CALIFORNIA ENERGY COMMISSION

Energy Research and Development Division

FINAL PROJECT REPORT

Desert Plant Response to Solar Energy Development

Trophic Interactions, Rare and Invasive Species, and Management Implications

Gavin Newsom, Governor
December 2020 | CEC-500-2020-076

PREPARED BY:

Primary Authors:
Steve Grodsky, Ph.D.
Karen E. Tanner
Rebecca R. Hernandez, Ph.D.

University of California, Davis
1 Shields Avenue
Davis, CA 95616
Phone: 530-752-1130 | Fax: 530-752-1552
http://www.WildEnergy.org

Contract Number: EPC-15-060

PREPARED FOR:
California Energy Commission

David Stoms, Ph.D.
Project Manager

Jonah Steinbuck, Ph.D.
Office Manager
ENERGY GENERATION RESEARCH OFFICE

Laurie ten Hope
Deputy Director
ENERGY RESEARCH AND DEVELOPMENT DIVISION

Drew Bohan
Executive Director

ACKNOWLEDGEMENTS

Additional funding for KET was provided by Kara Moore-O'Leary; BMP Ecosciences (Bruce M. Pavlik); the Ecology and Evolutionary Biology Department at University of California, Santa Cruz (UCSC); the Jean H. Langenheim Graduate Fellowship; the Hardman Award; Northern California Botanists; Southern California Botanists; the California Native Plant Society; the Marilyn C. Davis Memorial Scholarship; and the Jill Barrett Foundation.

The researchers thank the following people for advice, supporting information, and assistance in the field and/or lab: Angelita Ashbacher, Sailor Banks, Theadora Block, Viridiana Castro, Jon Clark, Joia Fishman, Sophia Haji, Tasya Herskovits, Zach Jordan, Michael Loik, Drew Maraglia, Margot McClaughry, Patrick McIntyre, James Nyenhuis, Chris Otahal, Ethan Peck, Pete Raimondi, Jordan Rainbow, Xochitl Ramirez, Fred Smith, Alison Stanton, Jere E. Tanner, Morris A. Tanner, Julia Toro, Juan Troncoso, Anita Wah, and Jared Young. The researchers also thank Parker lab members at the UCSC, and the legion of field technicians and undergraduate volunteers (from California State University Bakersfield, Mills College, UC Davis, UC Irvine, UC Riverside, and UCSC) who worked on this project.

PREFACE

The California Energy Commission's (CEC) Energy Research and Development Division supports energy research and development programs to spur innovation in energy efficiency, renewable energy and advanced clean generation, energy-related environmental protection, energy transmission and distribution and transportation.

In 2012, the Electric Program Investment Charge (EPIC) was established by the California Public Utilities Commission to fund public investments in research to create and advance new energy solutions, foster regional innovation and bring ideas from the lab to the marketplace. The CEC and the state's three largest investor-owned utilities—Pacific Gas and Electric Company, San Diego Gas & Electric Company and Southern California Edison Company—were selected to administer the EPIC funds and advance novel technologies, tools, and strategies that provide benefits to their electric ratepayers.

The CEC is committed to ensuring public participation in its research and development programs that promote greater reliability, lower costs, and increase safety for the California electric ratepayer and include:

- Providing societal benefits.
- Reducing greenhouse gas emission in the electricity sector at the lowest possible cost.
- Supporting California's loading order to meet energy needs first with energy efficiency and demand response, next with renewable energy (distributed generation and utility scale), and finally with clean, conventional electricity supply.
- Supporting low-emission vehicles and transportation.
- Providing economic development.
- Using ratepayer funds efficiently.

Desert Plant Response to Solar Energy Development: Trophic Interactions, Rare and Invasive Species, and Management Implications is the final report for the Optimizing Solar Facility Configuration Effects on Habitat, Managed Plants, and Essential Species Interactions project (Contract Number EPC-15-060) conducted by the University of California, Davis. The information from this project contributes to the Energy Research and Development Division's EPIC Program.

For more information about the Energy Research and Development Division, please visit the CEC's research website (www.energy.ca.gov/research/) or contact the CEC at 916-327-1551.

ABSTRACT

While California deserts are prioritized as environments for solar energy development, the effects of this development on desert plants are poorly understood. Solar energy helps reduce the risks of climate change for society at large, but local disturbance from solar development in desert ecosystems may negatively affect native plants and promote colonization by invasive species. The researchers in this project quantified the effects of concentrating solar power development, including site preparation and heliostat density, on soils, Mojave milkweed (Asclepias nyctaginifolia), and the queen butterfly (Danaus gilippus), using Ivanpah Solar Electric Generating System in the Ivanpah Valley, California as a model system. In Barstow, California, the researchers quantified the effects of simulated photovoltaic solar panels on three annual plant species, including the congeners Eriophyllum mohavense and E. wallacei and the exotic invasive annual Sahara mustard (Brassica tournefortii). At Ivanpah, the researchers determined that site preparation using bulldozing created uninhabitable soil conditions for nearly all plants and that preconstruction, plant-conservation islands of undeveloped desert within Ivanpah Solar Electric Generating System, known as halos, are effective for Mojave milkweed conservation and maintenance of Mojave milkweed-queen butterfly trophic interactions. For desert annuals, the researchers determined that microhabitat alteration from simulated photovoltaic panels did not affect reproduction for any of the species focused on, but effects of altered water availability and soil temperature may have population-level effects on these species over time and with varied climatic conditions. The team's results indicate that solar energy development in the Mojave Desert may have adverse effects on some desert plants and that the level of impact may be regulated, to some extent, by informed site preparation and management practices. The team's research provides a platform for future studies of the solar energy-ecosphere nexus in California's deserts and informs management for plants at solar facilities of methods to reduce environmental mitigation costs and ecological damage.

Keywords: concentrating solar power, conservation, ecology, invasive species, Ivanpah Solar Electric Generating System, management, photovoltaics, solar energy, sustainability, trophic interactions

Please use the following citation for this report:

Grodsky, S. M., K. E. Tanner, and R. R. Hernandez. 2020. *Desert Plant Response to Solar Energy Development: Trophic Interactions, Rare and Invasive Species, and Management Implications*. California Energy Commission. Publication Number: CEC-500-2020-076.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

EXECUTIVE SUMMARY

Introduction

Solar energy is a critical, growing renewable energy technology with the capacity for rapid buildout to meet growing human energy demands and to mitigate global climate impacts. In California, large-scale solar energy development is often located in deserts. However, disturbance associated with solar energy development may have localized ecological and social consequences. Desert species typically are poorly adapted to disturbance. Disturbance from solar energy development can occur from site preparation activities and the novel presence of solar panels or heliostats (mirrors) in these fragile desert ecosystems. Site preparation can disturb and compact soils, thereby affecting nutrient cycling and hydrology. Solar panels and heliostats create shade that can alter soil temperature, soil moisture, and the amount of light available for plants to photosynthesize. Panels and heliostats may also increase the volume and velocity of rainwater reaching the ground, resulting in runoff and decreased absorption in the soil.

These altered microhabitat conditions may affect the abundance, survival, and reproduction of native desert plants. Disturbance from solar energy development in deserts may also increase colonization by invasive species that are better adapted to manmade disturbance than native desert plants. More broadly, altered microhabitat conditions and more abundant invasive species can affect the ecosystem processes and food webs of deserts, because novel changes in environmental conditions affect ecological interactions. Sustainable solar energy that simultaneously meets human energy demand, conserves species and ecosystem services, and uses informed management and mitigation practices hinges on a basic understanding of the localized ecological effects of disturbance from solar energy development on desert soils, plants, and food webs. Such an understanding, specifically with regard to the recent surge in solar energy development, is still rudimentary.

Project Purpose

The purpose of this research project was to fill some of these knowledge gaps about the level of risk from solar energy development in Californian deserts on native species and their interactions throughout the food web. The research sought to answer questions related to solar energy development and plants, specifically those centered on alterations to microhabitat conditions resulting from the presence of solar panels and heliostats and the methods used to prepare sites for them. The project was conducted as two parallel studies to address these topics.

One study analyzed the effects of concentrating solar power development, including site preparation and heliostat density on soils, Mojave milkweed, and the queen butterfly at the Ivanpah Solar Electric Generating System in the Ivanpah Valley, California. Whereas most ecological studies investigate the interaction of a single species with its environment, this study was among the first to integrate the interactions across the food web.

In a second study, the researchers measured the effects of photovoltaic solar panels on the changing structure, or demography, of the populations of three annual plant species, including the related Mojave woolly sunflower and woolly daisy and the exotic invasive annual Sahara mustard. The woolly daisy is common, whereas the Mojave woolly sunflower is relatively rare.

If the rare and common species, with their similar evolutionary history, respond similarly to the effects of solar panels, then the common species may be used in place of its rare cousin in assessing impacts or testing strategies to protect them. Specifically, the second study investigated the following research questions:

1. How much do solar panels change abiotic or physical conditions in the microhabitats beneath or near them (that is, temperature, soil moisture, and light for photosynthesis)?
2. Are the effects of these microhabitat changes on belowground dynamics (seed banks) similar across rare, common, and invasive plants?
3. Are the effects of these microhabitat changes on aboveground dynamics (seedling emergence, survivorship, and reproduction) similar across rare, common, and invasive plants?
4. Do panel microhabitats influence community metrics (species richness, diversity) or relative abundance of native and exotic taxa?

The intent of both studies was to provide on-the-ground management recommendations to conserve desert plants and ecosystems. Simulated solar panels made from plywood were installed at study sites where the three species were found.

Project Approach

The researchers conducted field-based ecological studies involving desert ecosystems and solar energy development. The team generated and tested hypotheses related to the effects of habitat alteration from solar energy development, including concentrating solar power and photovoltaic panels, on desert plants in the Mojave Desert.

In the first study, the researchers defined treatments representing three unique site preparation treatments at the Ivanpah Solar Electric Generating System: (1) bladed — intensive site preparation via blading (that is, bulldozing); above- and belowground plant material removed; (2) mowed — moderate site preparation intensity via mowing with about one foot of aboveground biomass retained; and (3) halo — a pre-construction, plant conservation treatment that designated buffer zones around rare desert plants within the solar field that were left undisturbed. Control plots in undisturbed desert scrub habitat with Mojave milkweed were also studied. The researchers collected physical and biological data during spring and fall seasons over three years.

In the second study, the team installed panels to simulate photovoltaic panels at three sites near Barstow, California. Each site supported a large population of one of the three annual plant species. Plots at each site were divided into different microhabitats, including shade (beneath the panels where light and precipitation are blocked), runoff (along the southern edge of the panel where precipitation drains from the panel), and controls that corresponded to the other two types but under natural conditions. The researchers again collected data on physical conditions and ecological processes such as retention of seeds in the soil and the growth and reproduction of the annual plants in the different microhabitats.

Project Results

The researchers determined that site preparation at the Ivanpah Solar Electric Generating System via blading (bulldozing) created poor soil conditions for nearly all plants and that preconstruction, plant-conservation halos of undeveloped desert within the heliostat field are effective for Mojave milkweed conservation and maintenance of Mojave milkweed for use as host plants by queen butterflies. For desert annuals, the researchers determined that microhabitat alteration from simulated solar panels did not affect reproduction and mortality rates for any of the focal species, but that the effects of significantly altered growing conditions such as water availability and soil temperature may have population-level effects on these species over time and with varied climactic conditions. The researchers' results indicate that solar energy development in the Mojave Desert may have adverse impacts on some desert plants and that the level of impact may be regulated, to some extent, by informed site preparation and management practices. The team recommends preparing sites for solar energy development by mowing rather than blading to reduce disturbance in desert ecosystems. The team also recommends that both concentrating solar power and photovoltaic solar facilities incorporate a mosaic of undeveloped areas within solar fields for the benefit of plants and wildlife that use them.

Knowledge Transfer Activities

The project used a multimedia approach to engage with the diverse set of stakeholders interested in various aspects of utility-scale solar energy development. The research team developed a new website and its associated online content, academic journal articles, datasets, invited talks, and conference presentations. To make this knowledge transfer as effective as possible, the researchers also developed a framework to identify the groups and organizations that take action on solar energy development and the critical knowledge needed to act wisely. The report authors then targeted the products of their research and the new knowledge toward the appropriate audiences in the framework, such as regulatory agencies, renewable energy developers, scientists, and non-governmental organizations. This framework can also identify and prioritize knowledge gaps that should be addressed by future research.

The project was presented twice to the technical advisory committee—May 2017 and February 2019. The committee consisted of experts in desert ecology, market applications (solar energy developers), and regulatory and permitting agencies from the University of Arizona, the California Energy Commission, U.S. Fish and Wildlife Service, the National Renewable Energy Laboratory, SunPower, NRG, Bureau of Land Management, and San Bernardino County. The results of the project have been published in several leading scientific journals, with several other articles being written or reviewed.

Benefits to California

Part of the costs of developing and operating renewable energy facilities is the cost of minimizing environmental impacts. Uncertainty about potential impacts may lead to inappropriate permitting requirements — either overshooting or undershooting the actual problem. The research presented here assessed the effects of solar renewable energy site preparation treatments on a food web involving a rare milkweed and a butterfly that depends upon it and of the effects of solar panels on annual plants through changes in soil temperature and moisture. Specifically, this research informs conservation of desert plant species with economic, cultural, and social significance as well as the plant–animal interaction central to ecosystem function in the Mojave Desert. This work can support ecosystem resiliency and restoration by shedding light on the role of water and soils in desert plant performance at solar energy facilities that in turn can lead to sustained, plant-based ecosystem services from Mojave Desert plants. The researchers are informing managers and policy makers on how to reduce negative effects of solar energy development on Californian desert plants and animals of conservation concern. The research will lead to better-informed and more sustainable renewable energy development in the deserts of California. It also serves as a platform for future studies on effects of solar energy development on soils, plants, and wildlife that will save money for ratepayers in California.

CHAPTER 1: Introduction

Background

Renewable energy development in the United States continues to gain significant momentum as socioeconomic interests and climate change mitigation goals incentivize industrial "green energy". In contrast to finite fossil fuels, solar energy is unlimited and generates negligible greenhouse-gas emissions that contribute to climate change. Ground-mounted, utility-scale solar energy (USSE; 1 megawatt [MWDC]), including photovoltaic and concentrating solar power (CSP), has evolved into the most viable contemporary energy technology, with an energy-generating capacity orders of magnitude greater than that of any other renewable energy system (Tao et al. 2006). In 2016 alone, the United States installed more than 14 gigawatts of solar energy capacity (Solar Energy Industries Association 2016). Favorable environmental conditions and abundant public lands have made Californian deserts ideal environments for solar energy development. Californian deserts support exceptional biodiversity and many threatened and endangered species already stressed by climate change. Studies explicitly quantifying potential effects of solar energy development on desert ecosystems are limited.

Environmental benefits of USSE, including reduced greenhouse gas emissions, must be considered in conjunction with environmental costs to landscapes, ecosystems, and species. The development of USSE exists within a land-energy-ecology nexus, which spans local to regional scales and involves a wide range of political, socioeconomic, industrial, and scientific interests (Moore-O'Leary et al. 2017). In this conceptual framework, complex interactions exist among the physical landscapes where energy systems are sited, energy development and generation, and the populations of organisms and their habitats within and surrounding energy systems that together, holistically inform the sustainability of USSE. Anthropogenic disturbance associated with solar energy production can be extensive over space and time, especially when USSE installations are built on previously undisturbed land (Macknick et al. 2013). Connections between land, energy, and ecology become even more important to consider when USSE is deployed on highly sensitive aridlands, which are common recipient environments for current solar energy development (Hernandez et al. 2015a, Grodsky et al. 2017).

Conceptually, ecological disturbance events often lead to "winners and losers" among species. For example, clearcutting a forest will benefit wildlife species that thrive in early-successional vegetation communities but will tend to displace wildlife reliant on mature forest canopy. In desert ecosystems, the "winners" responding to disturbance may mostly consist of invasive species, such as Saharan mustard (Brassica tournefortii), because native desert species are often poorly adapted to frequent or large-scale disturbances. Colonization of invasive species may be further promoted by the fact that native desert communities often take centuries to recover naturally following disturbance (Webb et al. 2009). Anthropogenic disturbance in the form of solar energy development may alter desert disturbance regimes and facilitate spread of invasive species such as invertebrates and plants, which then may reshape interactions between species and between species and ecological processes.

While endemic desert flora and fauna are adapted to a relatively narrow range of environmental conditions and historically infrequent disturbance, invasive species can occur within a wide range of environmental and habitat conditions. Roads associated with solar facilities also may perpetuate spread of invasive plants. Once populations of invasive species become established in and around solar facilities, propagules may disperse to adjacent undisturbed desert and potentially outcompete native species for resources. Disturbance from solar energy development may facilitate the spread of flammable, invasive annual plants such as Schismus species. Southwestern deserts and the species that live there are not fire-adapted. As such, increased fire frequency resulting from a combination of abundant, invasive plant fuels and higher likelihood of anthropogenic ignitions could have potentially severe ecosystem effects in deserts, adversely affecting sensitive plant communities and wildlife.

Empirical evidence of solar energy development effects on native desert plants is lacking and ambiguous. For example, most utility-scale solar energy facilities in California have been sited within desert scrublands and near protected natural areas, presumably leading to decreased plant biodiversity relative to alternative solar siting locations such as rooftops and degraded lands. An analysis of 30 consecutive years of Landsat satellite imagery across the Lower Colorado Desert revealed no effect of solar energy development on vegetation canopy cover (Potter 2016). Further, a recent modeling study found that solar and wind energy development in the Sahara could locally increase vegetation, although it did not consider site preparation practices or their consequences (Li et al. 2018). However, field-based studies of solar energy development effects on desert plants are needed to draw informed conclusions meaningful to stakeholders.

The case of USSE development in the state of California (USA) represents a collision of conservation, political, and socioeconomic values, making this particular land-energy-ecology nexus a valuable experimental system to test ecological hypotheses regarding ecosystem responses to disturbance from operational renewable energy projects. Given the inertia supporting widespread implementation of USSE throughout the US and the globe, USSE provides a representative model for identifying synergies and trade-offs between conservation and energy goals (Moore-O’ Leary et al. 2017). In California, USSE development is bolstered by state-level initiatives to push renewable energy and combat climate change. Meanwhile, most USSE installations larger than 20 MW in California are sited in natural systems close to less than 7 kilometers or often within protected natural areas (Hernandez et al. 2015b). As of 2014, there are pending requests for more than 220,000 hectares in the Mojave Desert to install USSE on Bureau of Land Management land (Hernandez et al. 2014a). The Mojave Desert supports exceptional biodiversity and many endemic species of conservation concern. The Mojave Desert may be especially imperiled by USSE development because desert species are not adapted to disturbance, whereas biological invaders thrive on it, and climate change impacts may exacerbate effects from USSE-related disturbance (Ustin et al. 2009).

USSE may affect entire trophic systems, thus effective conservation in and near solar facilities will require comprehensive, ecosystem-based management approaches informed by species-species and species-process interactions (Grodsky et al. 2017, Moore-O’Leary et al. 2017). To date, research on renewable energy and wildlife conservation has focused on direct (for example, mortality) or indirect effects (such as displacement) of renewable energy systems on a single taxon or species (see Lovich and Ennen 2011, Hernandez et al. 2014b, and Grodsky et al. 2017 for review of scarce empirical, peer-reviewed studies of USSE and wildlife). Although these research efforts may effectively guide management for certain taxa and may cumulatively inform conservation efforts for wildlife communities, they do not advance the understanding of the ecological mechanisms responsible for ecosystem-level responses to renewable energy development. In contrast, an ecosystem-based approach elucidates effects of renewable energy development on biota by focusing on "bottom-up" interactions among soils, plants, and animals and energy production, which may subsequently reveal mechanisms behind ecological responses to renewable energy-associated (for example, USSE) disturbance and environmental change.

Specifically, USSE can disturb microhabitats in at least two ways. First, site preparation varies within and between sites. Some areas are bulldozed to remove all existing vegetation; others may be mowed to reduce the height of remaining vegetation but left in place beneath photovoltaic (PV) panels of heliostats. In some cases, small areas within solar arrays have been left relatively undisturbed to protect species of concern, such as the "halos" at the Ivanpah Solar Electric Generating System (ISEGS). Regardless of the site preparation treatment, the presence of the PV panels or heliostats modifies the microhabitat by shading (and therefore cooling) the surface beneath and by diverting precipitation from below the panels to a runoff area along the lower edge.

Report Organization

In this report, the researchers present two independent chapters pertaining to effects solar energy development on plants in the Mojave Desert. Chapter 2 involves the effects on microhabitat of site preparation and management activities for CSP on trophic interactions between Mojave milkweed and the queen butterfly at ISEGS. Chapter 3 involves the effects of simulated PV solar panels on microhabitats and consequently on the demography and community composition of desert annual plants, including invasive species. Chapter 4 embodies knowledge transfer activities and products, including insight into the knowledge system that may benefit and/or intersect with these deliverables. Knowledge systems are the complex networks of actors, organizations, and objects that perform knowledge-related functions, most notably linking knowledge with action, which may include research, innovation, development, demonstration, deployment, and adoption.

Objectives

In Chapter 2, the researchers' primary objective was to assess effects of microhabitat conditions in ISEGS (as affected by site preparation, heliostat configuration, and management [that is, halos]) and in undisturbed desert on:

- Seasonal (spring and fall) plant characteristics and long-term demographics of Mojave milkweed.
- Oviposition rates and abundance of eggs and caterpillars of monarch and queen butterflies using Mojave milkweed host plants.
- Physical and chemical defense traits of Mojave milkweed and linkages to herbivory.

- Larval toxicity of desert *Danaus* caterpillars and linkages backwards to Mojave milkweed defense traits and forwards to avian predation rates.

The researchers hypothesized that within shaded microhabitats in ISEGS, chemical and physical defenses of Mojave milkweed are reduced, herbivory on Mojave milkweed by desert *Danaus* caterpillars is increased, sequestration of defense chemicals by desert *Danaus* caterpillars is reduced, avian predation rates on desert *Danaus* caterpillars are low but invertebrate predation rates on desert *Danaus* caterpillars are high, and parasitism of desert *Danaus* caterpillars is increased.

In Chapter 3, the researchers' objective centered on four questions:

1. Did experimental solar panels drive differences in abiotic conditions across local microhabitats at each site?
2. Were panel microhabitat effects on belowground dynamics similar across rare, common, and invasive taxa?
3. Were panel microhabitat effects on aboveground dynamics similar across rare, common, and invasive taxa?
4. Did panel microhabitats influence community metrics (species richness, diversity) or relative abundance of native and exotic taxa?

Broad Goal

The underlying goal of both studies was to inform sustainable solar energy production in Californian deserts by providing science-based evidence of the ecological consequences, the efficacy of mitigation techniques, and the management implications of development and operation of industrial-scale solar facilities in desert ecosystems.

