05$ level.

Plant community.—In all years where data were available, we calculated species richness and abundance on the basis of surveyed microhabitat area: 0.372 m² for shade and control microhabitats and 0.096 m² for runoff and runoff control microhabitats (see Appendix S1: Plot sampling schemes for further details). We used the vegan package (Oksanen et al. 2018) to calculate the Shannon diversity index on the same basis. To test for an interaction between microhabitat and site (soil type) affecting community composition, we isolated abundance data for the seven taxa occurring on both the caliche pan and gravelly bajada habitat (five native and two exotic species, Appendix S1: Table S1). We used vegan to build

Bray-Curtis dissimilarity matrices, incorporating as many years of data as possible; data sets containing a preponderance of zeroes were discarded where they inhibited analysis (the final analysis for control vs. shade included 2015, 2017, and 2018 data sets; the runoff control vs. runoff analysis included 2015 and 2017 only). We used *vegan* to conduct permutational analysis of variance (PERMANOVA) on raw and standardized data, including year, site, microhabitat, and their three-way interaction as predictors. Standardized abundance data were generated by dividing cells in each species column by the total number of individuals observed for that species across years (column total). This procedure allowed us to consider whether site or microhabitat effects operate primarily at the level of the entire community, or have different relative effects across species. Results using raw and standardized data were qualitatively similar, so we present results using raw data here. Where PERMANOVAs revealed a significant site \times microhabitat interaction, we used similarity percentage analysis (SIMPER) to identify the species contributing most to community dissimilarity across microhabitats and sites.

To test for microhabitat effects on species richness, Shannon diversity, and plant abundance within each site, we built GLMs using the most appropriate family distribution and link function for each response variable. We used Poisson GLMs with log link functions to test for microhabitat effects on species richness and Gaussian GLMs with the identity link function to test for effects on Shannon diversity. To test for microhabitat effects on native and exotic abundance, we used the *glm.nb* family function from the MASS package (Venables and Ripley 2002) to specify negative binomial GLMs suitable for overdispersed count data (Warton et al. 2016). However, model diagnostics suggested that overdispersion was not entirely eliminated in analyses of abundance data at the gravelly bajada site. Full models for response variables at each site included year, microhabitat, and their interaction. We restricted statistical comparisons to microhabitats of the same dimensions (i.e., control vs. shade, and runoff control vs. runoff) for all analyses to avoid artifacts driven by the species-area curve (surveying in a larger area generally increases species richness and

abundance). We used the *car* package (Fox and Weisberg 2011) to extract model *P*-values and the *emmeans* package (Lenth 2019) to conduct post hoc comparisons on estimated marginal means for all response variables.

RESULTS

Abiotic effects of panels

Soil moisture.—The three-way interaction year \times site \times microhabitat had a significant effect on soil moisture ($df = 2$, $F = 5.44$, $P = 0.004$; Appendix S1: Table S4a). On caliche pan habitat in 2013, soil moisture was higher in the control and runoff microhabitats compared to shade (Fig. 3a, Appendix S1: Table S4b). In 2017, soil moisture remained higher in control than shade on caliche pan habitat, but there was no difference between the control and runoff microhabitats. Soil moisture was exceedingly low on gravelly bajada habitat due to very low water-holding capacity of soils at this site (Appendix S1: Table S2). As a result, there were no significant moisture differences across microhabitats, even though this site received more rainfall from storms in both 2013 and 2017 (Fig. 3b, Appendix S1: Table S4b).

Soil temperature.—Average soil temperature differences between microhabitats were strong and showed similar patterns across the caliche pan and gravelly bajada habitat (Fig. 4). Average temperatures were $\sim 7.4^\circ\text{C}$ lower in the shade near solar noon in fall and spring at the caliche pan site (Kruskal-Wallis $\chi^2 = 98.18$, $df = 1$, $P < 0.001$). At the gravelly bajada site, shade temperatures were $\sim 11^\circ\text{C}$ lower near solar noon in fall and spring (Kruskal-Wallis $\chi^2 = 217.32$, $df = 1$, $P < 0.001$).

Light environment.—Photosynthetically active radiation was significantly lower in shade compared to the control (morning sampling period, Welch's $T = -57.97$, $df = 59$, $P < 0.001$; solar noon sampling period, Welch's $T = -148.31$, $df = 59$, $P < 0.001$; afternoon sampling period, Welch's $T = -76.82$, $df = 59$, $P < 0.001$). Measurements near solar noon were on average $\sim 184 \mu\text{mol m}^{-2}\text{s}^{-1}$ in experimental shade compared to $\sim 1576 \mu\text{mol m}^{-2}\text{s}^{-1}$ in full sun. This observed $\sim 88\%$ reduction in PAR (Fig. 5c) was similar to measurements taken under a full-size

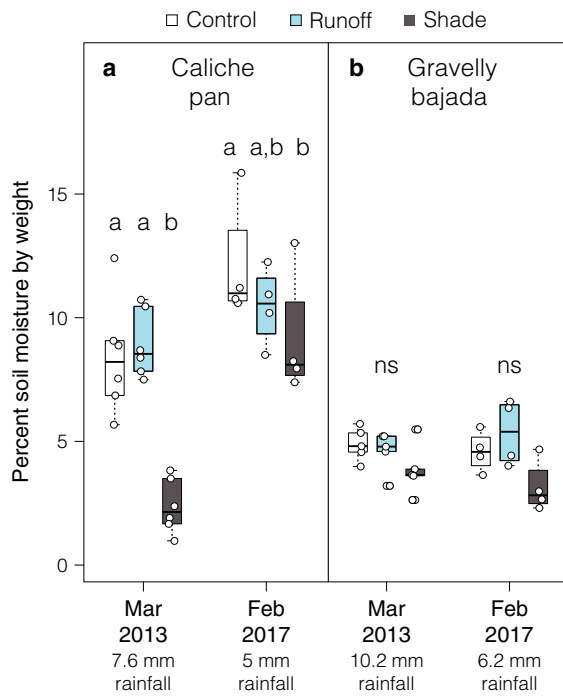


Fig. 3. Percentage moisture by weight of soil cores taken the day after storms at (a) the caliche pan site and (b) the gravelly bajada site. Boxplots show medians and interquartile range, with whiskers indicating the highest and lowest values excluding outliers. Open boxes indicate the control microhabitat, blue boxes the runoff microhabitat, and gray boxes the shade microhabitat. Open circles are actual data points. Different letters above boxplots indicate significant differences at the $P \leq 0.05$ level.