CHAPTER 2: Effects of Ivanpah Solar Electric Generating System on Mojave Milkweed-Queen Butterfly Interactions

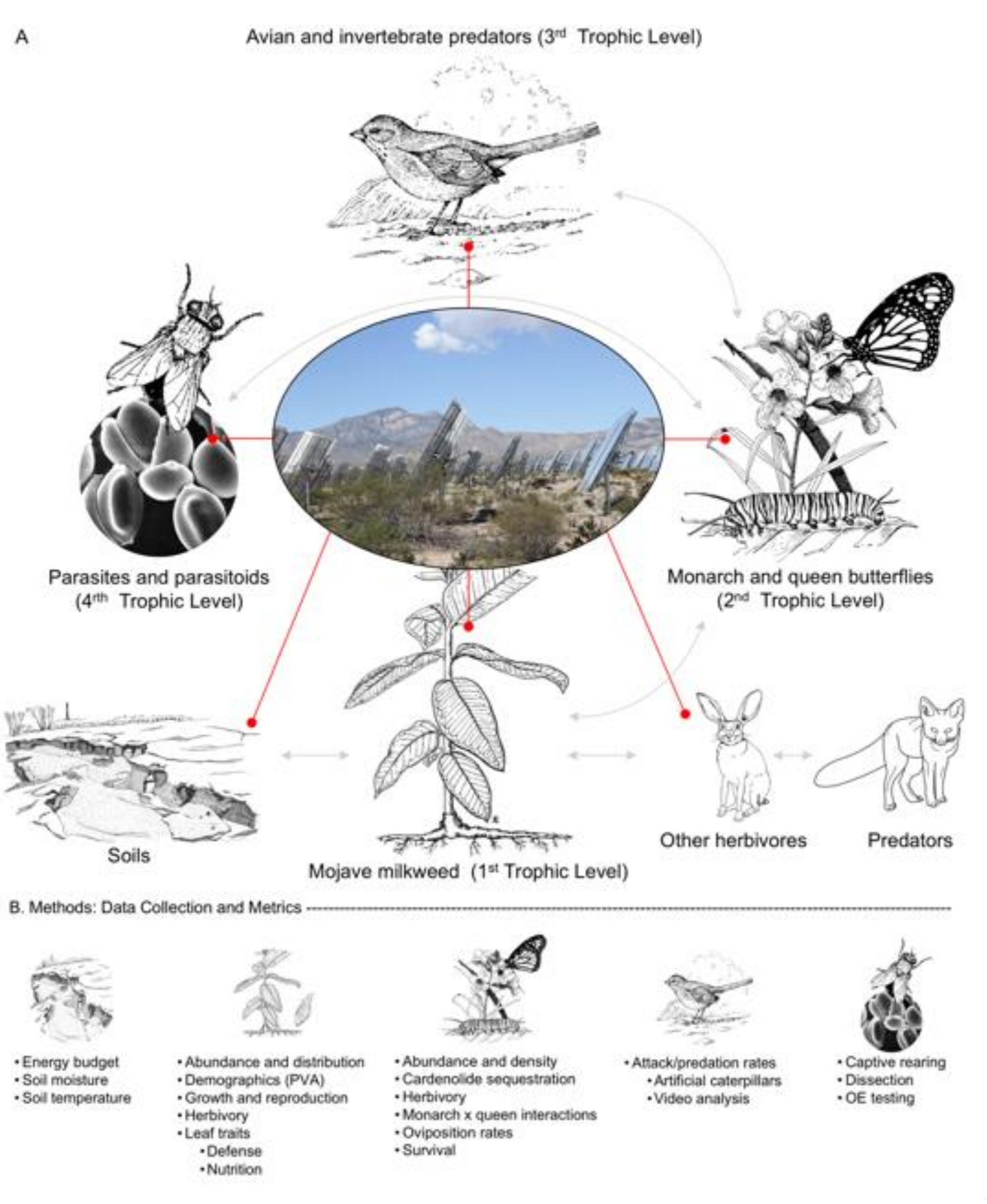
Introduction

When considering effects of solar energy development on entire desert ecosystems, a “bottom-up” approach can be useful for elucidating interconnected rather than isolated impacts on representative desert systems (Grodsky et al. 2017). For example, studying how solar energy facilities affect soils, which affect Mojave milkweed and the queen butterfly (a close relative of the monarch butterfly), which uses Mojave milkweed as a host plant, may reveal mechanisms behind ecological responses to solar energy-mediated disturbance and environmental change. In contrast, measuring response of one individual element of the soil-milkweed-queen nexus to solar-energy mediated disturbance may uncover patterns, but is less likely to reveal causation. Preconstruction site preparation at solar facilities may vary in intensity (for example, blading vs. mowing), which dictates levels of soil disturbance and consequently plant community response (Hernandez et al. 2014b). Heliostat presence and configuration may alter microclimate conditions of soils via shading and altered water dynamics, including availability, runoff, and erosion (Tanner et al. 2014). Soil variables may, in turn, affect milkweed physiology, photosynthetic rate, and overall plant health, potentially leading to variable rates of herbivory and granivory (Moore O’Leary et al. 2017). Positive and/or negative feedback loops between individual milkweed plants and queen caterpillars may result in further “bottom-up” implications, including individual caterpillar survival.

Research at the nexus of solar energy development and desert plant ecology may be essential for informing sustainable development of solar energy in the California. Among major renewable energy technologies, solar energy has a high propensity for large-scale development in undisturbed, sensitive desert ecosystems with high biodiversity (Hernandez et al. 2015). In contrast, wind energy facilities may be sited in agricultural areas with typically low biodiversity (McDonald et al. 2009, Grodsky et al. 2013), and woody biomass harvests for forest bioenergy often occur after timber harvest in industrial forests (Grodsky et al. 2018). Desert ecology studies on solar energy development may be enhanced by prioritizing research efforts that address species–species and species–process interactions, including “bottom-up” ecological interactions, ecosystem-wide effects, and landscape-level impacts.

This project encompasses a series of experiments aimed at determining interactive, “bottom-up” ecological responses to the development, operation, and maintenance of ISEGS in the Mojave Desert. The objectives were to address effects of ISEGS on soils, Mojave milkweed (*Asclepias nyctaginifolia*) — a rare desert plant — and butterflies in the genus *Danaus*, including queen (*D. gilippus*) and monarch (*D. plexippus*) butterflies. The goal was to inform sustainable solar energy development in Californian deserts through the study of the nexus of anthropogenic land-use changes and ecological interactions among soils, host plants, butterfly caterpillars (herbivores), adult butterflies (pollinators), and avian predators at ISEGS (Figure 1).

Figure 1: Conceptual Model of Trophic Interactions



Conceptual model of the Milkweed-Danaus Trophic System, including interactions among Ivanpah Solar Electric Generating System (red lines) and soils, plants, and animals (grey lines). (B) Links between methods and the Milkweed-Danaus Trophic System Conceptual Model.

Source: UC Davis

In addition to serving as an indicator species for other desert plants, Mojave milkweed is a critical host plant (*1st trophic level*) for two desert butterflies in the genus *Danaus* (hereafter "desert *Danaus* butterflies"): monarch butterfly (*Danaus plexippus*) and queen butterfly

(*Danaus gilippus*) (Figure 2). Given the dense but restricted distribution of *A. nyctaginifolia* and relatively low abundance of other milkweed species in Ivanpah Valley, Mojave milkweed likely provides critical resources for breeding desert *Danaus* butterflies in the region.

Figure 2: Mojave Milkweed (*Asclepias nyctaginifolia*)

Photo by Steve Grodsky

The fitness of desert *Danaus* butterflies is inextricably linked to the fitness of Mojave milkweed (Figure 3). Both monarch and queen butterflies oviposit on milkweed, especially regionally abundant Mojave milkweed. Of the desert *Danaus* butterflies, breeding populations of the queen are more common in the Ivanpah Valley than those of monarchs (S. Grodsky, personal observation). The peak oviposition period of desert *Danaus* butterflies typically coincides with the spring emergence of Mojave milkweed at ISEGS (Moore and Grodsky, *personal observation*, 2011 - 2017). Larvae (that is, caterpillars) of monarch and queen butterflies hatch from eggs on Mojave milkweed, eat their own egg casing (and possibly surrounding, unhatched butterfly eggs), and then begin rapidly consuming the milkweed leaves (*2nd trophic* level). As the caterpillars eat Mojave milkweed leaves, they sequester cardenolide glycosides used by the milkweed species as a chemical defense against herbivory from other animals and molt through a series of instars (monarch = 5; queen = 6) until they are large enough to pupate. Both monarch and queen butterfly caterpillars exhibit characteristic white, black, and yellow striping, a warning to predators that they are toxic and distasteful. Despite these chemical defenses, several bird and invertebrate species tolerate or even specialize on monarch and queen butterfly caterpillars as prey (*3rd trophic level*). Last, desert *Danaus* butterflies are hosts for several parasites and parasitoids (*4th trophic level*), including the virulent protozoan *Ophrocystis elektroscirrha* and tachinid flies, respectively. Mojave milkweed (Figure 2) is a rare, perennial plant species that occurs in an isolated range within the Ivanpah Valley, California (Grodsky et al. 2019b). Most known Mojave milkweed populations occur immediately within and near ISEGS. Mojave milkweed exhibits key traits of many endemic, herbaceous desert perennials, including iteroparous habit (seasonal emergence and reproduction), capacity to remain dormant during unfavorable conditions, and possession of belowground storage structures (for example, tubers).

Figure 3: Queen Butterfly (*Danaus gilippus*) Larva

Photo by Steve Grodsky.

Methods

Study Area

The researchers conducted the study in ISEGS and surrounding natural desert. ISEGS is located in the Desert Renewable Energy Conservation Plan area, about 45 miles south of Las Vegas, Nevada (Figure 4). ISEGS is located on a bajada at the base of Clark Mountain in the Ivanpah Valley, San Bernardino County, California (35°33′ 8.5″ N, 115°27′ 30.97″ W) in the Californian Mojave Desert. ISEGS consists of 173,500 heliostats (~350,000 individual mirrors). ISEGS was constructed in 2011 on a 1,400-ha tract of previously undeveloped Mojave Desert creosote scrubland near the Mojave River corridor, the Mojave National Preserve, and Mesquite and Stateline Wildernesses.

Figure 4: Location of Ivanpah Solar Electric Generating System

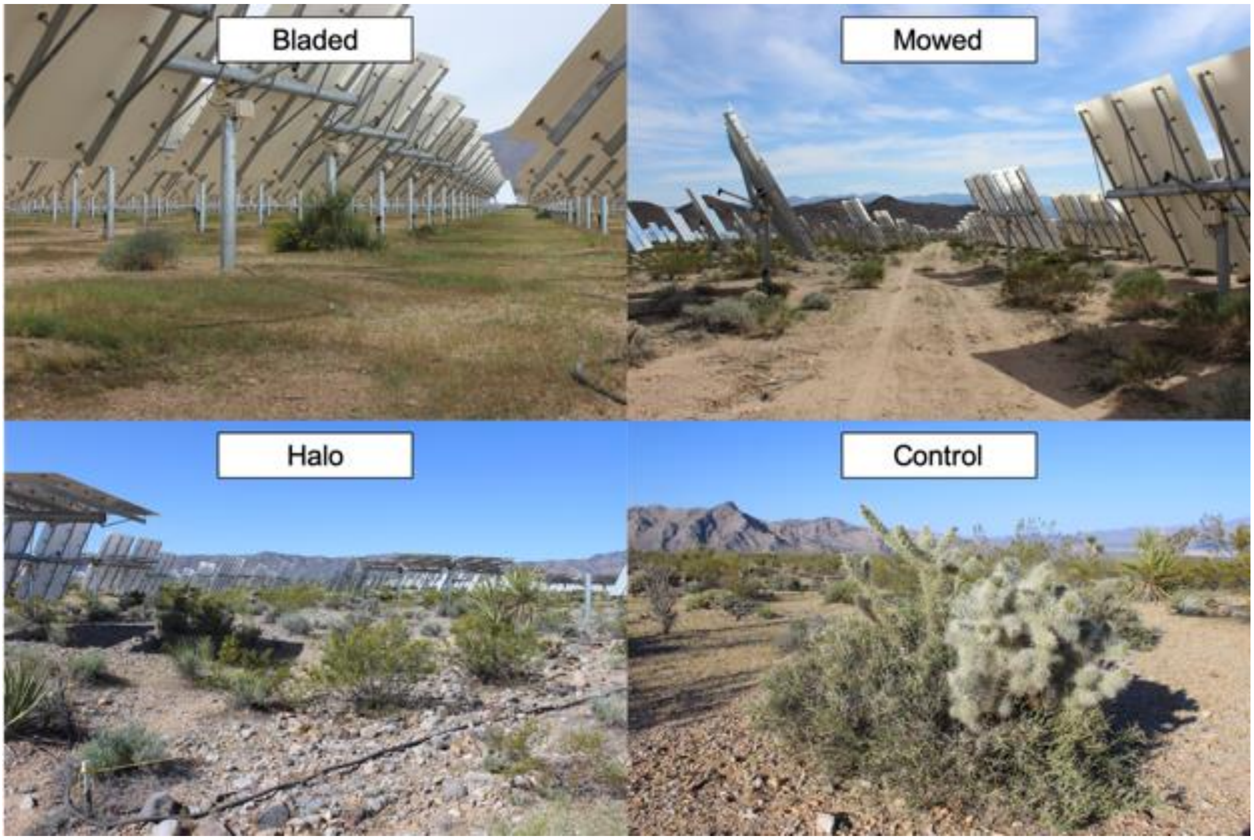
Location of Ivanpah Solar Electric Generating Facility in California's Desert Renewable Energy Conservation Plan Area.

Source: Map adapted from Moore and Pavlik 2014.

Study Design

The researchers quantified effects of concentrating solar power development, including site preparation and heliostat density, on soils, Mojave milkweed, and the queen butterfly using ISEGS as a model system. Within ISEGS, the researchers designated each of the three power blocks (that is, tower and associated heliostats as replicated blocks. The researchers defined treatments in each block representing three unique site preparation treatments as follows (see Figure 5): (1) bladed—intensive site preparation via blading (that is, bulldozing); above- and belowground biomass removed; (2) mowed—moderate site preparation intensity via mowing; ~0.30 m aboveground biomass retained; and (3) halo—a pre-construction, plant conservation decision that designated buffer zones around rare desert plants within the solar field, which were roped off and left undisturbed (that is, no site preparation, no heliostats). The bladed treatments have the highest heliostat density, given the physics of light reflection, and were used as a storage site for solar energy infrastructure during construction, which is why the developer opted not to mow in these areas. The researchers designated replicated control plots in natural desert scrub containing Mojave milkweed populations immediately surrounding ISEGS.

Figure 5: Experimental Treatments in Ivanpah Solar Electric Generating System



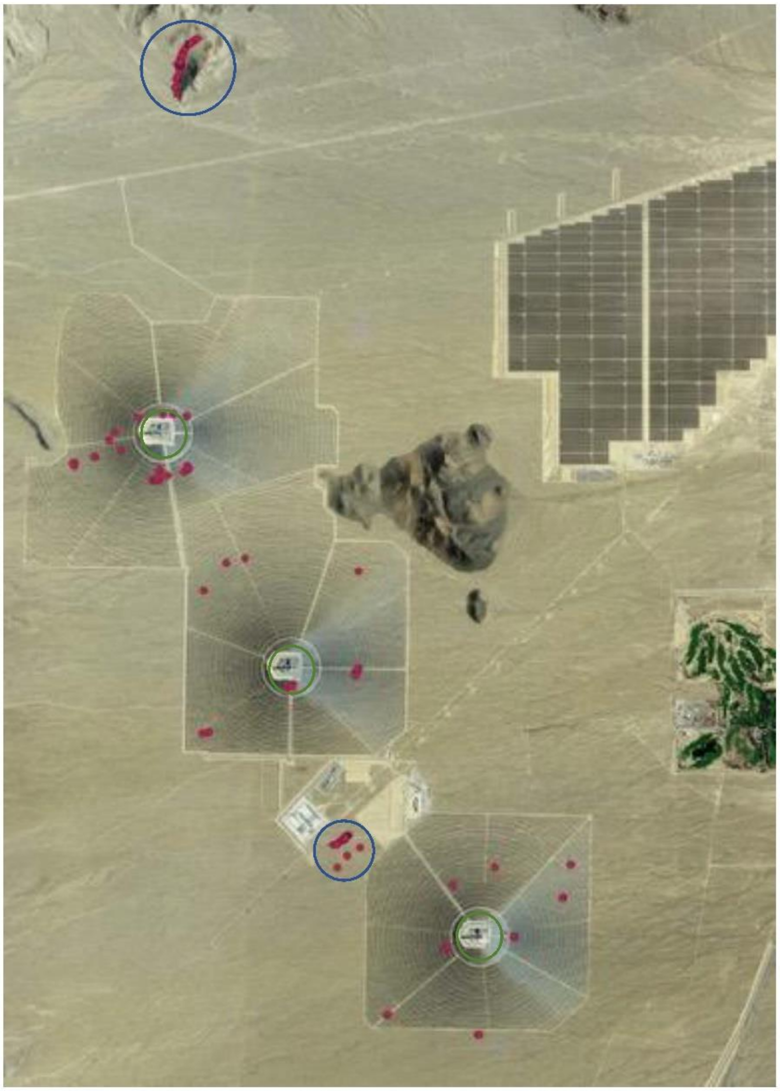
Bladed—intensive site preparation via blading (that is, bulldozing); above- and belowground biomass removed; (2) mowed—moderate site preparation intensity via mowing; ~0.30 m aboveground biomass retained; 3) halo—a pre-construction, plant conservation decision that designated buffer zones around rare desert plants within the solar field, which were roped off and left undisturbed (that is, no site preparation, no heliostats); and 4) control plots in natural desert scrub containing Mojave milkweed populations immediately surrounding ISEGS.

Photographs by Steve Grodsky.

Mojave Milkweed and Queen Caterpillar Sampling

During peak Mojave milkweed emergence and queen butterfly breeding activity, the researchers collected abiotic and biological data at all Mojave milkweed locations in treatments within ISEGS and at control sites during three spring field seasons (April – June 2017, April and May 2018; April and May 2019) and three fall field seasons (September 2017 – 2019) (Figure 6). The researchers collected a suite of field measurements and observations, including soil temperature, Mojave milkweed characteristics (for example, plant volume, number of stems, reproduction), and number of butterfly eggs and caterpillars on Mojave milkweed plants at all Mojave milkweed locations. The researchers recorded continuous video footage using self-sustaining, solar-powered camera arrays at 48 Mojave milkweed locations (12 cameras in each treatment and controls) to document real-time phenological events, including butterfly oviposition, pollinator visits, herbivory, and predation on caterpillars.

Figure 6: Mojave Milkweed Locations in Ivanpah Solar Electric Generating System and Controls



Location of Mojave milkweed in ISEGS (red dots). Orange circles indicate location of bladed treatments and blue circles indicate location of control populations of Mojave milkweed. No halo treatments (that is, mowed) were located within the boundary of each power block where a halo was not present. Halos treatments were located within blocks in locations containing rare plants found during the pre-construction phase.

Source: Map by Jason Whitney.

Abiotic Sampling

The researchers used *SoilDucks* (Figure 7), a type of I-button, to measure soil temperature at 40 locations throughout treatments in ISEGS and controls. The researchers deployed half of the *SoilDucks* at locations without plant cover and the other half at locations directly under the canopy of Mojave milkweed plants. The researchers buried each *SoilDuck* 10 cm below the soil surface and automatically recorded rea-time subterranean soil temperature each hour from 7 May 2017 to 20 September 2019. The researchers also recorded rainfall using rain gauges at each *SoilDuck* location.

Figure 7: *SoilDuck* Temperature Sensor Installed under Mojave Milkweed

Photograph by Steve Grodsky.

Concurrent Ecological Sampling

The researchers sampled plants in 15 spatially independent plots in each of the three treatment units in blocks (five plots/treatment/block) and in control sites (total plots = 60). The researchers situated plots in controls along five randomly selected transects – three north of each block and two south of two blocks. Each transect contained three plots stratified at 250 m, 500 m, and 1 km from the boundary of the nearest block. The researchers chose the upper limit of stratification based on spatial analysis of aerial photography, which indicated that plots established at a distance greater than 1 km from ISEGS would be confounded by other landscape features potentially affecting plants, including Clark Mountain to the north (for example, elevational plant community shift) and a golf course and highway to the south.

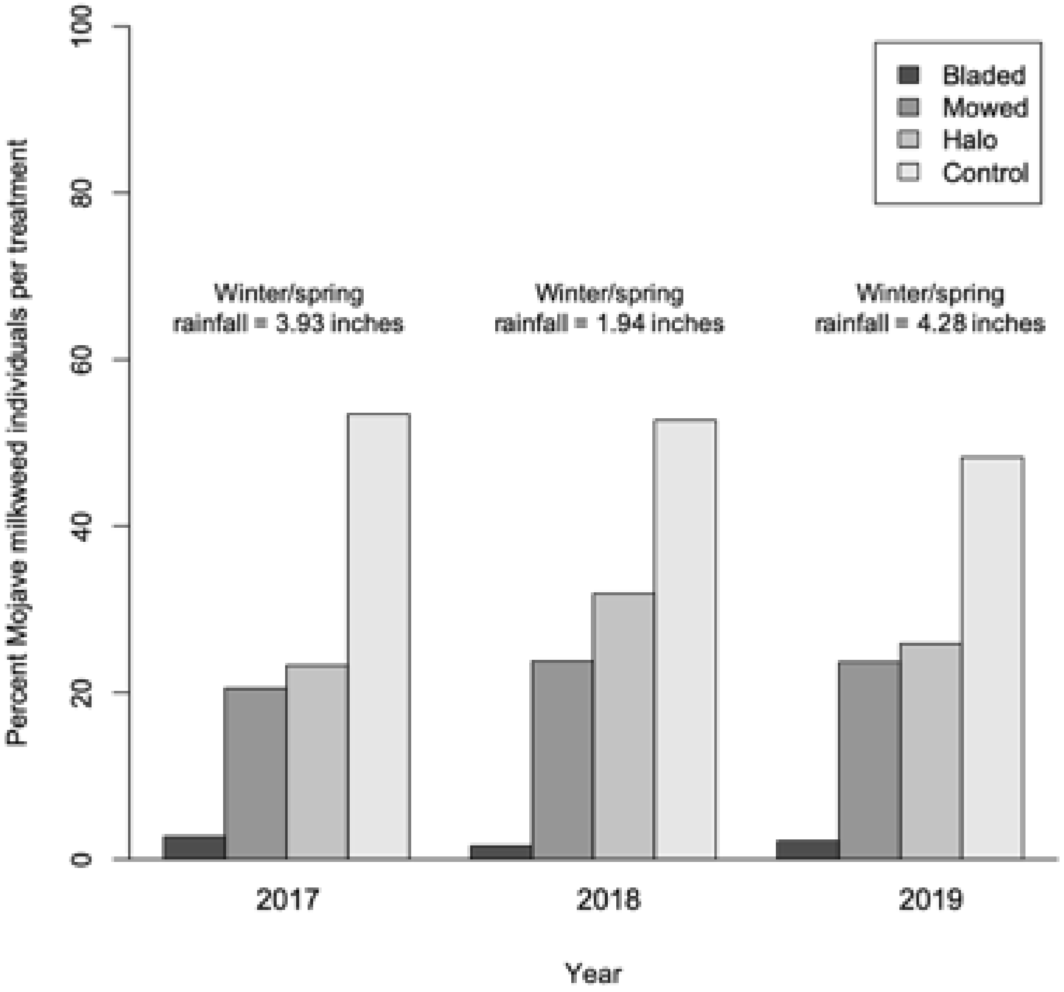
The researchers measured plant composition, plant structure, species richness, species diversity, and relative abundances of plants in each photosynthetic pathway, individual species, reproductive individuals, and clones using a combination of the line intersect method and whole-plot visual vegetation surveys during peak-spring growing season in the Mojave Desert, 28 April - 8 May 2018. The researchers established four, 10-m long transects radiating from the center of each plot in each cardinal direction. The researchers walked along each transect and measured each individual plant ≥2 cm that were encountered within 5 cm of either side of the transect line. For each plant intersecting the transect-line area, the researchers recorded species and cover [length of transect covered by plant canopy (cm)]. The researchers used a 2-m tall, 4.8-cm diameter rod marked at 1-decimeter increments to measure the maximum height of each individual plant and determined whether individuals were reproductive based on presence or absence of flowers on perennials and spikelets on grasses. For clonal species (for example, *Larrea tridentata*), the researchers considered individual stems ≤1 meter from one another as clones and counted the number of clones for each individual plant intersecting the transect-line area. After the researchers sampled vegetation along all transects in a plot, they visually surveyed the entire plot area (macroplot = 100m^2) and recorded all plant species undocumented during the line-intersect survey for use in community-level analyses.

The researchers calculated plant height per individual as the sum of heights for each individual plant in each plot divided by the total number of individual plants in each plot. The researchers calculated plot-level percent cover as the total plant cover divided by the total transect length in each plot; total transect length in the Bladed, Mowed, and Control treatment plots was 4,000 cm, and transect lengths in the Halo treatment plots were determined by the variable dimensions of each individual "halo". Because transects differed in length, the researchers calculated relative abundances for perennials, annuals, individual species, clones, and reproductive individuals by dividing number of individuals by total transect length in meters (that is, individual plants/meter). The researchers used counts of individual species and abundance of individual species pooled over the total plot area (that is, transects and macro-plots) to generate species richness and species diversity measures, respectively. To elucidate comprehensive patterns of species richness and evenness among treatments, the researchers computed mean Shannon diversity indices (H`) for each plot ("vegan" in R).

Results

The researchers recorded a larger percentage of Mojave milkweed individuals in controls than in any treatment within ISEGS during each spring growing season (Figure 8). The number of Mojave milkweed individuals increased from 2017 (*n* = 140) to 2019 (*n* = 230). The total number of Mojave milkweed individuals in ISEGS and controls increased through time (Figure 9).

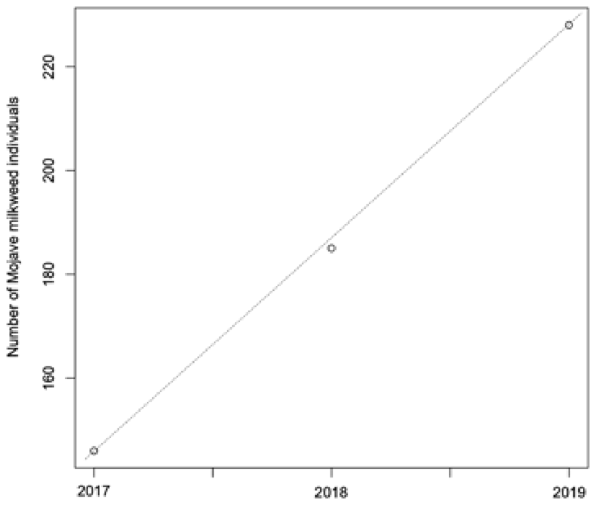
Figure 8: Percent Mojave Milkweed Individuals per Treatment



Percent Mojave milkweed individuals per treatment during each year of the study. Winter and spring rainfall data potentially affecting milkweed growth is presented in the figure for each year.

Source: UC Davis

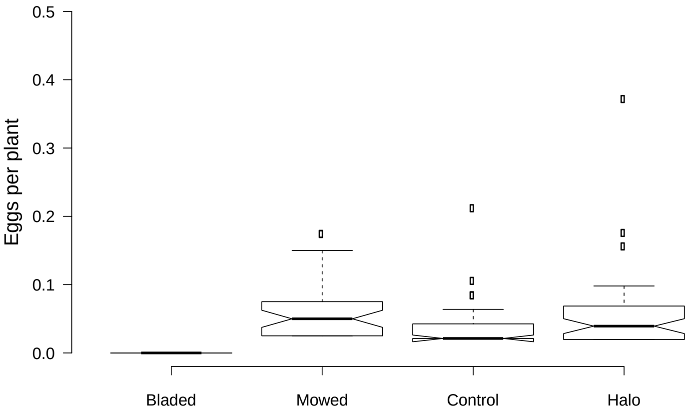
Figure 9: Number of Mojave Milkweed Individuals per Year



Source: UC Davis

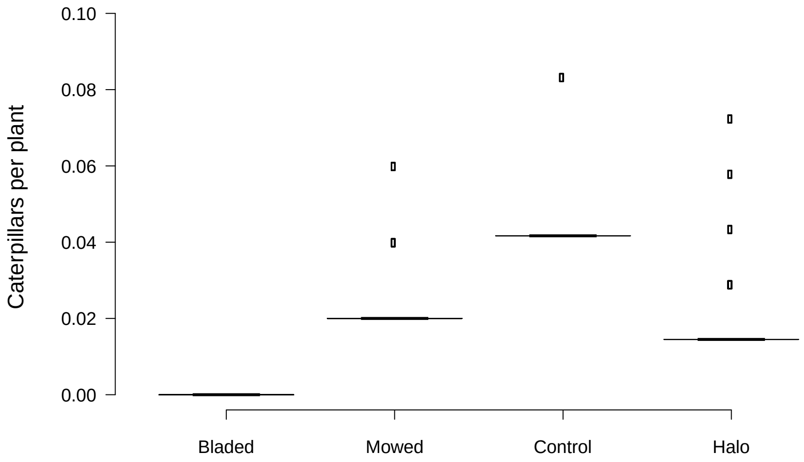
The researchers counted 310 queen butterfly eggs and 184 queen butterfly caterpillars, respectively, in the spring of 2017. Number of butterfly eggs was significantly lower in the bladed treatments than all other treatments, but did not differ among mowed, control, and halo treatments (Figure 10). Number of queen butterfly caterpillars was significantly lower in the bladed treatments than all other treatments and significantly higher in the control treatments than all other treatments (Figure 11). The researchers did not document any breeding activity by monarch butterflies in 2017 or any breeding activity by either queen or monarch butterflies in 2018. However, the researchers documented one monarch caterpillar on a Mojave milkweed plant during vegetation surveys in the fall of 2019. In the spring of 2019, the researchers counted 37 queen butterfly eggs and 6 queen butterfly caterpillars; they recorded all caterpillars and most eggs (84%) on Mojave milkweed plants in controls.

Figure 10: Number of Queen Butterfly Eggs per Plant (2017)



Source: UC Davis

Figure 11: Number of Queen Butterfly Caterpillars per Plant (2017)

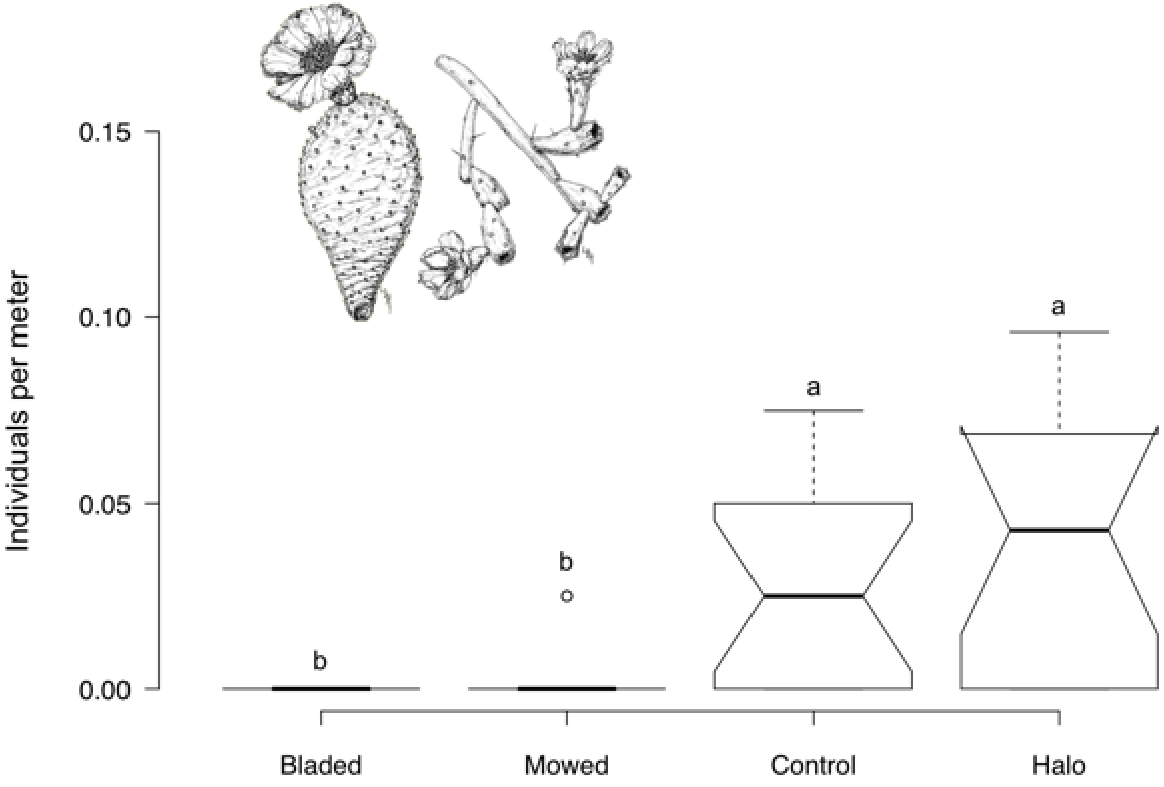


Source: UC Davis

The researchers determined that both structure and composition of perennials was lower in bladed treatments than in all other treatments and lower in mowed treatments than in halo treatments and controls. The researchers determined that the relative abundances of perennials, reproductive perennials, *Ambrosia dumosa*, and *Larrea tridentata* were lower in bladed treatments than in all other treatments and in controls; relative abundance of clonal perennials was lower in bladed treatments than all other treatments and lower in mowed treatments than in halo treatments and controls. The researchers determined that relative abundance of plants using the crassulacean acid metabolism (CAM) photosynthetic pathway was higher in controls and halo treatments than in mowed and bladed treatments (Figure 12), whereas relative abundances of the invasive grasses *Schismus* spp. (*S. arabicus* and *S. barbatus* were indistinguishable in the field) were higher in bladed treatments than in all other treatments and controls (Figure 13).

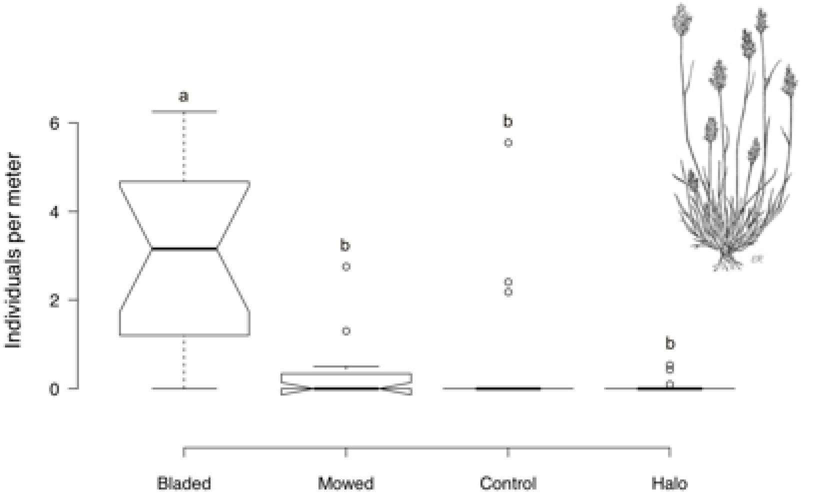
The researchers summarized their results on treatment-level on Mojave milkweed and other desert perennials in Figure 14.

Figure 12: Relative Abundance of CAM Plants in Treatments



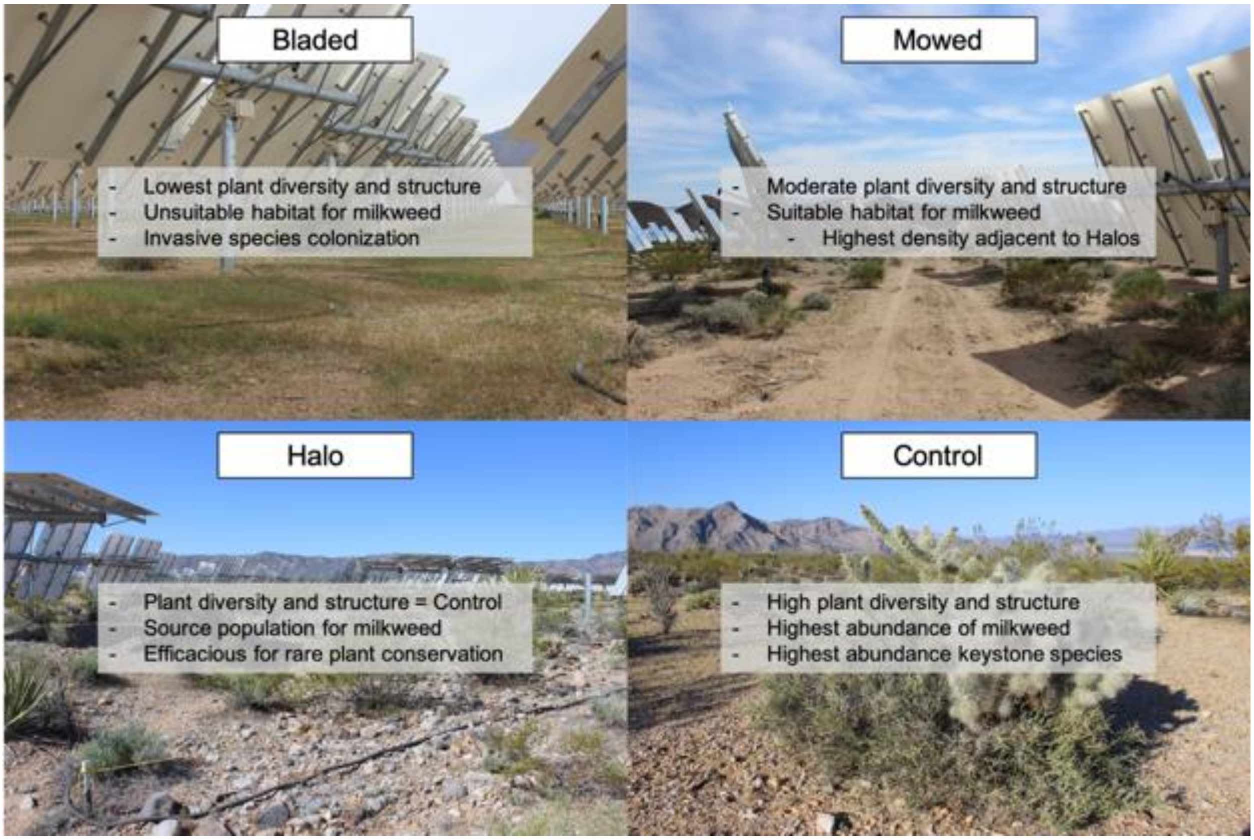
Source: UC Davis

Figure 13: Relative Abundance of *Schismus* spp. in Treatments



Source: UC Davis

Figure 14: Summary of Treatment-Level Effects on Plants



Source: UC Davis

Management Implications

Blading (that is, bulldozing) negatively effects desert perennials, including the rare Mojave milkweed, and plant-insect trophic interactions. Further, blading increases colonization of invasive grasses like *Schismus* spp., which, in turn, can increase risk of wildfire and decrease abundance of CAM species like cacti and yucca. Despite yearly differences in rainfall, Mojave milkweed was always more abundant in control population than in ISEGS. As a management practice, halos within solar facilities designed for rare plant conservation are efficacious for maintenance of Mojave milkweed populations inside ISEGS. The mowed areas of ISEGS appear to provide suitable habitat for Mojave milkweed, albeit sporadic and especially evident in comparison to bladed areas. Mojave milkweed was effectively unavailable to queen butterflies as a host plant in bladed areas. Although queen butterflies oviposited on Mojave milkweed in halos and mowed areas in 2017, caterpillar survivorship was highest in controls. Further, the researchers found most queen butterfly eggs and caterpillars in control treatments in 2019. These results suggest that ISEGS may negatively impact host-plant use by queen butterflies within the solar facility. When possible, blading should be avoided as a site preparation practice to limit negative ecological effects of solar energy development in the Mojave Desert. They also suggest that leaving undeveloped gaps akin to halos in CSP or PV installations will lead to positive ecological outcomes. As a rare plant, Mojave milkweed is persisting in ISEGS; however, ecological interactions between Mojave milkweed and beneficial insects were negatively impacted relative to controls.

CHAPTER 3:
Photolvoltaic-Annual Plant Nexus: Impacts of Simulated Solar Panels on Plant Demography and Annual Communities

Introduction

Solar energy facilities alter habitat through disturbance and infrastructure effects on light and water regimes (Smith, S.D., Patten, D.T., Monson, 1987; Tanner, Moore, & Pavlik, 2014). Inside site footprints, natural microhabitats created by topographic variation are replaced by novel shade and moisture gradients imposed by solar infrastructure, and activities required for facility operation (for example, panel washing). Typical management planning for both rare and invasive species may overlook how species response varies across micro-environmental gradients within energy facilities and mitigation areas. Altered microhabitats are likely to favor some species: for example, invasive plants may increase where microsite conditions favor invader success. In contrast, native species may be limited if fitness is reduced in altered microhabitats. Rare species can have narrow distributions because they occupy unusual habitats or specialized niche space, so abiotic changes imposed by solar infrastructure may disproportionately affect these taxa. Without insight into microhabitat effects, costly efforts to maintain populations of rare species affected by solar facilities or reduce the spread of invasive plants may be compromised. Furthermore, long-term mitigation and conservation outcomes will be strongly influenced by intrinsic and exogenous factors such as onsite soil characteristics and seasonal rainfall. These factors can mediate the effects of altered microhabitats, with downstream consequences for plant demographic performance and community structure.

Here, microhabitat effects on performance of three species are assessed at sites with distinct soil characteristics and variable rainfall across the study period. The focus on annual species is justified because they are critical components of desert ecosystems, and provide a tractable system for measuring population-level impacts on short timescales. The annual plant life history strategy may be especially sensitive to changes associated with energy development, because of the risk of mortality prior to successful reproduction (J. Beatley, 1967) and the lack of an aboveground link between generations (Morris et al., 2008). Nonetheless, in North American deserts where the environment is characterized by strong temperature fluctuations and highly variable rainfall (Went, 1948), annuals may comprise more than 40% of the flora (Leck, Parker, & Simpson, 1989). Dormant seed banks provide a means of persisting through periods unfavorable for aboveground growth (Tevis, 1958; Went, 1948); under unfavorable germination conditions only a fraction of seeds break dormancy, such that each generation spreads risk across multiple seasons – an important bet hedging strategy for desert species (Leck et al., 1989). Germination cues can be complex and variable among species (Freas & Kemp, 1983; Philippi, 1993) and these “germination niches” can contribute to community diversity via resource partitioning (Chesson, 2000) or drive directional shifts in community composition (Kimball, Angert, Huxman, & Venable, 2010). Seed bank dynamics are thus critical determinants of desert annual ecology, but remain challenging to observe because of their cryptic nature, and because of difficulties in assessing both seed age and shifts in age-dependent mortality for in situ seed banks (Adondakis & Venable, 2004; Clauss & Venable, 2000; Freas & Kemp, 1983). Furthermore, models of annual population growth are often sensitive to seed viability, germination, or survival rates (Venable, 2007), but little information is available to suggest how these belowground demographic transitions vary across microsites or with seed age (Philippi, 1993). Estimates of seed persistence in the seed bank and probability of germination in different microsites are necessary to understand how invasive species will respond to microhabitats imposed by solar infrastructure over time. For example, Brassica tournefortii is known to germinate under a range of temperatures and light regimes (Bangle, Walker, & Powell, 2008), but the effect of microhabitat on seed survival is unknown. Germination rate and seed survival rate in the soil over time are likely to differ among species, and further vary by microhabitat. Seed ecology may thus drive growth opportunities for plants populations at energy installations, where construction activities reshape topography and infrastructure imposes abiotic shifts (Armstrong, Ostle, & Whitaker, 2016; Smith, S.D., Patten, D.T., Monson, 1987; Tanner et al., 2014). These factors are likely to have differential effects on seed germination and seed bank survival, exerting an influence on community composition. It is therefore essential to conduct studies that yield sound information on seed ecology and assess how microsite conditions may affect belowground processes that contribute to plant population growth or decline. Furthermore, little is known about potential interactions between soil microbial communities and seed dynamics in desert systems. To the best of the researchers' knowledge, the importance of soil pathogens for seed survival in desert systems remains unexplored even in natural settings – but in tropical and grassland systems, microsite conditions and associated shifts in soil pathogen activity affect seed survival (Augspurger & Kelly, 1984; Mordecai, 2012; Pake & Venable, 1996). If seed-pathogen interactions are important drivers of survival and germination in deserts, renewable energy facilities offer an ideal opportunity to explore their effects, because site infrastructure creates strong departures from natural abiotic conditions.