mock solar panel at solar noon (Appendix S1: Table S6). Measurements under experimental panels varied over time with the sun's movement and were highest along the eastern edge of the shade footprint in morning and along the western edge in the afternoon (Fig. 5b, d). Morning and afternoon light were also elevated in the north compared to the center and south subplots, where there was less clearance between the panel and the ground. Near solar noon, more light leaked under the southern edge of panels on gravelly bajada habitat as a consequence of east-facing aspect (Fig. 5c).

Biotic effects of panels across sites

PERMANOVAs showed strong dissimilarity between communities in shade and control

microhabitats, with significant year \times site, year \times microhabitat, and site \times microhabitat interactions (Table 1a). SIMPER analysis revealed that four species accounted for 93% of observed dissimilarity (Table 2), and abundance plots revealed differences in the site effect versus the interaction between site and microhabitat as a driver of abundance. *Chaenactis stevioides* abundance differed strongly between sites, but not across microhabitats within site (Fig. 6a). *Erodium cicutarium* and *Gilia stellata* were both more common on caliche pan habitat, where shade also appeared to have a strong positive effect on these species (Fig. 6b, c). *Schismus arabicus* abundance was quite similar across habitat types in the open, but increased very sharply in shade on the caliche pan habitat only (Fig. 6d).

Community dissimilarity between the runoff control and runoff microhabitats was significantly affected by the year \times site interaction and marginally significantly affected by the year \times microhabitat interaction (Table 1b). We found no evidence for a site \times microhabitat interaction, suggesting that soil differences across sites did not influence community dissimilarity across the runoff control and runoff microhabitats.

Biotic effects of panels within sites

Shade vs. control.—The prevalence and direction of panel shade effects on plant communities differed between caliche pan and gravelly bajada habitat. We found a significant effect of the year \times microhabitat interaction on species richness at the caliche pan site (Table 3a), where shade significantly increased richness in three relatively dry years (Fig. 7a). Year was the only significant predictor of richness at the gravelly bajada site (Table 3c), but richness was marginally significantly different between the control and shade microhabitats in two years (Fig. 7b).

Community diversity on caliche pan habitat was affected by a significant year \times microhabitat interaction (Table 3b), with diversity higher in the shade for two out of three years where panel effects mattered (Fig. 7c). Only year had a significant effect on gravelly bajada habitat diversity, but shade had a marginally significantly positive effect on diversity at this site in 2018 (Table 3d, Fig. 7d).

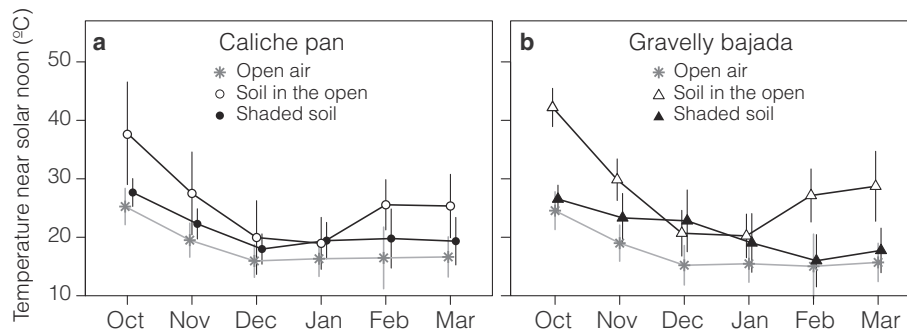


Fig. 4. Soil temperatures near solar noon for each month on (a) caliche pan habitat and (b) gravelly bajada habitat in 2017–2018, acquired using iButtons buried 7 mm below the soil surface (see Appendix S1: Soil temperature for more details). Open circles show the control microhabitat, and filled circles show the shade microhabitat at the caliche pan site. Open triangles show the control microhabitat, and filled triangles show the shade microhabitat at the gravelly bajada site. Air temperatures from the closest permanent weather stations are shown for reference (asterisks). Error bars are 1 SD.

Native abundance was affected by the year \times microhabitat interaction on caliche pan habitat, with higher abundance in shade where significant or marginally significant differences occurred (Table 4a, Fig. 7e). Year and microhabitat had significant effects on exotic abundance, and the year \times microhabitat interaction had a marginally significant effect (Table 4b); exotic abundance was higher in shade during three years on caliche pan habitat, but not in the two driest years, when sample sizes were inadequate to detect panel effects (Fig. 7g, Appendix S1: Table S7). On gravelly bajada habitat, a year \times microhabitat interaction affected native and exotic abundance (Table 4c, d). Native abundance was higher in the control microhabitat in two of three years where panel effects mattered, and exotic abundance was higher in the control for both years where panels had significant effects (Fig. 7f, h).

Site-specific trends for native abundance across the open and shaded locations persisted after reducing community data sets to the five species occurring on both habitat types (Appendix S1: Table S1, Fig. S3). For this shared set of natives, shade increased abundance on caliche pan habitat but generally reduced abundance on gravelly bajada habitat.