In this study the researchers examined the effects of solar infrastructure on the aboveground and belowground life stage transitions of three focal species - the native annuals Eriophyllum mohavense and E. wallacei, and the exotic invasive annual Brassica tournefortii. The choice of a rare-common native species pair is strategic. Data on population resilience and/or sensitivity are often in short supply because rare taxa can be difficult to locate or access; in addition, regulatory constraints may preclude manipulative studies if they might harm populations. Nonetheless, land managers are sometimes required to make management decisions even where data on rare species are lacking. If data are available for a common relative, they may be used instead under the assumption that shared evolutionary history or ecological niche will ensure reasonable estimates of rare species response. The effectiveness of this strategy is under debate (Andelman & Fagan, 2000; Caro, Eadie, & Sih, 2005; Murphy, Weiland, & Cummins, 2011), and the researchers take the opportunity here to evaluate the surrogate species approach from a demographic perspective, considered the most appropriate test of efficacy.

The researchers assessed belowground dynamics (germination and seed survival with age) in microhabitats created by experimental arrays simulating an operational fixed-panel photovoltaic facility. To explore the possibility that higher moisture conditions are associated with increased fungal attack, half of the artificial seed banks packets were treated with fungicidal agents protecting against fungal and oomycete pathogens, allowing comparison of seed survival rates in treated versus untreated packets. The researchers examined effects of energy infrastructure on microsite conditions and belowground seed dynamics, and assessed whether response differed for a closely related rare and common native species pair (Eriophyllum mohavense and E. wallacei), as well as a noxious weed (B. tournefortii). These experiments revealed differences in the seed dynamics of focal species and demonstrated that novel abiotic conditions created at energy installations can affect these dynamics. Demographic rates obtained (seed bank retention, seedling emergence, seedling survivorship, and fecundity) were used to refine existing matrix models of population growth for Eriophyllum species under different microhabitat conditions (Tanner, Moore-O'Leary, Parker, Haji, Pavlik & Hernandez, in review). Lastly, the researchers explore solar panel effects on overall annual community richness, diversity, and abundance. Panel microhabitat effects on plant abundance and performance are likely to vary across taxa, and effects on co-occurring native versus exotic species are of particular interest.

Taken together, this work provides insight into how microhabitat variation within solar facilities will affect rare and common native annual populations over time, informing their management across a range of environmental conditions present within solar fields and mitigation areas. It also provides an early indication of invasive species performance across microhabitats within solar facilities, which can inform control measures at early invasion stages.

Methods

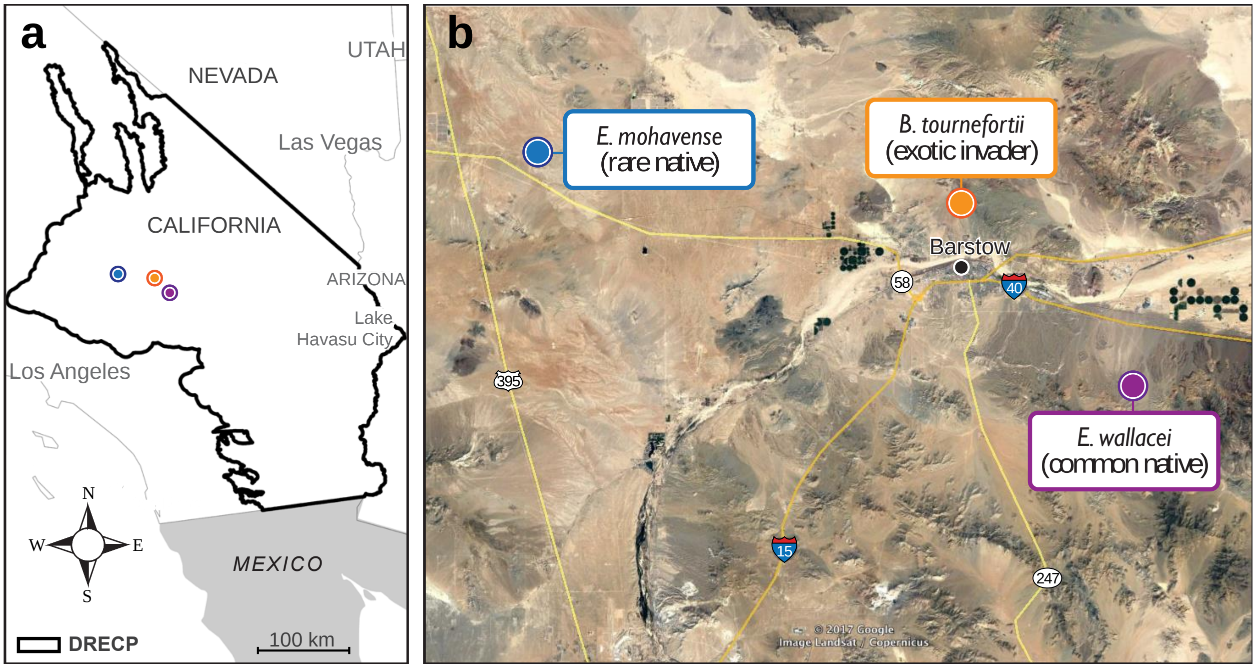
Sites and Species

The PV-Annual Plant Nexus comprises three experimental sites, each one supporting a large population of a different focal species (focal taxa do not co-occur across sites). Focal species include native congeners *Eriophyllum mohavense* (I.M. Johnst.) Jeps. and *E. wallacei* (A. Gray) A. Gray (Asteraceae), and the exotic invader species *Brassica tournefortii* Gouan (Brassicaceae). All three species are winter annuals, emerging in late fall or early winter, and completing their life cycle before the onset of the desert summer. *E. wallacei* is common in California's desert region, while *E. mohavense* holds the California Rare Plant Rank of 1B.2, and is a listed species of concern in the Desert Renewable Energy Conservation Plan (DRECP 2016, https://www.drecp.org/). *B. tournefortii* is native to north Africa and the Middle East, and is now widespread in the arid southwest (Curtis & Bradley, 2015), where it may suppress native species by drawing down soil moisture early in the growing season (Minnich & Sanders, 2000). Following senescence, *B. tournefortii* leaves behind substantial dry biomass, increasing the fuel load in invaded areas. *B. tournefortii* may thus have the potential to alter natural fire cycles in desert systems, as has already been described for exotic grasses (D'Antonio & Vitousek, 1992).

All three experimental panel array sites were established on Bureau of Land Management holdings in San Bernardino County, California (Figure 15: Map of PV-Annual Plants Study Sites). Sites were chosen on the basis of extant populations and to minimize visibility to passersby. The *E. mohavense* site is located at 720 m elevation near the intersection of highways 58 and 395, approximately 40 km northwest of Barstow. *E. mohavense* tends to occur in dense patches near the tops of low south-facing knolls at this site, in locations devoid of perennial vegetation (Figure 16 a). The *E. wallacei* site is at 934 m in the Newberry

Mountains, approximately 20 km southeast of Barstow. The site is situated on a gentle east-facing incline, and *E. wallacei* tends to occur in natural openings within a matrix of creosote bush scrub (Figure 16 b). The *B. tournefortii* site is situated on a shallow south-facing wash at 775 m elevation, ~ 3 km north of Barstow (Figure 16 c). See Appendix B – Site Selection and Characterization for more details.

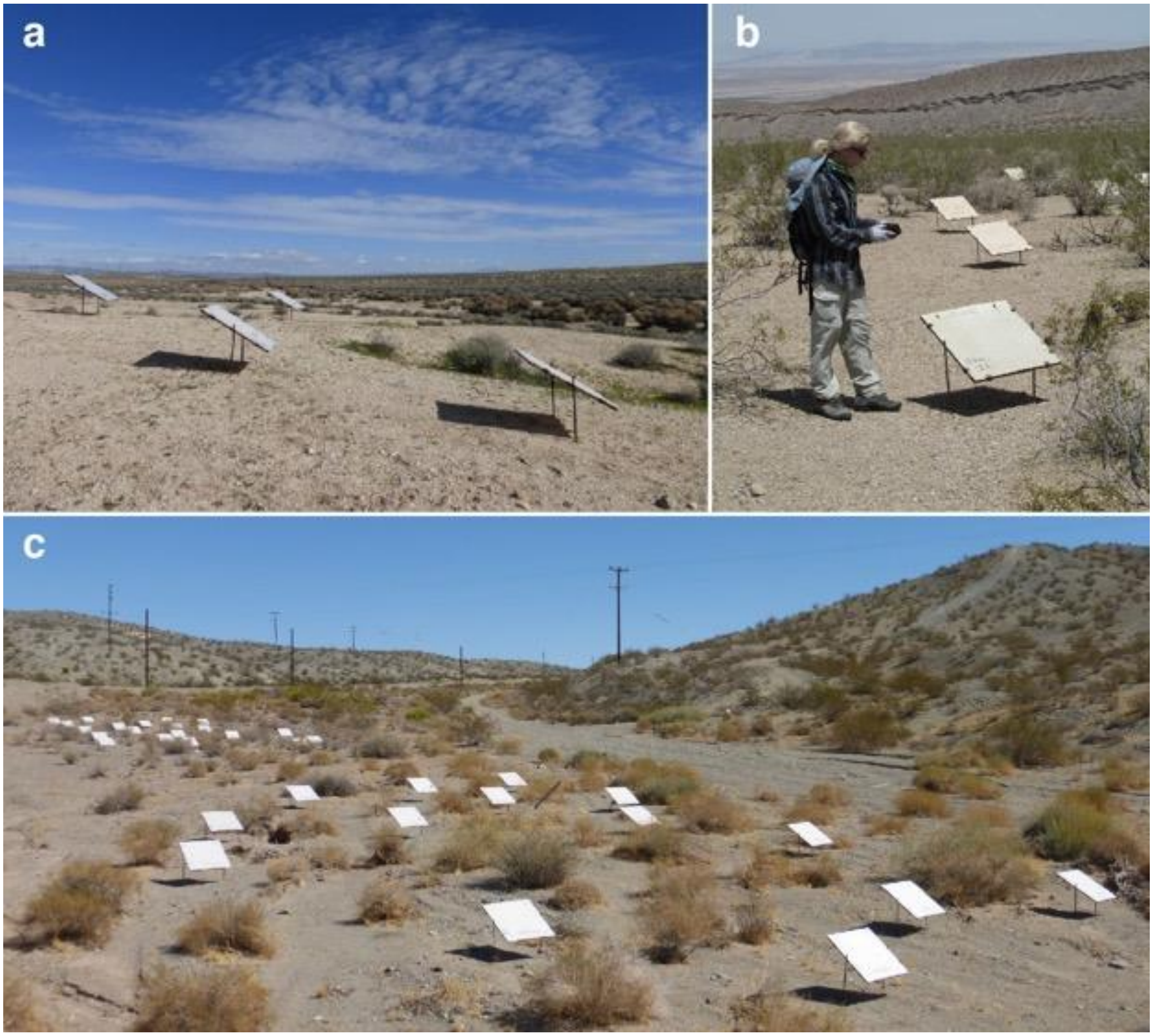
Figure 15: Map of PV-Annual Plants Study Sites



(a) Locations of the PV-Annual Plant Nexus experimental study sites within the Desert Renewable Energy Conservation Plan Area (DRECP; black boundary line) of California's Desert Region, and (b) location of sites relative to Barstow, California.

Source: a) Map adapted from Moore and Pavlik 2014; b) 2017 Google satellite imagery

Figure 16: Experimental Photovoltaic Panel Arrays



Experimental panel arrays at (a) the *E. wallacei* site; (b) the *E. mohavense* site; and (c) the *B. tournefortii* site.

Photos: Karen and Morris Tanner

Plot Selection

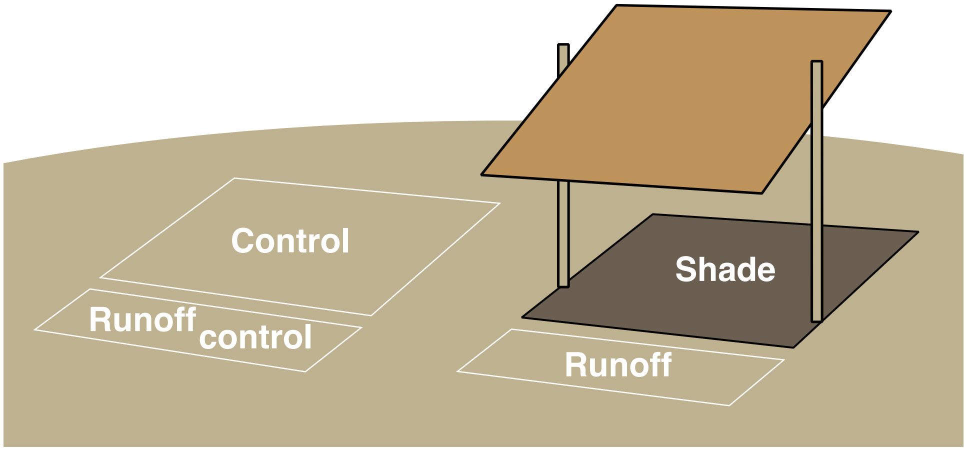
Plots at *Eriophyllum* sites were selected to contain minimum numbers of individuals depending on typical density for each species (target thresholds were n = 112 for *E. mohavense*, and n = 26 for *E. wallacei*), on the assumption that natural seed banks at these locations would produce seedlings that could be tracked in future seasons (high seed dormancy rates in these species made reliance on sown seed impractical).

The potential size of *B. tournefortii* natural recruits (measured range 6.4 – 117 cm in spring 2017) made reliance on natural emergence of seedlings at appropriate spacing inside each microhabitat unlikely, due to the relatively small scale of the plots. However, the high seed germination rate for this species suggested it would be possible to rely on sown seed to produce seedlings in each microhabitat (see Seedling Emergence Experiment below). Unfortunately, ants harvested much of the sown seed during 2017, requiring transplant of greenhouse-grown seedlings into plots during winter 2017 (see Appendix B - *B. tournefortii* Transplanting Effort for more details).

Experimental Panels

Panel frames measuring 2 x 2' were mounted on 3' legs at a 30º angle off horizontal (Figure B-2), the standard incline for fixed photovoltaic arrays (n = 34 per site, see Appendix B - Panel Construction for more details). The Shade microhabitat is defined by the shadow cast by panels at solar noon, and the Runoff microhabitat is defined as the patch of ground along the southern edge of panels that receives rainfall runoff (Figure 17). At each site twenty panels were assigned to artificial seed bank experiments, divided between fungicide-treated and untreated groups, and ten panels were assigned to monitor aboveground demographic performance. Remaining panels were used to characterize abiotic conditions across microhabitats.

Figure 17: Experimental Panel Microhabitats



Shade and Control microhabitats measure ~ 60 x 62 cm; Runoff and Runoff Control microhabitats measure 16 x 60 cm.

Source: UC Davis

Microhabitat Characterization

Soil Temperature

Thermochron iButtons (Maxim Integrated, DS1921G-F5#) were installed to monitor soil temperatures at four plots per site, with one unit deployed in the Shade, Runoff, and Control microhabitats at each plot (n = 12 units per site) in September 2017. Units were programed to record temperature every three hours and were buried 1.5 cm below the soil surface to reduce sensitivity to transient cloud cover and wind gusts. Units remained in the field until March 2018 (aligning with the growing season for plants studied here). Because radiation and soil temperature affect evapotranspiration, researchers isolated temperatures at ~solar noon (11:00 am or 12:00 pm, depending on daylight savings time) in analyses to compare conditions across the Shade and Control locations. See Appendix B – Soil Temperature for more details.

Soil Moisture

A time series of soil cores was initiated on February 19, 2017, following a weather system delivering at least 5 mm rainfall to each site. Cores 10 cm deep were collected at undisturbed locations inside the Shade, Runoff, and Control microhabitats at four plots per site. Each microhabitat was sampled across three consecutive days (n = 36 total samples per site). Cores were acquired using a 1"- diameter steel sleeve, and samples were immediately transferred to 50 mL Falcon centrifuge tubes (Corning 352070) with screw-top lids. Tubes were sealed into Ziplocs and stored in an ice chest until they could be transported back to UCSC. Tubes were weighed within 1.5 weeks, and samples were dried in an oven at 60º C for two weeks before reweighing to determine percent moisture by weight.

Light Environment

An Accupar LP-80 ceptometer (Decagon Devices) was used to measure the light environment in full sun and panel shade, quantifying photons received (μmol $m^{-2}s^{-1}$) in the photosynthetically active wavelengths (~400 – 700 nm). These measures allowed us to assess differences in photosynthetically active radiation (PAR) receipts that may affect photosynthetic rate and overall plant performance. Measurements were taken within 2 weeks of the spring equinox in the open and across the light gradient under panels (Appendix B Figure B-3) at ten plots per site. Because shadows cast by panels shift with the sun's movement through the day, measurements were taken in the morning, near solar noon, and in mid-afternoon. Measurements at each site (n = 30 per sampling location at each time) were averaged to generate light readings for each subplot, expressed as a percentage of the average full sun reading.

Response of Annual Plant Populations to Panels

Belowground Demographic Response

Artificial Seed Bank Packets

In summer 2016 artificial seed bank packets were constructed to characterize panel microhabitat effects on seed survival (see Appendix B – Seed Collection and Artificial Seed Bank Packet Construction for more details). The number of seeds per packet varied with seed supply for each species, and the 2015 seed cohort was employed in some *Eriophyllum* experiments to supplement the 2016 cohort (Table B-1). Artificial seed banks were buried under a shallow layer of soil in fall 2016 (Figure B-4). A set of six seed packets was installed in each microhabitat (Control, Runoff, Shade) at 20 plots; packets at ten of these plots were left to experience ambient experimental conditions (n = 180), and packets at the other ten plots were divided between control and fungicidal treatment groups (n = 90 per treatment). At the close of the 2017 growing season, a pair of packets was randomly selected for collection in each microhabitat at ambient experimental plots, and one untreated and one fungicide-treated packet were collected from each microhabitat at fungicide treatment plots. Untreated and fungicide-treated packets were stored separately in paper envelopes under laboratory conditions until seed could be inspected under a stereoscope to estimate the proportion of intact seed remaining in each packet. At the close of the 2018 growing season, a randomly selected pair of packets was again collected from each microhabitat at the *B. tournefortii* site, leaving a final pair of packets for collection in the 2019 growing season. At *Eriophyllum* sites all remaining packets were collected in spring 2018 – many packets were lost to apparent rabbit disturbance at the *E. wallacei* site between spring 2017 and spring 2018 (see Figure B-5 in Appendix B).

Fungicide Treatment

At fungicide plots Subdue MAXX (Syngenta, active ingredient Mefenoxam) and Cleary 3336^F (NuFarm, active ingredient thiophanate-methyl) were applied as a soil drench to offer broad protection against fungal and oomycete agents that may be present in the soil. The researchers mixed a solution of both agents to achieve manufacturer-recommended application rates (see Appendix B – Fungicide Treatment for more details) and applied treatments to half of the buried packets in October 2016 before the onset of fall rains (Figure B-6).

Assessing Seed Bank Retention Rate

All artificial seed bank packets harvested from sites were processed at UCSC. Seeds were removed from packets and observed individually under a stereoscope (Nikon SMZ800). Each seed was categorized as "intact" or "compromised" – in the latter category, the researchers commonly observed 1) broken seed coats; 2) empty hulls; or 3) remnants of radicle, stalk, or other plant material associated with the seed, all of which suggest germination (Figure B-7). Many seeds were compromised without clear evidence suggesting whether they germinated or simply decayed; the researchers therefore focus on the proportion of intact seeds recovered from each packet (total intact seed / total seed recovered). This proportion is defined as the "retention rate" in the soil seed bank.

Seed Survival via Tetrazolium Staining Assays

Because intact seeds may not actually be alive, tetrazolium assays were used to test for seed viability (respiring seed embryos turn red following exposure to tetrazolium stain, while dead tissue remains white). Because low respiration rates in truly dormant seed may result in minimal staining (Pake & Venable, 1996), this approach provides a conservative estimate of survival. After testing efficacy of this approach for these species (see Appendix B – Tetrazolium Treatment for more details), the researchers subjected a subset of intact seed recovered from seed bank packets to tetrazolium assays. After preparation, seeds of each species were soaked in a 1% solution of solid 2,3,5-Triphenyltetrazolium chloride and deionized water. Following soak, seeds were observed under the stereoscope for stained tissue. Seeds were scored as "viable" if red stain was observed on the seed embryo; seeds lacking any red color were scored as dead (Figure B-8).

Aboveground Demographic Response

Seedling Emergence Experiment

At each site, the researchers sowed known quantities of seed in late summer – early fall 2016. Seeding toothpicks were prepared to permit positioning of seed at appropriate soil depth for germination within each microhabitat (Figure B-9), and toothpicks served as markers allowing researchers to distinguish sown individuals from natural recruits (see Appendix B - Seeding Toothpick Preparation for more details). All seed sown at the *B. tournefortii* site came from the 2016 seed cohort; at the *E. mohavense* and *E. wallacei* sites seed from the 2015 as well as the 2016 cohort was used to boost sample sizes (Table B-1). Because *B. tournefortii* seed retention rate tended to be very low over time, new sets of seeding toothpicks were prepared and installed each year. Toothpicks were checked for seedlings on each visit after installation.

Survivorship to Reproductive Maturity

At *Eriophyllum* sites, plots were checked for seedlings emerging from the natural seed bank on early season surveys (late January in both years). Where seedlings were present, up to 55 individuals per plot across microhabitats were randomly selected and marked using plastic toothpicks. Marked plants were revisited on peak season surveys to determine the proportion surviving to reproductive maturity. Plants observed in bud, flower, or fruit by the end of the growing season were considered mature (Figure B-10). At the *B. tournefortii* site, six seedlings emerging in seeding toothpick arrays were randomly selected to follow through the season (two plants were selected per microhabitat; extra plants were weeded out to minimize competition). In 2017, *B. tournefortii* seedling toothpick arrays suffered heavy ant disturbance (Figure B-11). In this year the only marked *B. tournefortii* individuals were greenhouse transplants. For all species, survivorship was calculated as the number of mature plants divided by the total number of plants marked.

Reproductive Output

On peak season surveys in 2017 (March 26 – 31), randomly selected mature *Eriophyllum* individuals were collected for seed counts across Control, Runoff, and Shade microhabitats. *Eriophyllum* exhibits indeterminate fruit maturation, with some capitula dispersing seed while others remain in bud, so the researchers avoided collection of plants with buds or fresh flowers, focusing on individuals with dry or drying corollas that had not yet dispersed fruit. Individuals were stored in separate coin envelopes until dissection and seed counts could be carried out in the lab. During dissection only intact, fully black achenes were counted.

Marked plants at the *B. tournefortii* site were collected in March or April as individuals matured (when no more fresh buds or flowers were observed). Plants were stored in paper sacks until fruit and seed counts could be conducted in the lab. In a few cases, fruits dispersed seed before plants were collected, leaving visible peduncles and septa behind. Where present, these structures allowed us to account for missing fruit with high confidence.