Runoff vs. runoff control.—Only year was significant when comparing species richness and diversity in the runoff and runoff control microhabitats (Table 3), but estimated marginal means showed positive effects of runoff in two of

the driest years of our study. Gravelly bajada richness and diversity were significantly higher in the runoff microhabitat in 2012 (Fig. 7b, d), and richness was slightly higher in the runoff at the caliche pan site in 2013 (Fig. 7a).

We found that native abundance was affected by the year \times microhabitat interaction on both habitat types (Table 4a, c). Native abundance was lower in the runoff on caliche pan habitat in both years where differences were significant (Fig. 7e), and in two out of four years on gravelly bajada habitat (Fig. 7f).

Only year had a significant effect on exotic abundance at the caliche pan site (Table 4b), but the estimated marginal mean for the runoff microhabitat was significantly higher in one year (Fig. 7g). The year \times microhabitat interaction had a significant effect on exotic density at the gravelly bajada site (Table 4d), with marginally significantly more exotics in the runoff microhabitat in 2012, and significantly more exotics in the runoff control microhabitat in 2015 (Fig. 7h).

DISCUSSION

The high sensitivity of desert annual seed banks to rainfall transports seeds through barren, dry years and yields stunning superblooms in wet years (Went 1949, Beatley 1974, Chávez et al. 2019). Between these weather extremes, plants are distributed across a microhabitat mosaic created by topography and soil properties (Mabbutt and Fanning 1987, Parker 1991, Wondzell et al.

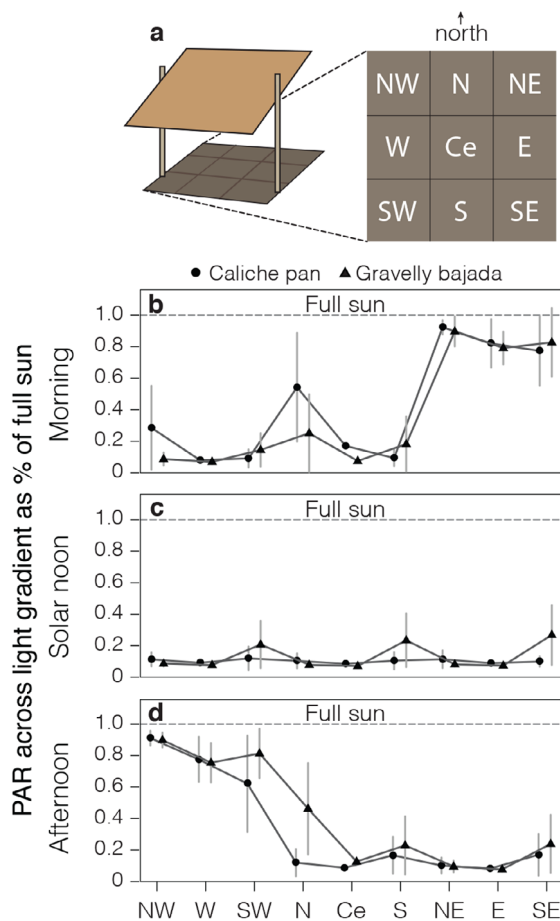


Fig. 5. PAR measurements across the light gradient under experimental panels for three sampling periods. (a) Measurements were taken in nine subplots under panels and expressed as a percentage of light received in full sun for (b) morning, (c) solar noon, and (d) afternoon. Filled circles indicate the caliche pan site, and filled triangles indicate the gravelly bajada site. In panel (a), Ce indicates the central subplot; all other subplots are named for cardinal or ordinal directions. Error bars show 1 SD.

1996). We found strong evidence that habitat physical properties, together with rainfall, affect the response of plant communities to imposed microhabitat variation. Panels had consistent effects on multiple abiotic factors at two experimental arrays, where these effects interacted with weather to drive variable response in each plant community. Our robust field study demonstrates that these communities are able to persist

Table 1. Results from PERMANOVA analyzing community composition across years and site for (a) control vs. shade microhabitats and (b) runoff control vs. runoff microhabitats.

Predictor by microhabitat comparison	df	F	P
(a) Control vs. shade			
Year	2	16.06	0.001
Site	1	49.74	0.001
Microhabitat	1	5.44	0.001
Year × site	2	13.25	0.001
Year × microhabitat	2	1.99	0.042
Site × microhabitat	1	4.83	0.003
Year × site × microhabitat	2	1.38	0.194
Residual	108	–	–
(b) Runoff control vs. runoff			
Year	1	10.97	0.001
Site	1	50.90	0.001
Microhabitat	1	0.12	0.990
Year × site	1	3.54	0.013
Year × microhabitat	1	2.07	<i>0.077</i>
Site × microhabitat	1	0.78	0.520
Year × site × microhabitat	1	1.48	0.193
Residual	65	–	–

Notes: Values in boldface indicate significant differences at the $P \leq 0.05$ level; italics indicate a marginally significant difference at the $P \leq 0.10$ level.

in altered microhabitats, at least over a relatively short time frame. However, long-term effects of solar infrastructure on resident plant communities remain difficult to predict. This suggests that effective management strategies for communities of conservation concern may be possible in some cases, but the retention of native diversity at energy sites over the long term may not be assured.

We found that panels had three distinct and consistent effects: they intercepted sunlight, reduced soil temperature, and diverted rainfall. These effects were broadly similar to those reported at commercial and full-scale artificial arrays. Reductions in PAR under experimental panels near solar noon align with measurements taken at operational photovoltaic facilities (~92% reduction; Armstrong et al. 2016); lower soil moisture in the shade is consistent with reduced rainfall under a full-size artificial array (Smith et al. 1987); and shifts in soil temperature between open and shaded locations match patterns reported in the USA, UK, and Chile (Armstrong et al. 2016, Smith et al. 1987, Suuronen et al. 2017).

Table 2. Results from SIMPER analysis identifying the species contributing most to dissimilarity in communities across the caliche pan and gravelly bajada sites for (a) the control microhabitat and (b) the shade microhabitat.

Species	Mean	SD	Ratio	Mean abundance		Cumulative % contribution
				Caliche pan	Gravelly bajada	
a) Control						
<i>Chaenactis stevioides</i>	0.36	0.31	1.16	0.10	89.10	0.46
<i>Schismus arabicus</i>	0.18	0.18	0.99	23.70	24.30	0.69
<i>Erodium cicutarium</i>	0.13	0.12	1.12	26.67	9.30	0.87
<i>Gilia stellata</i>	0.05	0.09	0.52	7.83	1.07	0.93
<i>Eriogonum maculatum</i>	0.02	0.04	0.52	0.03	3.70	0.96
<i>Eriogonum pusillum</i>	0.02	0.04	0.63	0.10	4.23	0.99
<i>Filago depressa</i>	0.01	0.02	0.52	0.13	1.53	1
b) Shade						
<i>Chaenactis stevioides</i>	0.31	0.25	1.23	0.33	102.40	0.40
<i>Schismus arabicus</i>	0.25	0.21	1.20	104.73	27.47	0.72
<i>Gilia stellata</i>	0.08	0.10	0.78	26.27	1.20	0.83
<i>Erodium cicutarium</i>	0.08	0.07	1.10	32.33	17.30	0.93
<i>Filago depressa</i>	0.04	0.10	0.36	0.03	10.47	0.97
<i>Eriogonum pusillum</i>	0.01	0.02	0.59	0.00	3.03	0.99
<i>Eriogonum maculatum</i>	0.01	0.02	0.57	0.13	2.70	1

Notes: The mean column shows the mean contribution of each species to overall dissimilarity in the Bray-Curtis matrix; the SD column shows the standard deviation of this contribution; and the ratio column shows the ratio of these two values by species. The caliche pan and gravelly bajada mean abundance columns show the mean number of plants in the relevant microhabitat (area = 0.372 m²) at each site. The cumulative % contribution column shows the cumulative contribution to dissimilarity as each species is added. Exotic species are indicated in boldface.

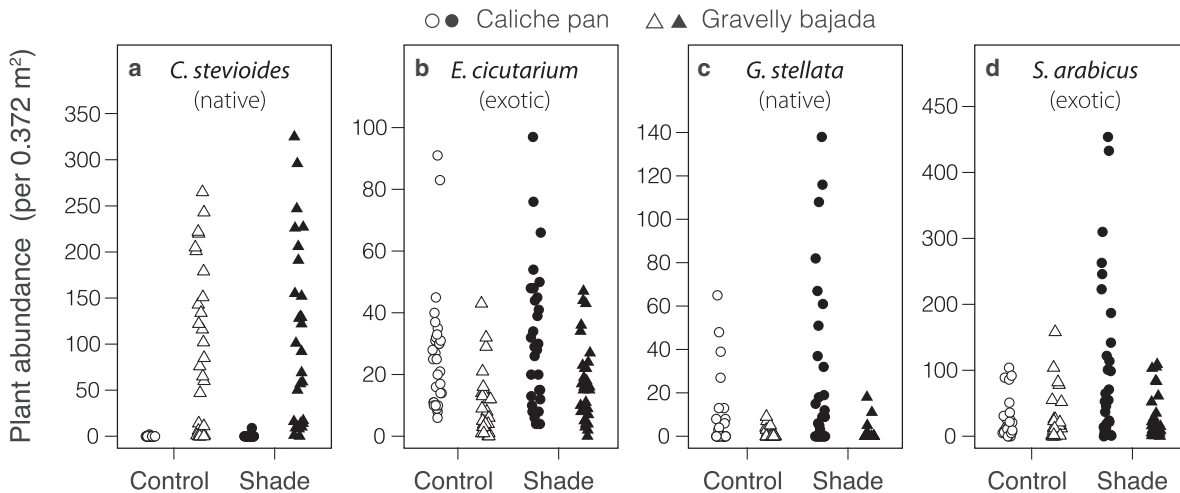


Fig. 6. Plant abundance (total individuals) in control and shade microhabitats at each site for the four species contributing most to community dissimilarity in SIMPER analysis; (a) *Chaenactis stevioides*, (b) *Erodium cicutarium*, (c) *Gilia stellata*, and (d) *Schismus arabicus*. Open circles show the control microhabitat, and filled circles show the shade microhabitat at the caliche pan site. Open triangles show the control microhabitat, and filled triangles show the shade microhabitat at the gravelly bajada site. Note the different scales on y-axes.

However, our seven-year study contrasted with previous single-year studies that found positive effects on diversity in desert systems (Smith et al. 1987, Suuronen et al. 2017).

Instead, we found shifting positive, negative, and neutral effects on two plant communities. Panel shade effects tended to be positive on caliche pan habitat but negative on gravelly

Table 3. Results from generalized linear models (GLMs) of species richness and Shannon diversity index across panel microhabitats on caliche pan habitat (a, b) and gravelly bajada habitat (c, d).