Annual Community Richness and Diversity

The Shannon Diversity Index was used to measure community diversity at *Eriophyllum* sites, which accounts for relative abundance of each species as well as the total number of species present in a community. This index often ranges from ~1.5 – 3.5 in ecological applications, with higher values corresponding to greater richness (total species counted) and evenness (relative abundances across species). The researchers surveyed annual communities present across microhabitats at *Eriophyllum* sites on peak season surveys (n = 20 plots per site). From first principles, the number of species found in a patch increases with patch size; therefore, comparisons are only appropriate between the Control and Shade microhabitats (60 x 62 cm footprint), and the Runoff Control vs. Runoff microhabitats (16 x 60 cm footprint). All species and individuals present in each microhabitat were counted at all plots, and plants were identified to family, genus, and species where possible. In cases where the phenological stage of plants did not permit assignment at the family or genus level, the researchers took photos and recorded morphological characteristics, allowing counts of individuals from "unknown" as well as identifiable species. In plots at the *E. mohavense* site, 31 annual and 2 perennial species were observed, including 9 unidentifiable taxa; at the *E. wallacei* site, 36 annual species including 7 unidentifiable taxa were observed (Table B-2). Data on annual communities at the *B. tournefortii* site were not collected because transplant of seedlings into microhabitats at plots incurred substantial disturbance.

Data Analyses

All programming and analyses were conducted in R (R Core Team 2016). Specific details of model construction, tests of difference, and reporting are provided for each experiment in the Appendix B – Data Analysis Methods section. The researchers used the plyr package (Wickham 2011) to generate summary statistics, and the Anova function of the car package (Fox & Weisberg, 2011) to extract *P*-values from generalized linear models where needed. All significant differences are reported at the $P \leq 0.05$ level, and marginal differences are reported at the $P \leq 0.10$ level.

Results

Panel Effects on Microhabitat

Soil Temperature

Soil temperatures near solar noon differed strongly across microhabitats (Kruskal-Wallis *X*-squared = 1530.8, df = 2, *P*-value < 0.001), with the average temperature ~9 ºC cooler in the Shade microhabitat than in the Control microhabitat (Figure B-12).

Soil Moisture

The number of days since precipitation (Day) had a significant effect and the Site*Microhabitat interaction had a marginally significant effect on soil moisture (Table B-3). As expected, soil moisture at each site generally declined from day one to day three. *Post-hoc* tests revealed significantly higher moisture in soil collected the first day in the Control versus Shade microhabitats at the *E. mohavense* site (Figure B-13 b). The researchers also found significantly higher moisture in soil collected the third day from the Runoff versus Shade microhabitats at the *E. wallacei* site (Figure B-13 c). The researchers never observed differences across microhabitat for soils collected from the *B. tournefortii* site (Figure B-13 a).

Light Environment

Measurements of photosynthetically active radiation under experimental panels were significantly lower than those taken in full sun during all sampling periods (Figure B-14; morning, Welch's $t = -65.312$, df = 59, *P*-value < 0.001; solar noon, Welch's $t = -145.37$, df = 59, *P*-value < 0.001; afternoon, Welch's $t = -79.222$, df = 59, *P*-value < 0.001).

Seed Bank Retention

B. tournefortii

Microhabitat and Year had significant effects on the proportion of intact *B. tournefortii* seeds recovered from artificial seed banks (Figure 18 a, Table B-4 a). The average retention rate across all microhabitats declined ~50% from 2017 to 2018, but held steady between 2018 and 2019 (actual retention rates for 2017, 2018, and 2019 were 12.6%, 6.1%, and 6.5%, respectively). Retention rates across microhabitat varied by year and showed some unexpected patterns. For packets collected in 2017 and 2019, significantly more intact seed was recovered from the Runoff microhabitat than the Shade microhabitat. For packets collected in 2018, significantly fewer intact seeds were found in the Shade microhabitat than in the Runoff or Control microhabitats.

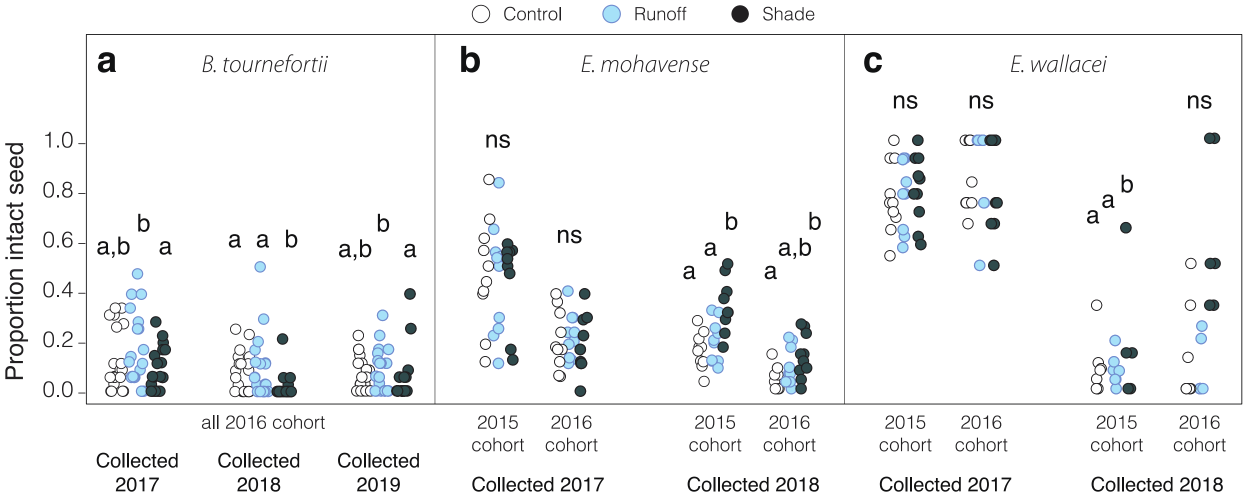
E. mohavense

Seed Cohort and the Microhabitat*Year interaction had significant effects on seed retention rate for *E. mohavense* (Figure 18 b, Table B-4 b). The researchers found no significant differences in retention rate across microhabitat for packets collected in 2017, for either seed cohort. In contrast, the researchers collected significantly more intact seed in 2018 from the Shade compared to the Control microhabitat for both cohorts. The average retention rate across microhabitats declined between 2017 and 2018 for both seed cohorts (45% to 22% for the 2015 cohort, and 20% to 9% for the 2016 cohort).

E. wallacei

The researchers found no effect of model predictors on *E. wallacei* seed bank retention in 2017 (Figure 18 c). In contrast, Microhabitat was a highly significant predictor of retention rate for packets collected during 2018 (Table B-4 b). The researchers recovered more intact seed from the 2015 cohort in the Shade microhabitat compared to the Control or Runoff (Fisher's exact tests: Control–Runoff, *P*-value = 0.704; Control–Shade, *P*-value < 0.004; Runoff-Shade, *P*-value < 0.003). No differences were observed across microhabitat for the 2016 seed crop collected in 2018 (Fisher's exact test: Control–Runoff, *P*-value = 1; Control–Shade, *P*-value = 0.108; Runoff–Shade, *P*-value = 0.128), likely related to low sample sizes. The average retention rate across all microhabitats declined between 2017 and 2018 for both seed cohorts (79% to 15% for the 2015 cohort, and 86% to 26% for the 2016 cohort).

Figure 18: Seed Bank Retention Rates



Seed bank retention rates in artificial seed bank packets by species, seed cohort, microhabitat, and burial duration. Results are shown for (a) *B. tournefortii*, (b) *E. mohavense*, and (c) *E. wallacei*. Letters indicate significant differences among microhabitats within a single year.

Source: UC Davis

Fungicide Experiment

There were no significant effects of Microhabitat, Fungicide or the interaction Microhabitat*Fungicide on seed bank retention for any species or seed cohort (Table B-6).

Seed Staining Experiment

There was no significant effect of Microhabitat on tetrazolium staining rates for any species or seed cohort (Figure B-15, Table B-8).

Seedling Emergence

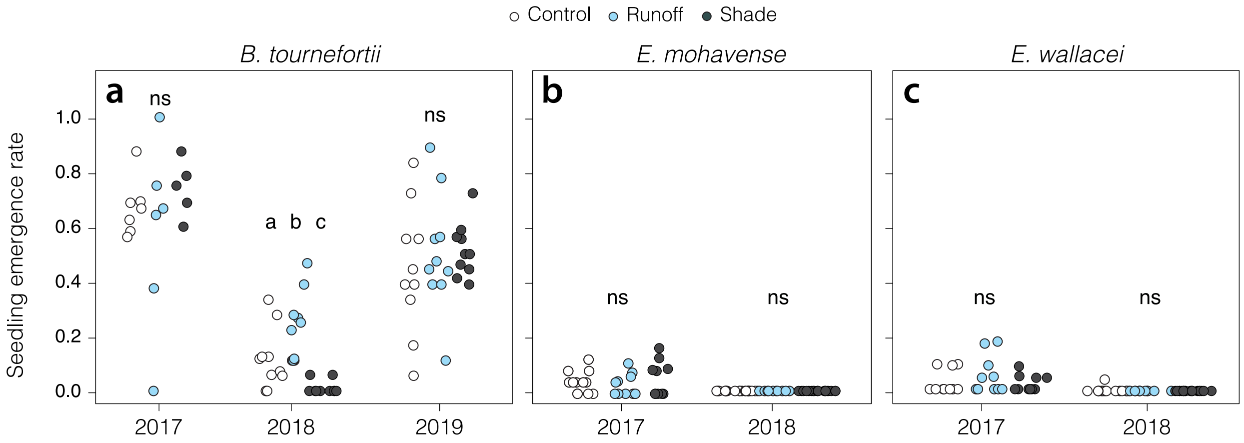
B. tournefortii

Microhabitat had a significant effect on seedling emergence in 2018 only, with more seedlings in the Runoff location than the Control, and the lowest number of seedlings in Shade (Figure 19 a; Fisher's exact tests, Control–Runoff *P*-value = 0.0142; Control–Shade *P*-value < 0.001; Control–Runoff *P*-value < 0.001). Microhabitat had no effect on *B. tournefortii* seedling emergence in 2017 or 2019 (Fisher's exact tests, *P*-value = 0.151 and 0.383, respectively).

Eriophyllum

Microhabitat had no significant effect on *E. mohavense* seedling emergence in 2017 (Figure 19b; Fisher's exact test, *P*-value = 0.399), or on *E. wallacei* emergence in either year (Figure 19 c; Fisher's exact tests, *P*-value = 0.196 and *P*-value = 1).

Figure 19: Seedling Emergence



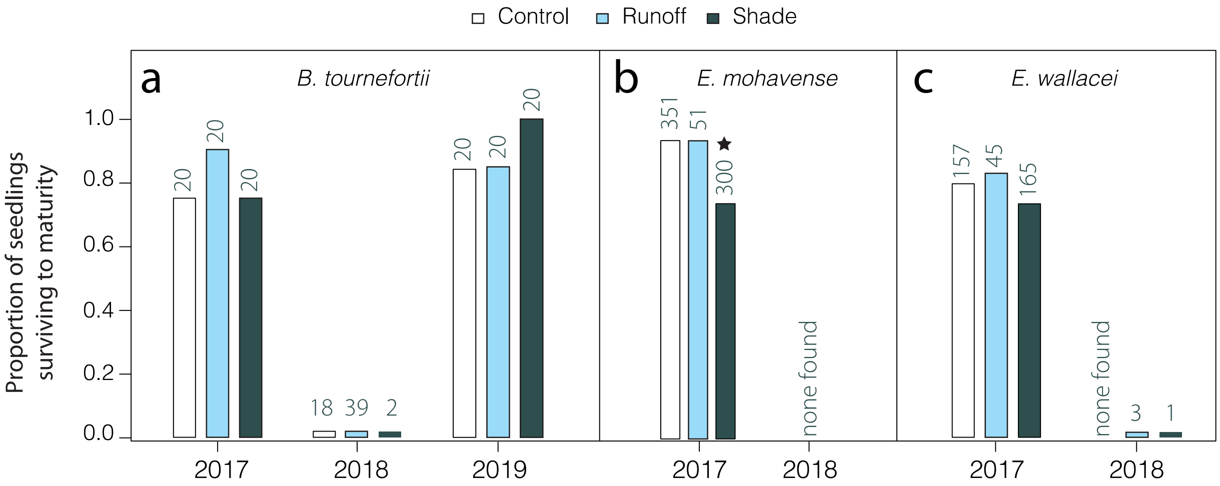
Seedling emergence by species, microhabitat, and season. Results are shown for (a) *B. tournefortii;* (b) *E. mohavense*; and (c) *E. wallacei*. Letters indicate significant differences among microhabitats within a single year.

Source: UC DavisFigure by Karen Tanner

Survivorship

Microhabitat had no effect on 2017 or 2019 survivorship of *B. tournefortii* seedlings (Figure 20 a; Fisher's exact test *P*-value = 0.444 in 2017, and *P*-value = 0.199 in 2019), or on survivorship of *E. wallacei* seedlings (Figure 20 c; Fisher's *P*-value = 0.276). *E. mohavense* seedling survivorship was higher in 2017 in the Control and Runoff microhabitats compared to the Shade microhabitat (Figure 20 b; Fisher's *P*-value < 0.001 and *P*-value = 0.005), but there was no difference between the Control and Runoff microhabitats (Fisher's *P*-value = 1).

Figure 20: Seedling Survivorship to Maturity



Survivorship by species, microhabitat, and season. Results are shown for (a) *B. tournefortii;* (b) *E. mohavense*; and (c) *E. wallacei*. Numbers above bars indicate sample sizes, and stars indicate significant differences among microhabitats within a single year.

Source: UC Davis

Reproductive Output

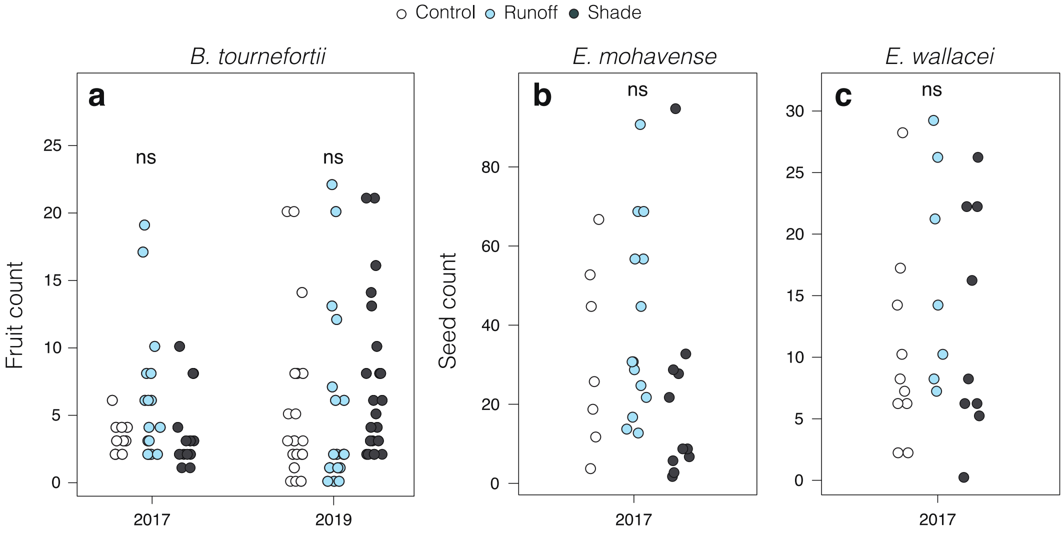
B. tournefortii

Only Year (that the fruit was produced) had a significant effect on *B. tournefortii* fruit number (Table B-9a, Figure 21 a).

E. mohavense and E. wallacei

Microhabitat had no effect on seed output in 2017, the only year in which the *Eriophyllum* taxa successfully reproduced (Figure 21 b, c; (Table B-9 b, c).

Figure 21: Reproductive Output



Reproductive output by species, microhabitat, and season. Results are shown for (a) *B. tournefortii;* (b) *E. mohavense*; and (c) *E. wallacei*. No *Eriophyllum* individuals survived to maturity in 2018. Note different scales on the y axis.

Source: UC Davis

Annual Community Response

Annual communities at the *E. mohavense* and *E. wallacei* sites were quite distinct; only seven species were present at both locations, including the common exotic species *Erodium cicutarium* and *Schismus arabicus* (Table B-2).

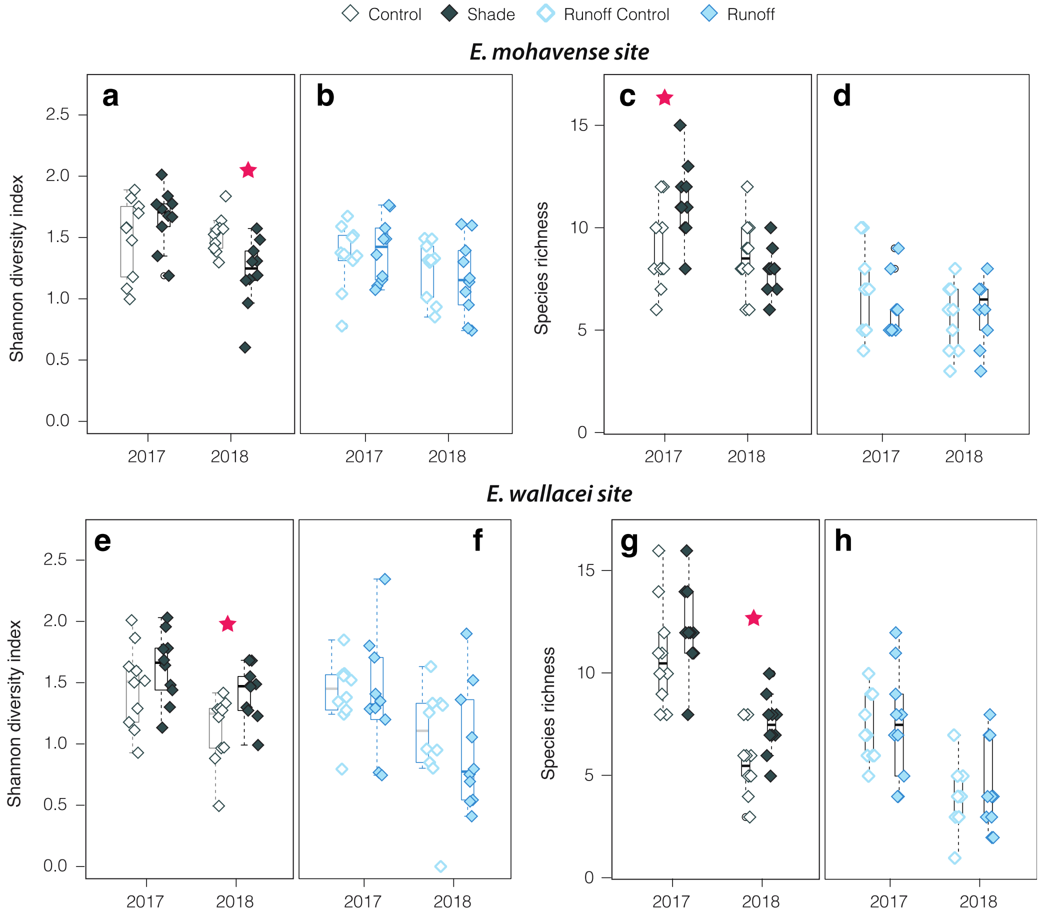
E. mohavense Community

The interaction Year*Microhabitat was significant for both Shannon diversity and species richness in the Control vs. Shade locations (Table B-10 a, b). In *post-hoc* tests of microhabitat difference within each year, the Shannon index was significantly lower in Shade than in Control in 2018 (Figure 22 a). In contrast, species richness was higher in the Shade than in the Control in 2017 (c). In the Runoff Control vs. Runoff locations, the researchers found a marginally significant effect of Year on Shannon diversity only. Native abundance in the Control vs. Shade locations was significantly affected by Year and marginally affected by Microhabitat (Table B-11 a). *Post-hoc* tests revealed significantly higher native abundance in Shade during 2017, but not in 2018 (Figure 23 a). In the Runoff Control vs. Runoff locations, the researchers found a significant effect of the Year*Microhabitat interaction on native abundance, with a trend for more natives in the Runoff Control in 2017, and more natives in the Runoff in 2018 (Table B-11 b, Figure 23 b). Both Year and Microhabitat had significant effects on exotic abundance, with more individuals in Shade in both years (Table B-11 b, Figure 23 c). Only Year affected exotic species in the Runoff Control and Runoff locations, with higher exotic abundance in 2018 (Table B-11 b), Figure 23 d).

E. wallacei Community

Year and Microhabitat affected Shannon diversity and species richness in the Control vs. Shade locations (Table B-10 a, b); in contrast to the *E. mohavense* site, there was no effect of the Year*Microhabitat interaction. Both diversity and richness were higher in Shade in 2018 (Figure 22 e, g). Native abundance was significantly affected by the Year*Microhabitat interaction in the Control vs. Shade locations (Table B-11 a), with significantly higher abundance in Shade in 2018 only (Figure 23 e). In the Runoff Control vs. Runoff locations, the Year*Microhabitat interaction had a marginally significant effect on native abundance, and *post-hoc* tests revealed significantly higher abundance in the Runoff during 2018 only (Figure 23 f). Microhabitat also affected exotic abundance across the Control and Shade locations, but *post-hoc* tests revealed only a trend for higher abundance in Shade (Figure 23 g). The researchers found no significant effects of model predictors on exotic abundance across the Runoff Control vs. Runoff locations (Figure 23 h).