Predictor	df	Deviance	Residual df	Residual deviance	<i>P</i>
Caliche pan					
(a) <i>Species richness</i>					
Control–shade					
Null	–	–	139	644.5	–
Year	6	480.9	133	163.6	<0.001
Microhabitat	1	18.0	132	145.6	<0.001
Year × microhabitat	6	37.0	126	108.6	<0.001
Runoff control–runoff					
Null	–	–	92	229.5	–
Year	6	181.9	86	47.5	<0.001
Microhabitat	1	0.04	85	47.5	0.845
Year × microhabitat	6	4.8	79	42.7	0.565
(b) <i>Shannon diversity index</i>					
Control–shade					
Null	–	–	119	59.6	–
Year	5	41.6	114	18.1	<0.001
Microhabitat	1	1.0	113	17.0	0.003
Year × microhabitat	5	4.1	108	12.9	<0.001
Runoff control–runoff					
Null	–	–	82	28.2	–
Year	5	21.0	77	7.3	<0.001
Microhabitat	1	0.03	76	7.2	0.596
Year × microhabitat	5	0.2	71	7.0	0.807
Gravelly bajada					
(c) <i>Species richness</i>					
Control - shade					
Null	–	–	139	282.3	–
Year	6	192.6	133	89.7	<0.001
Microhabitat	1	0.4	132	89.3	0.540
Year × microhabitat	6	6.5	126	82.8	0.365
Runoff control–runoff					
Null	–	–	139	238.4	–
Year	6	142.7	133	95.7	<0.001
Microhabitat	1	0.3	132	95.3	0.563
Year × microhabitat	6	5.1	126	90.3	0.536
(d) <i>Shannon diversity index</i>					
Control–shade					
Null	–	–	119	31.1	–
Year	5	15.1	114	16.0	<0.001
Microhabitat	1	0.5	113	15.5	0.052
Year × microhabitat	5	0.4	108	15.1	0.714
Runoff control–runoff					
Null	–	–	119	33.7	–
Year	5	16.7	114	17.0	<0.001
Microhabitat	1	0.2	113	16.8	0.288
Year × microhabitat	5	0.7	108	16.1	0.449

Notes: We used Poisson GLMs to model species richness and Gaussian GLMs to model diversity. Bold numbers indicate significant differences at the $P \leq 0.05$ level; italics indicate a marginally significant difference at the $P \leq 0.10$ level.

bajada habitat, while panel runoff effects were mixed. We examine how weather and physical factors interacted with panels to drive different community impacts below.

We found striking differences in annual plant emergence between the two study sites that we hypothesize are linked to a suite of physical properties. Our study encompassed a period of

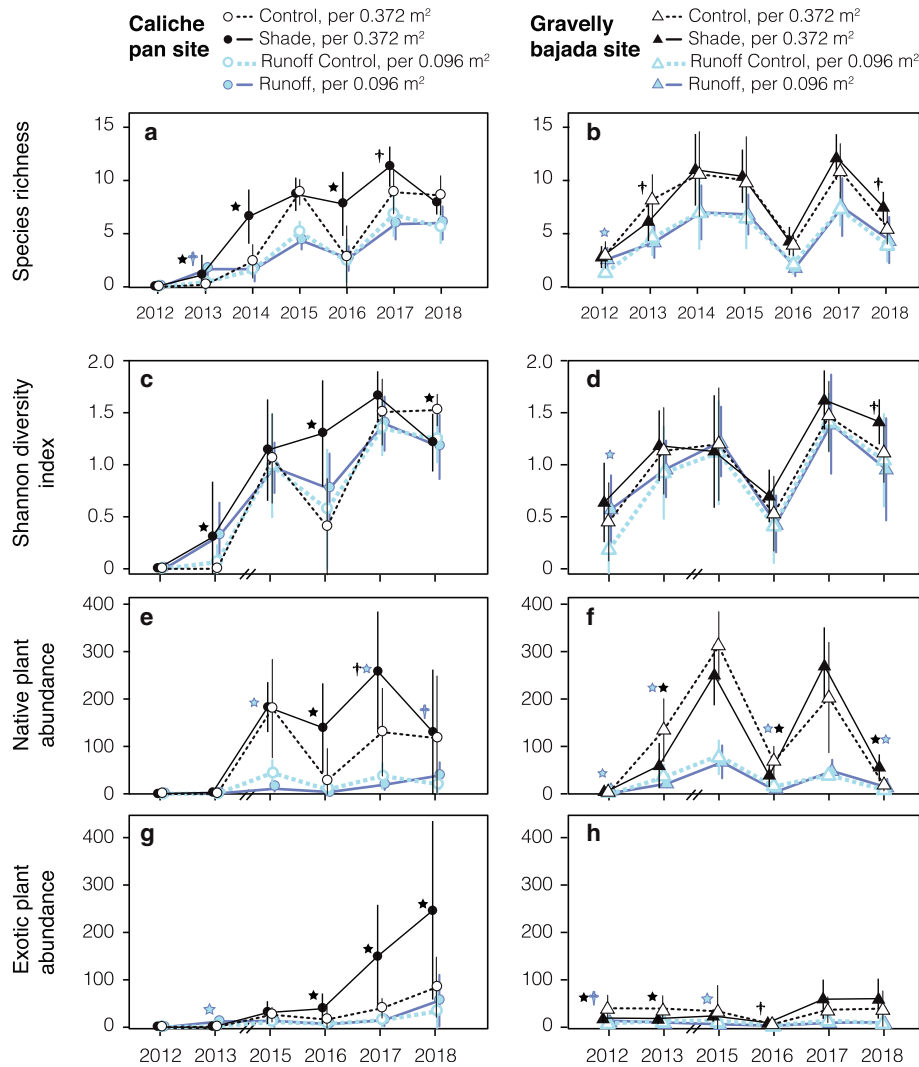


Fig. 7. Community metrics across sites and microhabitats, presented on the basis of actual microhabitat area surveyed (0.372 m^2 for control and shade and 0.096 m^2 for runoff and runoff control). (a, b) Species richness; (c, d) Shannon diversity indices; (e, f) native abundance (total plants counted); and (g, h) exotic abundance (total plants counted)—see Appendix S1: Table S1 for a list of species on each habitat type. Abundance data were not collected in 2014. Circles and triangles are color-coded to distinguish microhabitats; symbols with a black outline show the control microhabitat, and filled black symbols show shade. Symbols with a blue outline show the runoff control, and filled blue symbols show the runoff microhabitat. Stars indicate significant differences at the $P \leq 0.05$ level, and daggers indicate marginally significant differences at the $P \leq 0.10$ level; color-coding of these symbols identifies the relevant microhabitat comparison. A black star or dagger indicates a difference between control and shade, and a blue star or dagger indicates a difference between the runoff control and runoff. Error bars are 1 SD.

historic drought in California (Griffin and Anchukaitis 2014) as well as a superbloom year, with broadly similar patterns of annual rainfall from 2012 to 2018 across both sites (Fig. 2).

Annuals emerged on the more favorable gravelly bajada habitat even in the driest years, but no annual plants emerged on caliche pan habitat during 2012, and very few natives emerged in

Table 4. Results from generalized linear models (GLMs) of native and exotic community abundance (plant counts) across panel microhabitats on caliche pan habitat (a, b) and gravelly bajada habitat (c, d).

Predictor	df	Deviance	Residual df	Residual deviance	<i>P</i>
Caliche pan					
<i>(a) Native abundance</i>					
Control–shade					
Null	–	–	119	523.6	–
Year	5	372.8	114	150.8	<0.001
Microhabitat	1	15.6	113	135.2	<0.001
Year × microhabitat	5	25.0	108	110.2	<0.001
Runoff control–runoff					
Null	–	–	82	287.0	–
Year	5	194.4	77	92.5	<0.001
Microhabitat	1	1.5	76	91.1	0.226
Year × microhabitat	5	15.9	71	75.2	0.007
<i>(b) Exotic abundance</i>					
Control–shade					
Null	–	–	119	527.3	–
Year	5	395.9	114	131.5	<0.001
Microhabitat	1	11.5	113	119.9	0.001
Year × microhabitat	5	10.9	108	109.0	0.053
Runoff control–runoff					
Null	–	–	82	188.8	–
Year	5	96.3	77	92.4	<0.001
Microhabitat	1	2.5	76	89.9	0.111
Year × microhabitat	5	4.8	71	85.1	0.442
Gravelly bajada					
<i>(c) Native abundance</i>					
Control–shade					
Null	–	–	119	870.6	–
Year	5	695.3	114	175.3	<0.001
Microhabitat	1	0.3	113	175.1	0.594
Year × microhabitat	5	45.8	108	129.3	<0.001
Runoff control–runoff					
Null	–	–	119	517.4	–
Year	5	346.1	114	171.2	<0.001
Microhabitat	1	0.02	113	171.2	0.891
Year × microhabitat	5	36.1	108	135.1	<0.001
<i>(d) Exotic abundance</i>					
Control–shade					
Null	–	–	119	220.0	–
Year	5	72.5	114	147.5	<0.001
Microhabitat	1	0.3	113	147.2	0.569
Year × microhabitat	5	18.1	108	129.1	0.003
Runoff control–runoff					
Null	–	–	119	213.1	–
Year	5	75.2	114	137.9	<0.001
Microhabitat	1	1.3	113	136.5	0.248
Year × microhabitat	5	13.6	108	122.9	0.018

Notes: We used negative binomial GLMs to model both native and exotic abundance. Bold numbers indicate significant differences at the $P \leq 0.05$ level; italics indicate a marginally significant difference at the $P \leq 0.10$ level.

2013. Lower annual plant activity on caliche pan habitat in these years suggests that more rainfall is needed to stimulate seedling emergence and

growth at this site. Community assemblages are largely dissimilar across sites, so these emergence patterns could be related to inherent

species differences; however, the higher prevalence and generally positive effects of shade on caliche pan habitat suggest an ecological contrast between sites. We identified several factors that may increase plant stress on the caliche pan landform in comparison with the gravelly bajada: aspect, wind exposure, soil chemistry, and texture.

Situated on shallow south-facing knolls, plant communities on caliche pan habitat have greater sun exposure than communities on the gentle east-facing bajada slope. High sodium and boron content in caliche pan soil may also contribute to plant stress or present barriers to germination in the absence of sufficient rainfall (Berger 1949, Nable et al. 1997, Luan et al. 2009, Baskin and Baskin 2014). Sodium content in caliche pan soil was 75 times higher than levels in gravelly bajada soil and 13 times higher than averages reported from bajadas elsewhere in the Mojave (Titus et al. 2002). The caliche pan site is less than 25 km from the largest borax mine in the world (Rio Tinto in Boron, California, USA), and boron content was twice the recommended threshold for irrigation water in the American southwest (Magistad and Christiansen 1944). Soils at the caliche pan site were also finer, with higher clay content, cation exchange capacity, and water-holding capacity—explaining the higher soil moisture content on caliche pan habitat after storms that delivered more precipitation to the quick-draining gravelly bajada site (Fig. 3).

The prevalence of soil-borne pathogens or their effects on seed reserves in desert systems is largely unexplored (but see Li et al. 2019), and we observed higher fungal infection rates on seed buried at the caliche pan site compared to the gravelly bajada site (K. E. Tanner and S. Haji, *unpublished data*). Moisture favors fungal activity and increases seed mortality in other systems (Schafer and Kotanen 2003, Mordecai 2012), and we speculate that water-holding capacity may have influenced differences in fungal infection rates across sites. More study is needed to determine the role of fungal agents and to test whether infection rates affect plant population dynamics in this system.