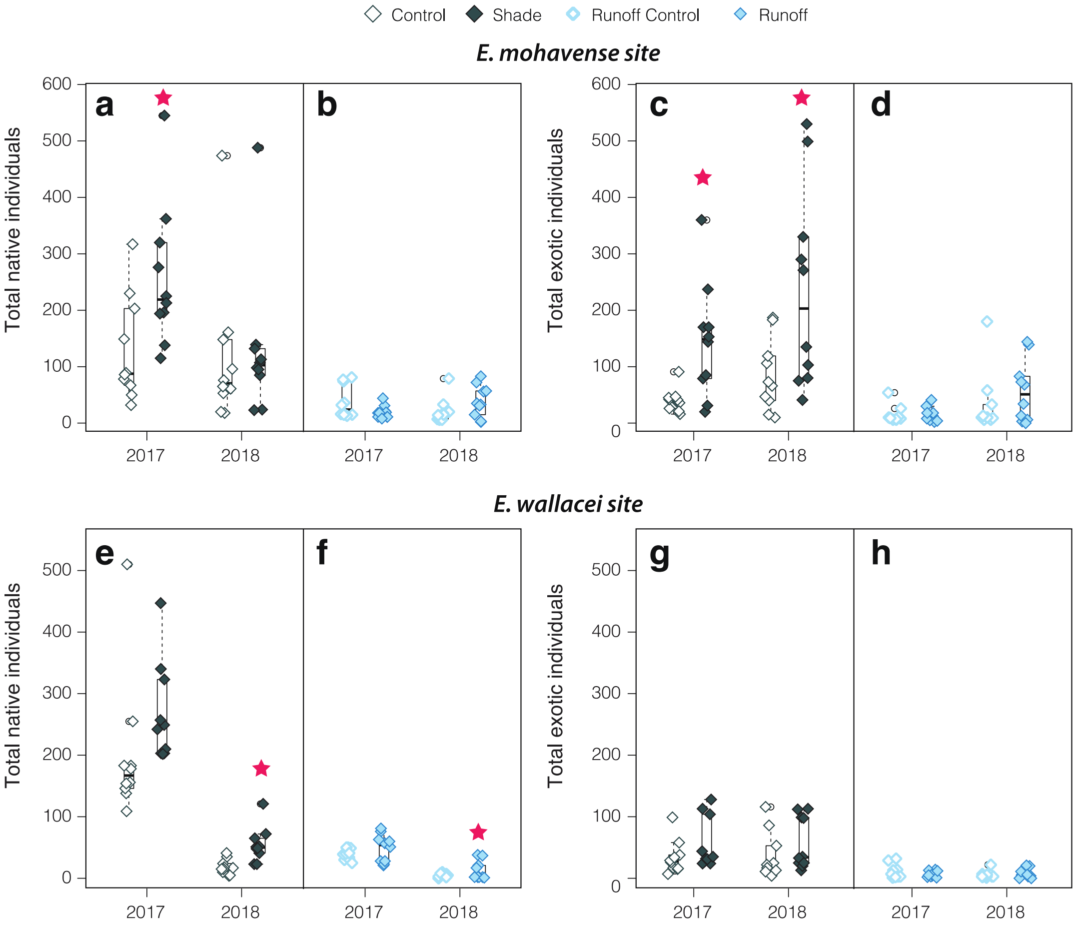
Figure 22: Community Diversity and Species Richness



Community metrics by microhabitat and season at the *E. mohavense* site (top row) and the *E. wallacei* site (bottom row). Metrics for the Control and Shade microhabitats were calculated from areas measuring 60 x 62 cm, and metrics for the Runoff Control vs. Runoff microhabitats were calculated from areas measuring 16 x 60 cm. Diversity results for the *E. mohavense* site are shown in (a) for the Control vs. Shade microhabitats, and (b) the Runoff Control vs. Runoff microhabitats. Species richness results are shown in (c) for the Control vs. Shade microhabitats, and (d) the Runoff Control vs. Runoff microhabitats. Diversity results for the *E. wallacei* site are shown in (d) for the Control vs. Shade microhabitats, and (f) the Runoff Control vs. Runoff microhabitats. Species richness results are shown in (g) for the Control vs. Shade microhabitats, and (h) the Runoff Control vs. Runoff microhabitats. Red stars indicate significant differences between microhabitats within a given year.

Source: UC Davis

Figure 23: Native and Exotic Community Abundance



Plant abundance by microhabitat and season at the *E. mohavense* site (top row) and the *E. wallacei* site (bottom row). Metrics for the Control and Shade microhabitats were calculated from areas measuring 60 x 62 cm, and metrics for the Runoff Control vs. Runoff microhabitats were calculated from areas measuring 16 x 60 cm. Native species abundance for the Control vs. Shade microhabitats is shown in (a, e), and for the Runoff Control and Runoff microhabitats in (b, f). Exotic species abundance for the Control vs. Shade microhabitats is shown in (c, g), and for the Runoff Control and Runoff microhabitats (d, h). Red stars indicate significant differences between microhabitats within a given year.

Source: UC Davis

Discussion

Ecological Effects

This work characterized experimental panel effects on abiotic conditions and the response of annual plants (rare, common, and invasive) at sites differing in physical properties. The researchers tested microhabitat effects on aboveground and belowground demographic transition rates over two weather years (2017 and 2018) for native taxa, and three weather years (2017–2019) for an exotic invader. The researchers also characterized species richness, community diversity, and the abundance of native and exotic taxa across microhabitats at two of three sites. The resulting data on biotic and abiotic response address four questions enumerated below.

Belowground demographic data for native taxa obtained here were used to improve existing matrix models of population growth, allowing researchers to examine the influence of seed bank survival on *Eriophyllum* population dynamics (Tanner, Moore-O'Leary, Parker, Haji, Pavlik & Hernandez, *in review*). Abiotic and community data obtained here also extend work done at *Eriophyllum* sites 2012 – 2016, allowing researchers to examine how rainfall and soil type mediate panel microhabitat effects (Tanner, Moore-O'Leary, Parker, Pavlik & Hernandez, *in review*).

1. Did experimental panels drive differences in abiotic conditions across local microhabitats at each site?
    - The researchers found significant effects of panel microhabitats on the local abiotic environments, and in some cases these effects varied across sites or weather years. Soil temperature effects were qualitatively consistent; near solar noon, when shade effects should be greatest, soil temperatures in the Shade microhabitat diverged sharply from those in the open. On average, soil temperatures were ~9 ºC hotter in the open than in the shade, consistent with strong differences measured at a Sonoran Desert artificial array (Smith, S.D., Patten, D.T., Monson, 1987). Such differences in local temperature should contribute to evapotranspiration rates, with reduced moisture loss in shaded locations. The high variability observed can be largely attributed to shifting conditions (for example, daily differences in air temperature, cloud cover, or wind speed affect monthly averages). The seemingly "cleaner" patterns of temperature difference at the *B. tournefortii* site may be related to site aspect and topography. All panels at this site faced directly south on nearly flat terrain, creating very uniform shadows. Panels at the other sites also faced south, but the *E. wallacei* array was installed on an east-facing slope, while the *E. mohavense* array was installed situated on a series of low knolls with distinct topographic shifts. As a result, shadows cast by panels were more irregular at the *Eriophyllum* sites, which may have contributed to variability in soil temperature measurements.
    - The researchers expected panels to intercept rainfall, with panel runoff driving higher soil moisture in the Runoff at the expense of drier conditions in the Shade. However, panel effects on soil moisture were variable across sites, and significant differences were rare. Rainfall during the 2017 storm that triggered soil sampling was fairly low, but typical for average volumes in this area – 5 mm at the *B. tournefortii* site, 5 mm at the *E. mohavense* site, and 6.2 mm at the *E. wallacei* site. The researchers never observed a significant moisture difference across microhabitats at the *B. tournefortii* site, but with the slight increase in rainfall volume at the *E. wallacei* site a trend of higher moisture in the Runoff microhabitat was detected. The *B. tournefortii* and *E. wallacei* substrates were similar, composed of sandy soils and coarse gravel with low water holding capacity (Tanner, Moore-O'Leary, Parker, Pavlik & Hernandez, *in review*). At both of these sites soil moisture declined noticeably over the three-day sampling period, in keeping with a fast-draining substrate. At the *E. mohavense* site soil moisture in the Runoff did not differ from the other microhabitats, and the researchers did not see a substantial decline in soil moisture over the same three-day period. However, soil moisture was substantially higher here than at the *B. tournefortii site*, despite receiving the same total volume of rainfall. These

    results demonstrate the potential for panel effects to depend on soil properties and prevailing weather, which can be locally variable (J. Beatley, 1974; Mabbutt & Fanning, 1987). Unfortunately, storm volumes during the 2018 growing season were too low to facilitate additional soil sampling and microhabitat characterization.

    - Panel effects on the light environment were qualitatively similar across sites, with drastic reductions in photosynthetically active radiation during each sampling period. Compared to an average full sun measurement of ~387 μmol m^2s^{-1}, morning shade measurements were ~150 μmol m^2s^{-1}, and mid-afternoon measurements were ~135 μmol m^2s^{-1}. The nearly 90% reduction in PAR at solar noon (~37 μmol m^2s^{-1}) is in keeping with strong reductions measured at other artificial and operational arrays (Armstrong et al., 2016; Smith, S.D., Patten, D.T., Monson, 1987). When the sun was low in the sky early or late in the day, sunlight penetrated underneath panels. Even though measured PAR reductions were striking, they will only affect plant performance if photosynthesis is light-limited. The researchers do not know the optimal light levels for peak photosynthetic efficiency in these focal species, but there is some evidence to suggest that shade can boost productivity in desert systems (Patten, 1978).
    - When considering panel effects of plant performance below, it is important to bear the size discrepancy between experimental and full-size commercial panels in mind (experimental panels are ~.37 m^2, while full-scale panels may be nearly 2 m^2). It is reasonable to expect that commercial panels will have more drastic effects than those observed in this study, because they intercept more light and divert larger volumes of rainfall – especially where panels are arranged in contiguous arrays.

2. Were panel microhabitat effects on belowground dynamics similar across rare, common, and invasive taxa?
    - Panel microhabitat effects on seed bank retention rate varied across species and depended on burial duration. *B. tournefortii* germination tends to be high (Bangle et al., 2008), in keeping with an opportunistic strategy exhibited by many successful annual invaders, and high germination likely drove low average seed bank retention (~12%) in the first year of burial. Retention held steady at ~6% in both the second and third seasons of burial. The researchers never found a significant difference in Control and Runoff retention rates, but Shade retention was lower than Runoff retention in 2017 and 2018, and lower than Control in 2018 only. In 2019 the typical pattern for Shade and Runoff reversed, with higher seed retention in Shade. This pattern is difficult to explain. *B. tournefortii* germinates readily when minimal moisture requirements are met, leaving few dormant seeds behind. It is tempting to attribute the higher 2019 Shade retention rate to moisture limitation under panels (that is, germination will be lower if moisture requirements are not met) - but the Shade retention patterns in 2017 and 2018 are inconsistent with this explanation. Another mechanism that can reduce seed retention is higher seed mortality – if the underlying mechanism varies, this could produce different patterns in Shade retention across years. However, it is not possible to distinguish between seed germination versus seed

    mortality as a driver of seed bank retention here. When individual seeds were inspected, the researchers could only reliably identify "intact" and "compromised" seed – with the latter potentially resulting from either germination or seed death at any point in the duration of burial.

    - In contrast, native Mojave Desert taxa tended to exhibit higher seed dormancy rates, in keeping with their evolutionary history in an uncertain rainfall environment. The researchers found no differences in seed bank retention across microhabitat for seed cohorts of either species following burial for one growing season, but the researchers did observe higher retention for *E. wallacei.* After a second season of burial, the researchers recovered more intact seed from the Shade than the Control microhabitat for both species and all cohorts. The effects of burial duration cannot be isolated from prevailing weather in each year, and desert annuals are known to have threshold moisture requirements (J. C. Beatley, 1974). It appears likely that in 2018, an already dry year, panel interception of rainfall drove greater moisture limitation in Shade. Low moisture could slow loss of seed from the seed bank, whether through germination or soil pathogen-mediated mortality.
    - Tetrazolium staining assays did not reveal any differences in the survival rate of intact seed across microhabitats for any species or seed cohort in a given burial period. The researchers did however observe a substantially higher proportion of live *B. tournefortii* seeds among intact seeds tested.

3. Were panel microhabitat effects on aboveground dynamics similar across rare, common, and invasive taxa?
    - Seedling emergence rates diverged strongly between native and invasive species, with *Eriophyllum* emergence ranging from 3.3% - 4.7% in a good rainfall year (2017), and 0% – 0.1% % in a poor rainfall year (2018). *B. tournefortii* emergence was very high in good rainfall years (67.5% and 48.7% in 2017 and 2019, respectively) and remained much higher than *Eriophyllum* emergence even under low rainfall conditions in 2018 (12%). The researchers found no difference in *Eriophyllum* emergence among microhabitats in either year, possibly related to the very low numbers of emergent seedlings. The researchers also found no microhabitat effects on *B. tournefortii* emergence in good rainfall years, but microhabitat had a strong effect during 2018 when conditions were dry. The researchers found the most seedlings in the Runoff microhabitat, and the fewest in the Shade microhabitat, where moisture limitation was likely strongest.
    - Patterns in survivorship among native and invasive taxa showed some striking differences. The researchers found little difference in survivorship across microhabitats for any of the species in 2017 or 2019, both good rainfall years. Survivorship was fairly high across the board, and the only significant finding was a negative effect of Shade on *E. mohavense* survival. In 2018, when early rainfall that typically drives emergence was very low, the researchers found only four *E. wallacei seedlings* in plots, and no *E. mohavense* seedlings. In contrast, the researchers found a total of 59 *B. tournefortii* seedlings in plots. Of the seedlings

found, none survived to maturity. The opportunistic strategy that serves the invader species well in good rainfall years backfires under low rainfall conditions, when profligate germination and emergence can result in high mortality. The researchers found no significant effects of microhabitat on reproductive output for any of the focal species, so panels appear to have the strongest effects on seedling emergence and survivorship rates.

4. Did panel microhabitats influence community metrics (species richness, diversity) or relative abundance of native and exotic taxa?
    - Panel microhabitat effects depended on the metric considered and were not consistent across sites or weather year. Because Shannon diversity accounts for the relative abundance of each species as well as the total number of species present in a community, this metric may best characterize panel effects. In a high rainfall year (2017), the researchers found that Shade had no effect on Shannon diversity index. In contrast, Shade had significant effects at both sites in a dry year (2018) – but these effects were in opposition. Shade effects on diversity were negative at the *E. mohavense* site, but positive at the *E. wallacei* site. Where Shade affected species richness, it had a positive effect at both sites – however, Shade affected richness under wet conditions at the *E. mohavense site*, while effects at the *E. wallacei* site were restricted to dry conditions. Panel effects on abundance were more consistent, with higher abundance in Shade for seven out of eight comparisons where differences were significant.

CHAPTER 4:
Knowledge Transfer Activities

The overall purpose of knowledge transfer for the project was to:

1. Broadly define the knowledge system for the projects herein and ground-mounted, utility-scale solar energy development projects in general.
2. Disseminate results and lessons learned to the knowledge system, including key federal state agencies and stakeholders.
3. Facilitate public access to and assimilation of the project's critical information and data to the knowledge system, including those that serve to overcome barriers to the achievement of the State of California's statutory energy goals.
4. Maximize the return on investment in the project by creating research and public engagement products that further the project's capacity to enhance sustainability of energy projects and development across diverse sectors, firms, and individuals.

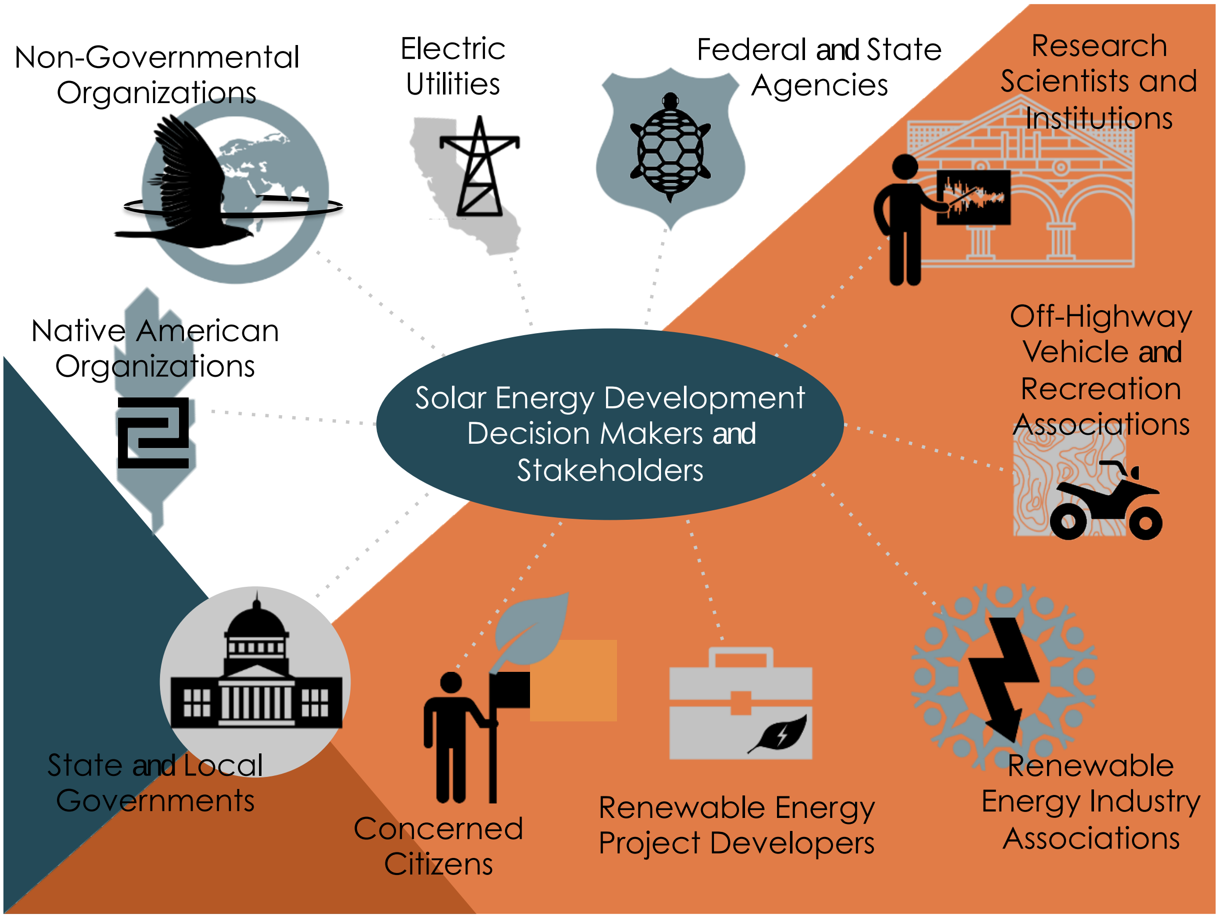
Energy development decision makers and stakeholders represent diverse bodies of varying interests, values, and goals (Figure 24), and each entity was strategically targeted for inclusion of goals (1) through (4) for audience designations (see list starting on page 46). Overall, this chapter serves as an important pathway through which products created from this project were and continue to be used to foster sustainable solar energy development and achievement of California's energy goals. Further, this chapter serves as a tool to facilitate a synthetic dialogue on solar energy development knowledge systems and transfers therein from which novel research and information might also emerge.

The Knowledge System for Ground-Mounted, Utility-Scale Solar Energy Development Projects

Background

Boundaries between scientific knowledge and decision making are determined by the nature and quality of communication of knowledge created within a knowledge system. Knowledge systems are the complex networks of actors, organizations, and objects that perform knowledge-related functions, most notably linking knowledge with action, which may include research, innovation, development, demonstration, deployment, and adoption (McCullough et al. 2016, Cash et al. 2003). California is a model system for elucidating the knowledge system of solar energy development. California is a leader in the technological advancement and adoption of solar energy. The development of the world's first utility-scale (that is, ≥ 1 MW) solar energy power plant occurred in 1982 near Hesperia, California. Since that time, California has been positioned at the vanguard of ground-mounted, utility-scale solar energy development and advancements globally. California has also been the stage on which tension over the impact of energy development on species of concern, energy sprawl, land-cover change, and conservation broadly has emerged. Overall, little research has been done on the solar energy-related knowledge systems.

Figure 24: Knowledge Network Map of Ground-Mounted, Utility-Scale Solar Energy Development Projects.



Links occur across these knowledge network actors, organizations, and objects but these links have yet to be studied empirically. Colors do not indicate attributes.

Source: UC Davis

Here, the team provides a knowledge network map for the project and ground-mounted, utility-scale solar energy development projects, broadly (Figure 24 and list on page 46) and a complementary detailed list of individual knowledge network actors, organizations, and objects. Several questions remain, which they present here as a tool to foster an introspective and iterative evolution of the knowledge transfer goals:

A. Are all actors, organizations, and objects represented in the knowledge system?

B. How do actors most efficiently achieve goals (1) through (4) as the knowledge system itself evolves?

C. What is the nature, frequency, and magnitude of interactions across the knowledge system?

D. Which actors, organizations, and objects confer the greatest influence on solar energy development decisions and outcomes, including those related to sustainability?

E. In the decision-making process, what are the values and perceptions of individual network actors, organizations, and objects on solar energy development throughout the lifespan of a solar energy development project.

List of Knowledge System Actors for This Project and Ground-Mounted, Utility-Scale Solar Energy Development Projects Broadly

A. Key Federal and State Agencies
   - Bureau of Land Management
   - California Department of Fish and Wildlife
   - California Department of Parks and Recreation
   - California Energy Commission
   - California Independent System Operator
   - California Public Utilities Commission
   - California State Lands Commission
   - Desert Renewable Energy Conservation Plan
   - Governor Brown's Office
   - National Park Service
   - National Renewable Energy Lab
   - U.S. Department of Defense
   - U.S. Department of the Interior
   - U.S. Environmental Protection Agency
   - U.S. Fish and Wildlife Service
   - U.S. Geological Survey

B. State and Local Governments
   - California, USA (encompasses project sites)
   - San Bernardino County, California (encompasses project sites)
   - Imperial County, California
   - Inyo County, California
   - Kern County, California
   - Los Angeles County, California
   - Riverside County, California
   - San Bernardino County, California
   - City of Lancaster, California

C. Renewable Energy Project Developers
   - NRG
   - BrightSource
   - EnXco
   - First Solar
   - Iberdrola Renewables
   - K Road

  - SunPower Corporation
  - Terra Gen
  - Wells Fargo

D. Research Scientists and Institutions
  - Lawrence Berkeley National Laboratory
  - University of California
  - University of Nevada
  - Stanford University

E. Renewable Energy Industry Associations
  - CALWEA
  - Geothermal Energy Association
  - Large Scale Solar Association

F. Non-Governmental Organizations
  - American Geophysical Union
  - California Environmental Justice Association
  - California Council of Land Trusts
  - California Native Plant Society
  - Center for Biological Diversity
  - Center for Energy Efficiency & Renewable Technologies
  - Defenders of Wildlife
  - Electric Power Research Institute
  - Ecological Society of America
  - Friends of the Desert Mountains
  - Natural Resources Defense Council
  - National Parks Conservation Association
  - Sierra Club
  - The Nature Conservancy
  - The Wildlands Conservancy
  - University of California, Davis
  - University of Nevada, Las Vegas

G. Electric Utilities
  - Imperial Irrigation District
  - Los Angeles Department of Water and Power
  - Pacific Gas & Electric
  - Sempra Energy Utilities
  - Southern California Edison

H. Native American Organizations
    - California Association of Tribal Governments
    - Desert Renewable Energy Tribal Coalition
    - Colorado River Indian Tribe
    - Fort Mohave Indian Tribe
    - Chemehuevi Indian Tribe

I. Off-Highway Vehicle Associations/Recreation
    - California Off-Road Vehicle Association
    - Off-Road Business Association

Knowledge Created by the Project

- Predicted the likelihood of long-term persistence of rare plants within and adjacent to solar energy installations;
- Provided mechanisms for and early indication of the threat of invasive plants within and adjacent to solar energy installations;
- Develop and apply a "bottom-up" approach to understanding the effects of solar energy infrastructure on complex, food web interactions; and
- Increase the effectiveness of mitigation strategies, thus creating a potential for reduced costs of species management plans.