Caliche soil horizons exacerbate drought conditions, trapping soil moisture at shallow depths where evaporation is rapid (Schlesinger et al. 1987, McAuliffe 1994). Hardpan caliche layers

occur ~15 cm below the soil surface in this area (ERT 1988, and as encountered during panel installation). Hardpan carbonate layers limit shrub establishment and subsequent survival (McAuliffe 1994), and knolls at our site are almost completely devoid of shrub cover (Appendix S1: Fig. S1). The vacant, shallow soils above the caliche layer are colonized by winter annuals, and two rare species may even specialize on these locations—*Eriophyllum mohavense* and *Chorizanthe spinosa*. Endemism is often high where soil properties create harsh growing conditions (Whittaker 1954), but apparent specialization can also result from the simple exclusion of intolerant species (Barbour 1970, Moore and Elmendorf 2011). *E. mohavense* has been associated with boron-enriched caliche soils (ERT 1988), but whether this distribution reflects edaphic specialization or merely competitive release (e.g., from perennial shrubs) remains unknown. No rare or endemic annual plants were identified on the gravelly bajada habitat, although this community had higher species richness. Extreme environments may reduce diversity by filtering out species unable to tolerate or adapt to prevailing conditions (Odum and Barrett 1971, Whittaker 1972), but because the identities of taxa present on each habitat type were largely different (Appendix S1: Table S1), it is difficult to assess the relative importance of edaphic constraints versus regional species pools as drivers of community composition.

The absence of shrub cover on caliche pan habitat likely increased wind-driven moisture loss. Wind exposure drives moisture loss from plant tissue and soils (Whitehead 1962, Hanks et al. 1967), affects transpiration rates (Martin and Clements 1935, Caldwell 1970), and reduces plant biomass (Bang et al. 2010). High winds often made fieldwork at the caliche pan site difficult or uncomfortable for workers between January and March (the aboveground growing season). Compared to the gravelly bajada site, the number of days with winds over 35 km/h increased 72% on caliche pan habitat, and the number of days with winds over 65 km/h increased 300%. Shrubs can reduce wind velocity up to 80% (Ash and Wasson 1983), and well-developed creosote bush cover likely slowed moisture loss on gravelly bajada habitat as well as improving human comfort.

Panel effects on plant communities

Our experiment produced ninety-eight opportunities to detect panel effects on annual plant communities: two microhabitat contrasts (control vs. shade, and runoff vs. runoff control) \times two sites \times six years \times four response variables—plus two extra years for species richness. We found significant differences between communities in the control and shade microhabitats in fifteen cases and differences between the runoff and runoff control microhabitats in ten cases. Panel effects were therefore relatively rare, occurring only 26% of the time. However, because experimental panels are smaller than panels at operational arrays, our panels divert less rainfall and allow greater sunlight penetration early and late in the day; thus, our findings should be conservative estimates of impacts from full-size panels, especially where they are arranged in continuous arrays.

Species richness and diversity were only affected by panel shade on caliche pan habitat, where shade effects were almost uniformly positive. In light of work showing that reductions in physical stress lead to higher diversity in arid systems (Danin 1976, Smith et al. 1987), this finding supports our hypothesis of higher stress on caliche pan habitat. Panels intercept wind and solar radiation that contribute to soil moisture loss (Hanks et al. 1967), two functions that may be especially important where shallow, sodium-enriched soils are regularly scoured by high winds. Wind speeds can drop sharply under panels at operational arrays, and relative humidity is higher under panels (Armstrong et al. 2016, Suuronen et al. 2017). Smith et al. (1987) also showed that panels slowed springtime moisture depletion in the top ten centimeters of soil, the zone most relevant to diminutive desert annuals (Forseth et al. 1984). We found that shade increased the number of *E. mohavense* plants surviving to maturity on caliche pan habitat in the spring of 2013 and 2014 (K. E. Tanner, *unpublished manuscript*), coincident with positive effects on richness and diversity presented here. We speculate that reduced evapotranspiration in the shade allowed more species to persist under challenging conditions, boosting richness and diversity.

Plant abundance was also higher in shade on caliche pan habitat, in keeping with work

showing that more moderate microclimates under shrub canopies can boost desert annual density and productivity (Patten 1978, Tewksbury and Lloyd 2001). Shade continued to exert some positive influence on caliche pan habitat even during the highest rainfall year (2017), when many numerically common species remained more abundant in shade (Appendix S1: Fig. S4). However, conditions that favor high density do not necessarily favor high fitness (Kadmon and Shmida 1990), and we found that shade effects on modeled *E. mohavense* growth switched from positive to negative in 2017 (K. E. Tanner, *unpublished manuscript*). The positive effects of shade on caliche pan communities reported here may disappear under higher rainfall conditions, but this is difficult to predict from our data set because the highest rain year in the study was close to the historic median. It should be noted that Smith et al. (1987) found lower winter annual biomass under full-scale panels in the Sonoran Desert, especially in the deep shade of the panel interior. Plant abundance and biomass may have different responses to shade, or differences in panel size may have contributed to divergent responses.

Panel effects on gravelly bajada habitat generally contrasted with those on caliche pan habitat, mediated by differences in physical stress between sites. Winds were less frequent and slower at the gravelly bajada site, soils contained much lower levels of sodium and boron, and an east-facing site aspect reduced radiation exposure. Panel shade never had a significant effect on species richness or diversity at this site, and plants tended to be more plentiful in the open where differences were significant. We speculate that the combination of coarse soil and low rainfall drove stronger moisture limitation on gravelly bajada habitat (Noy-Meir 1973), with the driest conditions in shade. Thus, the negative effect of panel rain shadows appeared to overwhelm any otherwise protective benefit. The interpretation of panels effects primarily mediated through rainfall blocking at this site is supported by patterns observed in 2015 and 2017. During these two years of highest native abundance, when rainfall was above the 47th percentile, we saw no difference between shade and the open—suggesting that rainfall was adequate to relieve moisture limitation even under panels.