Goal of Knowledge Transfer

The goal was to use a multi-media approach to engage with the knowledge system's actors, organizations, and objects and facilitate knowledge transfer through the development of a new website, associated online content, academic journal articles, datasets, reports, photographs, invited and contributed talks, and conference presentations.

Knowledge Transfer Products

Web-Based Content

The team developed a new initiative, the Wild Energy Initiative of the John Muir Institute of the Environment, and associated website, www.WildEnergy.org, to host content for the project (Figure 25). Through a comprehensive development process with all members, leading to a strategic plan, the team created the following content to orient website visitors with the research:

Figure 25: Homepage for Wildenergy.org

- Statement of Purpose. The Wild Energy Initiative facilitates impartial research and education on interactions between energy development and Earth, including its systems and species, to address urgent sustainability issues.
- Institutional Affiliations. The Wild Energy Initiative is a part of the John Muir Institute of the Environment at the University of California, Davis in northern California (The Barn, 501 Engineering Bikeway, Davis, CA 95616). Current offices are located approximately fifteen miles from the Capital Mall in Sacramento, California. Future offices may include the UC Davis Aggie Square satellite campus located near downtown Sacramento in Oak Park.
- Mission Statement. The mission is to:
    - Produce non-partisan and actionable research products that promote better understanding of the ecology of energy for human use, including ecological effects, trade-offs, and synergies of energy systems;
    - Develop scientific data and consensus to support planning and policy decisions related to sustainable energy development; and
    - Support knowledge transfer across global communities of energy and environmental stakeholders, including but not limited to communities and tribes, concerned citizens, industry, intergovernmental and governmental agencies, non-profit organizations, scientists, and urban planners.

Washington Post Article

The team was featured in a Washington Post article (content provided by UC Davis), entitled "Can Solar Energy and Wildlife Coexist?". This article to date has over one million readers. The article is embedded with a feature mini documentary that has also been widely watched and well received.

Academic Journal Articles

The team intends to develop the following articles (online, open-access) for publication and work with media writers at UC Davis to develop complementary press releases timed for release when publication embargos are lifted to promote maximum exposure to all members of the knowledge system (Target Audience: A-I):

- Effects of Ivanpah Solar Electric Generating System on Mojave Milkweed-Queen Butterfly Interactions (Chapter 2)
    - Hare don't care! Consumption of a rare, desert milkweed containing phytochemicals by the black-tailed jackrabbit. Published: *Journal of Arid Environments*.
    - An ecosystem service value system of desert plants reveals trade-offs for concentrating solar power. *Submitted*. Target Journal: *Nature Sustainability*.
    - SoilDucks for Earth Science: Taking the destruction and cost out of temperature monitoring. *In Preparation*. Target Journal: *PLOSOne*.
    - Shedding light on "bottom-up" interactions: Effects of solar energy development on an intricate, desert trophic web. *In Preparation*. Target Journal: *Proceedings of the National Academy of Sciences*.
    - Long-term, demographic effects of utility-scale solar energy development on a rare, desert milkweed. *In Preparation*. Target journal: *Conservation Biology*.
    - Fitness trade-offs in a monarch-milkweed system affected by solar energy development. *In Preparation*. Target Journal: *Ecology*.
- PV-Annual Plant Nexus Project (Chapter 3)
    - Simulated solar panels create altered microhabitats in desert landforms. Published. Journal: *Ecosphere.*
    - Microhabitats associated with solar energy development alter demography of two desert annuals. *Submitted*. Target Journal: *Ecosphere.*
    - Unearthing the buried treasure of seed bank survival. *In Friendly Peer Review*. Target Journal: *New Phytology*.
    - Impacts of simulated photovoltaic panels on soil temperature using iButtons. *In Preparation*. Target Journal: *Applied Soil Ecology*.
    - Solar energy development impacts seed bank demography through microclimate effects. *In Preparation*. Target journal: *Conservation Biology*.
    - Impacts of solar development on invasive plant demography and structure of annual communities. *In Preparation*. Target journal: *Biological Invasions*.

Datasets

The researchers developed and will make available (after publication in peer-review journals) on the research websites the following reports and complementary datasets:

- Final CS-Milkweed-Monarch Environmental Data Summary Report
- Final PV-Annual Plant Environmental Data Summary Report
- Final PV-Annual Plant Nexus Data Summary Report

- Final CS-Milkweed-Monarch Nexus Data Summary Report

Reports

The researchers developed and made available online (CEC website, WildEnergy.org) this final report.

Invited and Contributed Talks

The team presented more than 25 invited and contributed talks and posters to diverse audiences. Examples of such talks and presentations include:

- Amherst University, Ecology Department, Rebecca R. Hernandez (Invited Talk, 3 October 2019), The Sustainability and Ecology of Renewable Energy in an Unprecedented Energy Transition, Audience: D.
- Environmental Protection Agency, NEPA Environmental Review Branch, Steven M. Grodsky, Karen Tanner (Invited Talk, 25 November 2019) Optimizing Solar Facility Configuration Effects on Habitat, Managed Plants, and Essential Species Interactions, Audience: A.
- Electric Power and Research Institute, Rebecca R. Hernandez (Invited Talk, January 2017), Talk: Siting Solar Energy: From Mitigating Adverse Impacts to Optimizing Techno-Ecological Synergies, Audience: A-G.
- First Solar, San Francisco, California, Rebecca R. Hernandez (Invited Talk, January 2017), Talk: *Utility-scale solar energy development: Impacts, Synergies, and Co-Benefits*, Audience: C & E.
- School of Life Sciences Seminar Series, University of Nevada, Las Vegas, Rebecca R. Hernandez (Invited Talk, December 2016), Talk: *Energy Geographies, Nexus Issues, and the Future Energy Landscape,* Audience: A & E.
- SunPower Founder, Vice President of Operations, and Staff, Energy Efficiency Center, University of California, Davis, California Rebecca R. Hernandez (Invited Talk, October 2016), *Talk: Utility-scale solar energy development: Impacts, Synergies, and Co-Benefits*, Audience: C & E.

Costs of conference attendance and travel were not covered by the CEC.

CHAPTER 5: Conclusions and Recommendations

Effects of Ivanpah Solar Electric Generating System on Mojave Milkweed-Queen Butterfly Interactions

Blading (that is, bulldozing) negatively affects desert perennials, including the rare Mojave milkweed, and plant-insect trophic interactions. Further, blading increases colonization of invasive grasses like *Schismus* spp., which, in turn, can increase risk of wildfire and decrease abundance of CAM species like cacti and yucca. Mojave milkweed was always more abundant in control populations than in ISEGS, whether in wet or dry years. As a management practice, halos within solar facilities designed for rare plant conservation are efficacious for maintenance of Mojave milkweed populations inside ISEGS. Mojave milkweed plants conserved in halos may serve as a source population for the spread of Mojave milkweed outside of halos into areas with heliostats in ISEGS, although this hypothesis was not evaluated in this study. The mowed areas of ISEGS appear to provide suitable habitat for Mojave milkweed. Mojave milkweed was effectively unavailable to queen butterflies as a host plant in bladed areas. Although queen butterflies oviposited on Mojave milkweed in halos and mowed areas in 2017, caterpillar survivorship was highest in control treatments. Further, the researchers found most queen butterfly eggs and caterpillars in control treatments in 2019. These results suggest that ISEGS may negatively impact host-plant use by queen butterflies within the solar facility, although pre-construction data would be needed to test this hypothesis. When possible, blading should be avoided as a site preparation practice to limit negative ecological effects of solar energy development in the Mojave Desert. The researchers also suggest that leaving undeveloped gaps akin to halos in CSP or PV installations will lead to positive ecological outcomes. As a rare plant, Mojave milkweed is persisting in ISEGS; however, ecological interactions between Mojave milkweed and beneficial insects were negatively impacted relative to control treatments.

Photovoltaic-Annual Nexus

Utility of Common Species as “Surrogates” for Rare Species

California’s deserts support many rare plants (Moore and André 2014, California Native Plant Society Rare Plant Program 2018), some occurring in areas identified for renewable energy development. Loss of rare species in other systems has been linked to changes in land use (Lavergne, Thuiller, Molina, & Debussche, 2005), so it is important to understand how landscape changes imposed by energy development are likely to affect rare plants present. However, experimental studies on rare species are often hindered by regulatory or logistical constraints. To make management decisions when data on rare species are sparse, a closely related common species may be substituted. The tacit assumption is that the response of the common species can provide insight into that of the rare one, as a consequence of shared evolutionary history or ecological niche (Caro et al., 2005). This strategy has however been challenged, and remains a topic of lively debate (Andelman & Fagan, 2000; Murphy et al., 2011). In the current two-year study, the researchers found no strong differences in panel microhabitat effect on belowground dynamics of the rare and common native taxa. In artificial seed banks buried for a single growing season, microhabitat had no effect on seed survival. After a second season of burial, seed survival rates were higher in Shade for both species and cohorts. Under dry conditions, Shade may promote retention of seeds in the seed bank for both species, at least temporarily. The researchers found no effect of microhabitat on reproductive output for either species in the single year where plants successfully matured (2017). In contrast, Shade effects on survivorship differed across the rare and common species. While survivorship remained quite high for both species in 2017, Shade had a negative effect on the rare *E. mohavense* only. Because these species were tested at sites differing in physical characteristics (for example, soil texture) the researchers cannot rule out a role for the local environment in driving these outcomes. Local physical conditions could play a role, and in fact seem to contribute to differences in microhabitat effects across sites differing in soil characteristics (Tanner, Moore-O'Leary, Parker, Pavlik & Hernandez, *in review*). This result does nonetheless highlight the risk of inferring rare species response from a closely related relative, and this risk may be heightened when the species observed do not experience the same environmental conditions. Although the researchers found limited evidence for strong microhabitat impacts here, subtle effects can be compounded across generations to drive population-level consequences (Tanner, Moore-O'Leary, Parker, Haji, Pavlik & Hernandez, *in review*)

Panel Effects on Exotic Invasive Species

B. tournefortii germinates and emerges readily, an opportunistic strategy that works well when moisture is not strongly limiting, but can cause mass mortality when conditions after emergence are dry. In a single season, nearly 90% of seeds in the soil seed bank may germinate, leaving behind a relatively small seed bank. As such, a series of naturally dry years, or a series of consecutive years of control efforts at solar facilities, should drive population densities down. However, *B. tournefortii* may still do well where it receives water runoff subsidies (along roadsides, near panel driplines) so active control efforts may be required in these areas even in relatively dry years. Unfortunately, even though the number of *B. tournefortii* seeds retained in the seed bank was low in this study, > 80% remained viable for two years - a much higher viability rate than observed for native annuals. This result suggests that *B. tournefortii* populations may reinvade from belowground reserves when growing conditions are again favorable – at least over the timescales observed in this study. The authors recommend managing for invasive species (for example, herbicides), which may be promoted by solar panels, in and around photovoltaic solar facilities.

CHAPTER 6:
Benefits to Ratepayers

Part of the costs of developing and operating renewable energy facilities is the cost of minimizing environmental impacts. In the absence of sound scientific data about impacts, regulatory and permitting agencies cannot be certain whether requirements should be imposed on renewable energy developers or what the requirements should be. This uncertainty could hypothetically lead to unnecessary costs or to unintended environmental consequences. This project assessed the effects of site preparation treatments for solar CSP on an interconnected food web and of solar PV panels on native and invasive annual plants in the Mojave Desert. This research informs conservation of desert plant species with economic, cultural, and social significance as well as the plant-animal interaction central to ecosystem function in the Mojave Desert. This work can inform ecosystem resiliency and restoration by shedding light on the role of water and soils in desert plant performance at solar energy facilities that in turn can lead to sustained, plant-based ecosystem services from Mojave Desert plants. Plant-mediated ecotourism and quality of life for desert residents can be better sustained as a result of conservation informed by this study. The researchers are informing managers and policy makers on how to reduce negative effects of solar energy development on Californian desert plants and animals of conservation concern. This research will lead to better informed and more sustainable renewable energy development in the deserts of California. This work serves as a platform for future studies on effects of solar energy development on soils, plants, and wildlife that will save money for ratepayers and inform a just energy transition in California.

LIST OF ACRONYMS

Term	Definition
CAM	Crassulacean acid metabolism
CEC	California Energy Commission
CSP	Concentrating solar power
DRECP	Desert Renewable Energy Conservation Plan
EPIC	Electric Program Investment Charge
GLM	Generalized linear models
GLMM	Generalized linear mixed-effects models
ISEGS	Ivanpah Solar Electric Generating System
m^2	Square meter
PAR	Photosynthetically active radiation
PV	Photovoltaic (solar energy)
UCSC	University of California Santa Cruz
UC Davis	University of California Davis
USSE	Utility-scale solar energy

REFERENCES

Adondakis, S., & Venable, D. L. (2004). Dormancy and Germination in a Guild of Sonoran Desert Annuals. Ecology, 85(9), 2582–2590.

Andelman, S. J., & Fagan, W. F. (2000). Umbrellas and flagships : Efficient conservation surrogates or expensive mistakes ? Proceedings of the National Academy of Sciences, 97(11), 5954–5959.

Armstrong, A., Ostle, N. J., & Whitaker, J. (2016). Solar park microclimate and vegetation management effects on grassland carbon cycling. Environmental Research Letters, 11(7), 1–11. https://doi.org/10.1088/1748-9326/11/7/074016

Augspurger, C. K., & Kelly, C. K. (1984). Pathogen mortality of tropical tree seedlings: studies of the effects of dispersal distance, experimental seedling density, and light conditions. Oecologia, 61(2), 211–217.

Bangle, D. N., Walker, L. R., & Powell, E. . (2008). Seed Germination Of The Invasive Plant Brassica Tournefortii (Sahara Mustard) In The Mojave Desert. Western North American Naturalist, 68(3), 334–342.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. <doi:10.18637/jss.v067.i01>

Beatley, J. (1967). Survival of Winter Annuals in the Northern Mojave Desert. Ecology, 48(5), 745–750. https://doi.org/10.2307/1933732

Beatley, J. (1974). Effects of rainfall and temperature on the distribution and behavior of Larrea Tridentata (Creosote-Bush) in the Mojave Desert of Nevada. Ecology, 55(2), 245–261.

Beatley, J. C. (1974). Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology, 55(4), 856–863.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. (2008). Generalized linear mixed models : a practical guide for ecology and evolution. Trends in Ecology and Evolution, 24, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Cash, D. W. et al. Knowledge systems for sustainable development. Proc. Natl. Acad. Sci. U. S. A. 100, 8086–91 (2003).

Caro, T., Eadie, J., & Sih, A. (2005). Use of Substitute Species in Conservation Biology. Conservation Biology, 19(6), 1821–1826. https://doi.org/10.1111/j.

Carruthers, E., Lewis, K., Mccue, T., & Westley, P. (2008). Generalized linear models: model selection, diagnostics , and overdispersion. Memorial University of Newfoundland.

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics, 31, 343–366.

Clauss, M. J., & Venable, D. L. (2000). Seed Germination in Desert Annuals: An Empirical Test of Adaptive Bet Hedging. The American Naturalist, 155(2), 168–186. https://doi.org/10.1086/303314

Curtis, C. A., & Bradley, B. A. (2015). Climate Change May Alter Both Establishment and High Abundance of Red Brome (Bromus rubens) and African Mustard (Brassica tournefortii) in the Semiarid Southwest United States. Invasive Plant Science and Management, 8(3), 341–352. https://doi.org/10.1614/IPSM-D-14-00040.1

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological Invasions by Exotic Grasses , the Grass / Fire Cycle. Annual Review of Ecology and Systematics, 23(1992), 63–87.

ERT. (1988). Fort Collins, Colorado. E503 Luz SEGS VII sensitive plant salvage soil survey technical report, prepared by James Nyenhuis for Luz Engineering Corporation, Los Angeles, California.

Fox, J. and Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Freas, K. E., & Kemp, P. R. (1983). Some relationships between environmental reliability and seed dormancy in desert annual plants. Journal of Ecology, 71(1), 211–217. https://doi.org/10.2307/2259973

Kimball, S., Angert, A. L., Huxman, T. E., & Venable, D. L. (2010). Contemporary climate change in the Sonoran Desert favors cold-adapted species. Global Change Biology, 16(5), 1555–1565. https://doi.org/10.1111/j.1365-2486.2009.02106.x

Lavergne, S., Thuiller, W., Molina, J., & Debussche, M. (2005). Environmental and Human Factors Influencing Rare Plant Local Occurrence , Extinction and Persistence : A 115-Year Study in the Mediterranean Region. Journal of Biogeography, 32(5), 799–811.

Leck, M. A., Parker, V. T., & Simpson, R. L. (1989). The Ecology of Soil Seed Banks. The Ecology of Soil Seed Banks. Academic Press, Inc. San Diego, California.

Lenth, R. 2018. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.2.1. https://CRAN.R-project.org/package=emmeans

Mabbutt, J. A., & Fanning, P. C. (1987). Vegetation banding in arid Western Australia. Journal of Arid Environments, 12, 41–59. Retrieved from vegetation

Mangiafico, S.S. 2016. Summary and Analysis of Extension Program Evaluation in R, version 1.18.1. rcompanion.org/handbook/.

McCullough, E. B. & Matson, P. A. Evolution of the knowledge system for agricultural development in the Yaqui Valley, Sonora, Mexico. Proc. Natl. Acad. Sci. U. S. A. 113, 4609–14 (2016).

Moore, K. A., & André, J. M. (2014). Rare Plant Diversity In The California Deserts: Priorities for Research and Conservation. Fremontia, 42(1), 9–14.

Mordecai, E. a. (2012). Soil moisture and fungi affect seed survival in California Grassland annual plants. PLoS ONE, 7(6). https://doi.org/10.1371/journal.pone.0039083

Morris, W. F., Pfister, C. a., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., … Menges, E. S. (2008). Longevity can buffer plant and animal populations against changing climatic variability. Ecology, 89(1), 19–25. https://doi.org/10.1890/07-0774.1

Murphy, D. D., Weiland, P. S., & Cummins, K. W. (2011). A Critical Assessment of the Use of Surrogate Species in Conservation Planning in the Sacramento-San Joaquin Delta. California (U.S.A.). Conservation Biology, 25(5), 873–878. https://doi.org/10.1111/j.1523-1739.2011.01711.x

Pake, C. E., & Venable, D. L. (1996). Seed Banks in Desert Annuals : Implications for Persistence and Coexistence in Variable Environments. Ecology, 77(5), 1427–1435.

Patten, D. T. (1978). Productivity and Production Efficiency of an Upper Sonoran Desert Ephemeral Community. American Journal of Botany, 65(8), 891. https://doi.org/10.2307/2442185

Philippi, T. (1993). Bet-Hedging Germination of Desert Annuals : Beyond the First Year. The American Naturalist, 142(3), 474–487.

Porter, R. H., Durrell, M., & Romm, H. J. (1947). The Use of 2,3,5-Triphenyl-Tetrazoliumchloride as a Measure of Seed Germinability. Plant Physiology, 22(2), 149–159. https://doi.org/10.1104/pp.22.2.149

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Smith, S.D., Patten, D.T., Monson, R. K. (1987). Effects of artificially imposed shade on a Sonoran Desert ecosystem: microclimate and vegetation. Journal of Arid Environments, 13, 65–82.

Soil Survey Staff. (2017). Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link: https://websoilsurvey.sc.egov.usda.gov/. Accessed [12/08/2017].

Tanner, K., Moore, K., & Pavlik, B. (2014). Measuring impacts of solar development on desert plants. Fremontia, 42(2), 15–16.

Tanner, K. E., Moore-O'Leary, K. A., Parker, I. M., Pavlik, B. M., Hernandez, R. R. Simulated solar panels create altered microhabitats in desert landforms. In review.

Tanner, K. E., Moore-O'Leary, K. A., Parker, I. M., Haji, S., Pavlik, B. M., Hernandez, R. R. Microhabitats associated with solar energy development alter demography of two desert annuals. In review.

Tevis, L. J. (1958). A population of desert ephemerals germinated by less than one inch of rain. Ecology, 39(4), 688–695.

Venable, D. L. (2007). Bet hedging in a guild of desert annuals. Ecology, 88(5), 1086–1090. https://doi.org/10.1890/06-1495

Went, F. W. (1948). Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. Ecology, 29(3), 242–253. https://doi.org/10.2307/1930988

APPENDIX A:
Supporting Literature for "Effects of Ivanpah Solar Electric Generating System on Mojave Milkweed-Queen Butterfly Interactions"

Link to peer-reviewed paper entitled on Mojave milkweed herbivory "*Hare don't care! Consumption of a rare, desert milkweed containing phytochemicals by the black-tailed jackrabbit*": https://static1.squarespace.com/static/575188ec59827e7457af8c5b/t/5d4232d18f5a6b0001a855b3/1564619476870/Hare_Milkweeds_Grodsky_6.2019.pdf

Link to peer-reviewed book chapter on solar energy and the biosphere: https://static1.squarespace.com/static/575188ec59827e7457af8c5b/t/5b5bad5c352f53124f3c66b1/1532734815065/Solar+Energy+and+the+Biosphere.pdf

APPENDIX B: Technical Details of the PV-Annual Plant Nexus Study

Site Selection and Characterization

To avoid introducing the invader *B. tournefortii* into locations where it does not already occur, the researchers conducted surveys on BLM land in spring 2016 around Barstow, California (Zone 11S, 498560.02 m E, 3861625.84 m N) to identify extant populations. The researchers chose a location north of Barstow on a gentle south-facing slope flanked by a wide, active wash to the east, and a county-maintained flood control berm on the west shielding the site from passersby on Fort Irwin Road. *B. tournefortii* grows abundantly at this location, and the site can experience flooding from the adjacent wash, though the researchers saw no evidence of strong flood activity during the study period. The substrate here is classified as Cajon gravelly sand, 2 – 15 percent slope (Soil Survey Staff, 2017).

Earlier work determined that soils in the vicinity of the *E. mohavense* site are dominated by the Norob soil series (ERT, 1988). The substrate at the *E. wallacei* site is a heterogeneous soil-gravel mix, but soil taxonomy is not available for this location from the Web Soil Survey (Soil Survey Staff, 2017).

Weather

Weather stations were installed within 20 meters of experimental panels at the *E. wallacei* and *E. mohavense* sites, and ~ one km southeast of the *B. tournefortii* site to reduce visibility and risk of theft. Stations comprise a HOBO® Pendant Data Logger UA-003-64 inside a RS1 solar radiation shield acquiring hourly temperatures, and an RG3-M rain gauge collecting cumulative rainfall data. The researchers also downloaded precipitation and air temperature data for the period 1944 – 2016 from KDAG (Barstow-Daggett Airport) and KEDW (Edwards North Air Force Base), the closest monitoring stations to the *E. wallacei* | *B. tournefortii* and *E. mohavense* sites, respectively (Figure B-1). Subject to availability, precipitation and air temperature data were downloaded from the following sources (in order of preference): National Oceanic Atmospheric Administration NOWData (http://w2.weather.gov/climate/xmacis.php?wfo=vef); Armstrong Flight Research Center, Edwards Air Force Base (https://weather.dfrc.nasa.gov/wxclimatology.htm); and Weather Underground (https://www.wunderground.com/history/airport/KEDW/).