The rain shadow effect on gravelly bajada habitat suggested an explanation for otherwise perplexing patterns in the panel runoff microhabitat. We expected water diversion by panels to drive higher moisture in the panel runoff zone, but moisture never differed between the open and runoff microhabitat on either habitat type (Fig. 3). This outcome might be explained if (1) soils reached field capacity in both locations, or (2) panels did not divert enough water to drive measurable differences. Low-volume rain events are characteristic of the Mojave region; approximately 30% of storms on caliche pan habitat and 40% of storms on gravelly bajada habitat delivered less than 5 mm of rain during our study (data not shown). However, neither alternative explains why abundance was often lower in the runoff microhabitat at both sites.

We had the opportunity to visit the gravelly bajada site during the 2013 storm that preceded our soil coring effort, and we observed no water falling from panel driplines. We also saw obvious effects of windblown rain—a strong westerly breeze during the storm created visibly drier patches of soil to the east of panels. Because the runoff microhabitat is quite small, winds can offset panel rain shadows to encompass this area, potentially driving the negative effects observed on both landforms. While this may initially seem like a surprising result, shrub canopies can also negatively affect understory annuals by blocking rainfall when moisture is limiting (Tielbörger and Kadmon 2000).

It is interesting to note that most departures from overall trends in panel effects occurred in 2018 on both habitat types. The usual fall rains were delayed to January this year, and shade effects switched from positive to negative for diversity on caliche pan habitat and from negative to positive for native abundance on gravelly bajada habitat. It is not easy to interpret these results given the predominant pattern of shade effects on each habitat type—however, it does demonstrate that the timing of rain events can influence outcomes. Venable et al. (1993) showed that Sonoran Desert annuals have different responses to temporal environmental fluctuations that drive shifts in community composition from year to year. Late rain may favor a different set of species than early rain, and/or these taxa may have a different response to conditions in

panel microhabitats. Visualizations of common species in wet, dry, and late rain years at our sites show shifts in relative species abundance with changing rainfall, as well as (in some cases) shifts in panel effects (Appendix S1: Fig. S4). These patterns are consistent with a body of work showing that temporal niche differences are an important driver of species coexistence in fluctuating environments (Whittaker 1972, Hallett et al. 2019, Chesson 2000). Desert annual performance is also known to vary under shrub canopies depending on weather conditions (Tielbörger and Kadmon 2000). To the extent that solar infrastructure creates varying microhabitats within the natural range of conditions that desert plant communities experience, long-term impacts may be limited. However, it seems likely that conditions under full-scale continuous arrays will push these boundaries, driving uncertain outcomes.

Panel effects on the shared plant community

Annual plant assemblages at each site were unique, possibly reflecting differences in habitat preference or local species pools. Out of sixty-three taxa observed, only seven species occurred on both habitat types, including the ubiquitous exotics *Erodium cicutarium* and *Schismus arabicus*. Of the four species that contributed most to community dissimilarity, three had markedly higher abundance in shade on caliche pan habitat, supporting our interpretation that panels reduced a suite of abiotic stressors more important than moisture limitation under panels. Importantly, two of the three species benefitting from shade on caliche pan habitat were the exotic invaders *E. cicutarium* and *S. arabicus*. Present at roughly equal abundance in the open at both sites, *S. arabicus* increased sharply in the shade on caliche pan habitat. *E. cicutarium* was more plentiful in the open on caliche pan habitat and shade benefits there were not as strong, suggesting this species is more tolerant of ambient conditions at this site; *E. cicutarium* has a taproot and may be more successful at acquiring water under dry conditions (Pitt and Heady 1978). Naturalized in many ecosystems of California and beyond, these two invaders exhibit broad environmental tolerance but clearly remain capable of positive response where solar microhabitats reduce stress. To the extent that generalist invaders are present on

solar development sites, they may experience disproportionate benefit from shade—particularly where soils are stressful. These results highlight the potential for divergent panel impacts on native and exotic species, including the potential for some invaders, like *S. arabicus*, to proliferate under panel arrays.

Deserts around the globe are priority targets for solar energy development, and these landscapes are often characterized by landforms with distinct physical properties and plant communities. While energy infrastructure may impose some abiotic changes consistently, weather and physical features of the landscape can interact with these changes to alter community impacts. Most studies to date have examined the ecological impacts of renewable energy development at a single site, for good reasons; facility access can be difficult to acquire and differences in site preparation methods or solar technology hinder direct comparison of effects (Suuronen et al. 2017). Here, we used experimental panels to impose identical treatments on two habitat types differing in environmental drivers and tracked annual community response over seven years. Significant panel effects were found in 26% of cases, and the mechanisms driving these effects appeared to differ across microhabitats. Annual plants tended to be less abundant in the runoff zone on both habitat types, where plants experienced ambient insolation and temperature regimes but may have received less rainfall due to panel rain shadows. Yet, panel runoff did improve richness and diversity on gravelly bajada habitat in the driest year. Multiple environmental factors were altered simultaneously in panel shade. Panels blocked solar radiation and wind as well as rainfall, and the net effect of these changes on shaded plant communities differed across sites. On caliche pan habitat, shade mitigated stress by blocking sunlight and buffering wind, tending to increase plant community abundance and diversity. On gravelly bajada habitat, moisture stress was exacerbated in panel shade, tending to reduce plant abundance. These results suggest that even where site disturbance regimes and energy technology are held constant, weather and site-specific factors will be important determinants of ecological impact. Solar energy impacts may also be strengthened where environmental conditions are most

stringent, and exotic species may be able to take advantage of panel microhabitats. Endemic species also tend to be most common where habitat conditions are harsh, increasing the potential conflict between human goals for conservation and sustainable energy.

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