B. tournefortii Transplanting Effort

In December 2016, individual seeds were randomly drawn from the 2016 *B. tournefortii* seed collection and inserted into the cells of a plastic seedling flat filled with a 4:7 mixture of sand and potting soil (Premiere Horticultural ProMix Hp). Flats were lightly watered and chilled in a 40º refrigerator for two weeks. Following germination, flats were transferred to a greenhouse and seedlings were allowed to grow under ambient light and temperature conditions until individuals had two whorls of true leaves. In January 2017, greenhouse seedlings were transported to the experimental study site and six individuals were transplanted into each plot (two plants per microhabitat). Before transplanting, extant annual seedlings of all species were cleared, and a trowel was used to transplant two seedlings into each microhabitat (Shade, Runoff, Control). Transplanted seedlings were then showered with 500 mL of water from a watering can. Additional watering treatments of 500 mL were applied the next day, and 5 days after transplanting. All seedlings survived through the third week in the field, suggesting that no seedlings died as a direct result of the transplanting process. The researchers then followed these plants in 2017, harvesting them for fruit and seed counts at the close of the growing season.

Panel Construction

Experimental panel arrays were installed at *Eriophyllum* sites (n = 26 panels per site) in spring of 2011, as part of an earlier research project. These arrays were augmented with additional panels (n = 8 per site) in 2016, when 34 new panels were installed at the *B. tournefortii* site. Original panels were welded in-house from ½″ rebar; new panels were fabricated from ½″ cold rolled steel by Brian's Welding in San Jose, California, using the same design. Solar shields were constructed from ¼″ Columbia PureBond (low formaldehyde plywood) and bolted to frame mounting brackets. Sheets of clear corrugated plastic (2′ squares of 4 mm Coroplast, CorrugatedPlastics.Net) were screwed to shields to improve rainfall runoff. At all plots, panels were positioned facing south, and legs were pounded into the ground until the southern edge of the panel was ~20 cm off the ground. Control microhabitats at all sites were defined to be at least 1 meter from adjacent panels and shrubs to avoid unintentional shading (Figure B-2).

Soil Temperature

Units were sealed into 4 mil plastic bags using a vacuum sealer to protect them from moisture, after confirmed that bags did not affect temperature readings. After burial, squares of hardware cloth were installed over units to protect them from disturbance. Units were downloaded at ~2.5 month intervals to minimize overwriting of data.

Light Environment

Measurements were taken March 28 – 30, 2017 and March 25 – 27, 2018. The light gradient under panels was divided into 9 subplots to allow sampling across a north to south as well as an east to west gradient (Figure B-3). To restrict measurements to individual subplots, the ceptometer wand was wrapped in tinfoil with a 20 cm section exposed, thus constraining measurements to subplot dimensions. Morning samples were taken from ~10:30 – 11:00, samples near solar noon were taken ~12:45 – 13:30, and afternoon samples were taken ~15:00 – 15:30.

Seed Collection

In April 2016, mature *B. tournefortii* fruits were collected from six sites within 15 km of Barstow, California. At each site fruits were harvested from at least 19 individuals spanning the size range of plants present. Equivalent proportions of cleaned seed from each site were mixed together, and seed was randomly selected for use in artificial seed banks and seeding toothpick array experiments.

In March of 2015 and 2016, a randomly selected subset of fruiting *Eriophyllum* were collected in the open (n = 133 in 2015 and n = 113 in 2016 for *E. mohavense*; n = 176 in 2015 and n = 71 in 2016 for *E. wallacei*). Mature achenes (intact and black in color) were identified under a stereoscope and combined into a single lot per cohort. Achenes (hereafter referred to as seed) were randomly selected from these collections for use in artificial seed bank packet and seeding toothpick array experiments. Due to the limited supply of 2016 achenes, the 2015 cohort was used in some experiments.

Artificial Seed Bank Packet Construction

Seed packets were constructed from white polyorganza fabric, with polyester thread seams dividing each packet into cells, each cell containing a single seed (the number of cells per packet depended on seed cohort availability by species –Table B-1). Packets installed at fungicidal treatment plots were 2.5 x 9 cm, with cells sewn in a double column. Within each microhabitat, packets were laid out in two rows to achieve spatial separation between control and treated packets. At plots with ambient experimental conditions, packets were 1.5 by 18 cm with cells in a single column, laid out in a single row within microhabitat. Rows of packets were arranged with the long edge running east-west in the Shade, and north-south in the Runoff microhabitat, to allow packets to span relevant experimental gradients in each case. Layout in the Control microhabitat followed that in the Runoff microhabitat. After burial packets were covered with a square of ½" hardware cloth secured by 5" nails to protect against disturbance (Figure B-4), but this preventative measure was not always successful (Figure B-5).

Fungicide Treatment

The researchers mixed a treatment solution at the rate of 4 drops Subdue MAXX and 2.5 mL Cleary 3336^F per gallon in accordance with guidelines for small-scale soil drench treatments. At each plot, a 6 x 6" open-ended aluminum barrier box was centered on packets to be treated and hammered ~ 3 cm into the soil to isolate the treated area from the surrounding soil and untreated packets (Figure B-6). Six ounces of solution was adequate to wet the soil to a depth of 3 cm (buried packets were < 1 cm below the soil surface); at untreated locations, the same volume of water was applied as a control. Plastic bottles were pre-marked to allow dispensing of 6 ounce increments, and caps were perforated with small holes to allow slow, even delivery of liquid, avoiding exposure of buried packets.

Tetrazolium Treatment

Before conducting formal assays, the tetrazolium staining approach (Porter, Durrell, & Romm, 1947) was tested on field-collected seed from the 2017 cohort of each species. The researchers intentionally "killed" some of these seeds by boiling them in water for 2 minutes and confirmed that tissue of boiled seeds remained white after exposure to stain.

Seeds were prepared for staining by placing them on wetted filter paper for 24 hours to promote imbibition. Seeds were then cut longitudinally using a precision knife (Xacto #11) to expose embryo and pericarp. Seeds of *B. tournefortii* and *E. mohavense* seeds were soaked in stain solution for 24 hours at 17º C. *E. mohavense* was more refractory to staining in pilot trials, with best results following a 6 hour soak at 35º C, so the method was varied accordingly for this species.

Seeding Toothpick Preparation

Toothpicks were prepared by attaching one randomly selected seed of the appropriate species to the midpoint of plastic toothpicks (Ward's Science 159850), using a minimal quantity of

Elmer's glue mixed in a 1:1 ratio with water. Arrays of toothpicks were installed across microhabitats at each site.

Data Analysis Methods

Microhabitat Characterization

Temperature data were strongly bimodal so Kruskal-Wallis tests were used to assess temperature differences across microhabitats. Soil moisture data were analyzed using a generalized linear mixed effects model (GLMM) with Site, Microhabitat, Day, and their three-way interaction as fixed effects, and Plot nested inside Site as a random effect. The emmeans package (Lenth 2018) was used to carry out pairwise *post-hoc* tests on estimated marginal means from each microhabitat. The researchers tested for differences in photosynthetically active radiation (PAR) during each sampling period (morning, solar noon, afternoon). Data collected across the shade footprint were used to generate an average Shade measurement for each site and sampling period, and Welch's *t*-tests were used to compare these values to measurements in full sun.

Seed Bank Retention

The response variable was the proportion of intact seed retained in seed bank packets, and the distribution of these data tended to be strongly non-normal. Generalized linear models (GLMs) provide more flexible tools for handling non-normal data (Bolker et al., 2008), so the researchers built GLMs or GLMMs using the lme4 package (Bates et. al. 2015). A GLM or GLMM approach was chosen for each species depending on whether Plot could be included as a random effect – packets deployed at a given plot are relatively close together, and are more likely to experience similarities in local conditions (soil texture, surface runoff patterns, etc.) compared to packets at different plots. Where blocks were complete for all plots in a data set (that is, seed bank retention estimates from all three microhabitats at each plot), Plot was included as a random effect in a GLMM. This was the case for *B. tournefortii*, but not the *Eriophyllum* data sets, which always contained incomplete blocks.

The researchers specified binomial or quasibinomial models with logit link functions, using the proportion of intact seed retained as the response, and weighting proportions by the number of seed recovered from a given microhabitat and plot (this approach combines seed if multiple packets were collected in the same microhabitat and plot). The quasibinomial family was chosen for *Eriophyllum* models to help control overdispersion (Carruthers, Lewis, Mccue, & Westley, 2008), but this approach did not eliminate the problem - so *P*-values should be considered approximate. For full models, fixed effects included Microhabitat (Control, Shade, Runoff), Year (the year packets were collected – 2017 or 2018), and the Microhabitat*Year interaction. Seed Cohort was also included as a fixed effect in *Eriophyllum* models, so the full interaction term was Microhabitat*Year*Seed Cohort (all *B. tournefortii* seed came from a single cohort). Diagnostic plots of model residuals versus fitted values confirm an approximately linear relationship between predictor and response variables, and diagnostic QQ plots (standardized residuals plotted against theoretical quantiles) showed points falling along an approximately straight line, suggesting models met the assumptions of lack of bias and homogeneity. The researchers used the emmeans package (Lenth 2018) to conduct pairwise *post-hoc* comparisons of marginal means across microhabitats.

For *E. wallacei*, low sample size in 2018 was a concern, particularly because there was a strong Year effect for this species. The researchers therefore chose to create separate GLMs by year for this species and conducted Fisher's exact tests on the 2018 data to identify significant effects of Microhabitat and Seed Cohort. Where Fisher tests reported predictor significance, the pairwiseNominalIndependence function in the rcompanion package (Mangiafico 2018) was used to carry out *post-hoc* tests revealing differences among microhabitats.

Fungicide

The researchers built quasibinomial GLMs or GLMMs with logit link functions appropriate for overdispersed data to model the weighted proportion of intact seed in packets collected in 2017 (the only year in which the fungicidal treatment was applied). The fixed effects Microhabitat, Fungicide, and the Microhabitat*Fungicide interaction were included in models for each species. Two outlying data points were dropped from the *B. tournefortii* data set before analysis.

Seed Staining

The researchers built quasibinomial GLM models with logit link functions for each species using stain presence (indicating seed survival) as the response variable for individual seeds. The full *B. tournefortii* model included the fixed effects Microhabitat, Year, and the Microhabitat*Year interaction; full *Eriophyllum* models included Microhabitat, Year, Seed Cohort, and all interactions. The quasibinomial approach used in the *E. mohavense* model did not eliminate overdispersion, so *P*-values should be regarded as approximate. The emmeans package (Lenth 2018) was used to conduct *post-hoc* tests comparing marginal means on the basis of season, microhabitat, and seed cohort (where relevant). Because there were very few intact *B. tournefortii* seeds to work with, and the Microhabitat*Year interaction was a marginally significant predictor in the full model, a Fisher's exact test to determine whether there was an effect of microhabitat within year.

Survivorship

The researchers used Fisher's exact test for look for differences in survivorship across microhabitats in the relevant years for each species (that is, years in which at least some individuals survived). Where significant effects were observed, the rcompanion package (Mangiafico 2018) was used to carry out *post-hoc* tests identifying differences among microhabitats.

Reproductive Output

Fruit and seed count data sets failed the Shapiro-Wilkes test, so researchers used negative binomial GLMs to test for effects of Year, Microhabitat, and Year*Microhabitat on *B. tournefortii* fruit count, and for the effects of Microhabitat on *Eriophyllum* seed counts in 2017 only (the sole year in which *Eriophyllum* reproduced).

Community Response

To limit statistical tests to comparisons between microhabitats with equivalent plot area, the researchers created two data sets – one containing data associated with the Control and Shade microhabitats, and the other containing Runoff Control and Runoff data sets. The Shannon diversity index and species richness data sets passed the Shapiro-Wilkes test of normality, so two-way ANOVAs including the fixed effects Microhabitat, Year, and

Year*Microhabitat were built. Native and exotic abundance data sets were not normally distributed, and negative binomial GLMs were used to test for effects of Microhabitat, Year, and Year*Microhabitat on native and exotic abundance at both *Eriophyllum* sites. Where predictors were significant, the emmeans package (Lenth 2018) was used to test for differences between microhabitats with year.

Tables and Figures

Table B-1: Seed Allocations to Experiments

Species	Seed Cohort	Year Installed	Artificial Seed Bank Experiments				Seedling Emergence Experiments	
			Untreated Seed Packets		Fungicide Seed Packets			
			# Packets	Seeds in Packet	# Packets	Seeds in Packet	Arrays per Site	Seeds per Array
E. mohavense	2015	2016	-	-	180	18	30	12
E. wallacei	2015	2016	-	-	180	14	30	12
E. mohavense	2016	2016	180	9	-	-	30	12
E. wallacei	2016	2016	180	2	-	-	30	12
B. tournefortii	2016	2016	180	18	180	18	30	16
B. tournefortii	2016	2017	-	-	-	-	30	18
B. tournefortii	2016	2018	-	-	-	-	30	18

Source: UC Davis

Table B-2: Species List

Family	Genus	Species	Life Form	Exotic	CRPR Rank	Present at *E. mohavense* Site	Present at *E. wallacei* Site
Alliaceae	*Allium*		P			x	
Asteraceae	*Ambrosia*	*dumosa*	P			x	
	Chaenactis	*stevioides*	A			x	x
	Eriophyllum	*mohavense*	A		1B.2	x	
	Eriophyllum	*wallacei*	A				x
	Lasthenia	*californica*	A			x	
	Logfia	*depressa*	A			x	x
	Leptosyne	*calliopsidea*	A				x
	Leptosyne	*bigelovii*	A			x	
	Malacothrix	*californica*	A			x	
	Malacothrix	*coulteri*	A				x
	Monoptilon	*bellioides*	A				x
Boraginaceae	*Amsinckia*	*tessellata*	A				x
	Cryptantha	*circumscissa*	A				x
	Cryptantha	*pterocarya*	A				x
	Cryptantha	*sp.*	A			x	
	Nama	*demissum*	A				x
	Pectocarya	*platycarpa*	A			x	
	Pectocarya	*recurvata*	A				x
	Phacelia	*distans*	A				x
	Phacelia	*fremontii*	A				x
Brassicaceae	*Caulanthus*	*lasiophyllus*	A			x	
	Lepidium	*flavum*	A			x	
	Lepidium	*nitidum*	A			x	
Fabaceaea	*Astragalus*	*sp.*	A			x	
	Lupinus	*sp.*	A				x

Family	Genus	Species	Life Form	Exotic	CRPR Rank	Present at *E. mohavense* Site	Present at *E. wallacei* Site
	Lupinus	*concinnus*	A				x
	Lupinus	*sparsiflorus*	A				x
Geraniaceae	*Erodium*	*cicutarium*	A	x		x	x
Lamiaceae	*Salvia*	*comunbaria*	A				x
Loasaceae	*Mentzelia*	*albicaulis*	A				x
Onagraceae	*Eremothera*	*refracta*	A				x
	Tetrapteron	*spp.*	A			x	
Papaveraceae	*Eschscholzia*	*minutiflora*	A				x
Poeaceae	*Schismus*	*arabicus*	A	x		x	x
Polemoniaceae	*Gilia*	*stellata*	A			x	x
	Linanthus	*parryae*	A				x
Polygonaceae	*Chorizanthe*	*brevicornu*	A				x
	Chorizanthe	*spinosa*	A		4.2	x	
	Eriogonum	*maculatum*	A			x	x
	Eriogonum	*palmerianum*	A				x
	Eriogonum	*pusillum*	A			x	x
	Eriogonum	*sp.*	A				x
	Eriogonum	*trichopes*	A			x	
Unknown 1-9			A			x	
Unknowns 10-16			A				x

Species observed inside plots at the *E. mohavense* and *E. wallacei* sites (taxa with "sp" listed in the Species column could be identified to genus only). Species life form is designated as P (perennial) or A (annual); exotic (non-native) status and California Rare Plant Rank (CRPR) are shown where applicable. In addition to species listed, 9 unknown species were encountered at the *E. mohavense* site, and 7 unknown species at the *E. wallacei* site. Unknown species were not observed at a life stage permitting identification.

Source: UC Davis

Table B-3: Soil Moisture Table Statistics

Approach	Predictor	Df	***F*-value**	***P*-value**
GLMM	Site	2.00	87.62	**<0.001**
	Microhabitat	2	7.09	**0.001**
	Day	2	11.47	**<0.001**
	Site*Microhabitat	4	2.07	*0.081*
	Site*Day	4.00	1.15	0.330
	Microhabitat*Day	4	1.59	0.173
	Site*Microhabitat*Day	8.00	0.92	0.496

Source: UC Davis

Table B-4: Seed Bank Retention Model Statistics for (a) *B. tournefefortii*

Species and Approach	Predictor	Df	***F*-value**	***P*-value**
B. tournefortii	Microhabitat	2	17.88	**<0.001**
GLMM (binomial)	Year	2	34.24	**<0.001**
	Microhabitat*Year	4	1.88	0.106

Results from GLMM and GLM models of seed bank retention rate for (a) *B. tournefortii.*

Source: UC Davis

Table B-5: Seed Bank Retention Model Statistics for (b) *E. mohavense* and *E. wallacei*

Species and Approach	**Predictor**	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev**	***P*-value**
E. mohavense	Null	–	–	117	520.28	–
GLM (quasibinomial)	Microhabitat	2	21.57	115	498.71	**0.002**
	Year	1	110.22	114	388.49	**<0.001**
	Seed Cohort	1	140.11	113	248.38	**<0.001**
	Microhabitat*Year	2	25.13	111	223.25	**0.002**
	Microhabitat*Seed Cohort	2	1.52	109	221.73	0.681
	Year*Seed Cohort	1	0.26	108	221.47	0.711
	Microhabitat*Year*Seed Cohort	2	0.40	106	221.07	0.901
E. wallacei	Null	–	–	59	80.60	–
2017 GLM (quasibinomial)	Microhabitat	2	0.41	57	80.19	0.838
	Seed Cohort	1	3.05	56	77.14	0.120
	Microhabitat*Seed Cohort	2	0.57	54	76.57	0.796
2018 GLM (quasibinomial)	Null	–	–	33	79.90	–
	Microhabitat	2	18.09	31	61.81	0.016
	Seed Cohort	1	3.06	30	58.75	0.222
	Microhabitat*Seed Cohort	2	0.22	28	58.53	0.948

Results from GLMM and GLM models of seed bank retention rate for (b) *E. mohavense* and *E. wallacei.*

Source: UC Davis

Table B-6: Fungicide Experiment Seed Bank Retention Model Statistics for (a) B. tournefortii and E. wallacei

Species and Approach	Predictor	Df	*F*-value	*P*-value
B. tournefortii	Microhabitat	2	2.00	0.132
GLMM (binomial)	Fungicide	1	1.83	0.169
	Microhabitat*Fungicide	2	0.15	0.858
E. wallacei	Microhabitat	2	2.97	*0.057*
GLMM (binomial)	Fungicide	1	0.08	0.781
	Microhabitat*Fungicide	2	2.19	0.113

Results from GLMM and GLM models of seed bank retention in the fungicide experiment for each species.

Source: UC Davis

Table B-7: Fungicide Experiment Seed Bank Retention Model Statistics for (b) E. mohavense

Species and Approach	Predictor	Df	Deviance	Resid. Df	Resid. Dev	*P*-value
E. mohavense	Null	-	-	57	174.94	-
GLM (quasibinomial)	Microhabitat	2	0.54	55	174.40	0.916
	Fungicide	1	0.16	54	174.24	0.821
	Microhabitat*Fungicide	2	0.02	52	174.22	0.996

Results from GLMM and GLM models of seed bank retention in the fungicide experiment for each species.

Source: UC Davis

Table B-8: Seed Staining Model Statistics

Species and Approach	Predictor	Df	Deviance	Resid. Df	Resid. Dev	*P*-value
B. tournefortii	Null	–	–	228	130.97	–
GLM (quasibinomial)	Microhabitat	2	0.28	226	130.69	0.750
	Year	1	2.09	225	128.60	0.148
	Microhabitat*Year	2	5.76	223	122.84	*0.056*
E. mohavense	Null	–	–	401	552.02	–
GLM (quasibinomial)	Microhabitat	2	2.94	399	549.08	0.260
	Year	1	7.57	398	541.51	**0.014**
	Seed Cohort	1	1.47	397	540.03	0.235
	Microhabitat*Year	2	0.35	395	539.69	0.896
	Microhabitat*Seed Cohort	2	2.84	393	536.84	0.286
	Year*Seed Cohort	1	0.97	392	535.87	0.332
	Microhabitat*Year*Seed Cohort	2	2.08	390	533.79	0.365
E. wallacei	Null	–	–	202	224.38	–
GLM (quasibinomial)	Microhabitat	2	0.39	200	223.99	0.869
	Year	1	1.14	199	222.85	0.309
	Seed Cohort	1	2.31	198	220.54	0.153
	Microhabitat*Year	2	3.18	196	217.36	*0.060*
	Microhabitat*Seed Cohort	2	0.75	194	216.61	0.242
	Year*Seed Cohort	1	11.00	193	205.61	**0.001**
	Microhabitat*Year*Seed Cohort	2	0.00	191	205.61	1.000

Results from GLM models of seed staining rate for each species

Source: UC Davis

Table B-9: Reproductive Output by Species Results from GLM Models of Reproductive Output for Each Species

Species and Approach	Predictor	Df	Deviance	Resid. Df	Resid. Dev	*P*-value
(a) *B. tournefortii* GLM (negative binomial)	Null	–	–	40	54.05	–
	Microhabitat	2	3.60	38	50.46	0.166
	Year	1	5.16	37	45.30	**0.023**
	Microhabitat*Year	2	0.39	35	44.91	0.823
(b) *E. mohavense* GLM (negative binomial)	Null	–	–	31	38.69	–
	Microhabitat	2	3.48	29	35.21	0.176
(c) *E. wallacei* GLM (negative binomial)	Null	–	–	25	31.46	–
	Microhabitat	2	2.08	23	29.39	0.354

Results from GLM models of seed staining rate for each species

Source: UC Davis

Table B-10: Community Richness and Diversity by Site

Microhabitats		**Predictor**	**Df**	**_F_-value**	**_P_-value**
(a) Shannon diversity index					
E. mohavense	Control vs. Shade	Year	1	7.11	**0.011**
		Microhabitat	1	0.99	0.327
		Year*Microhabitat	1	8.51	**0.006**
		Residuals	36	-	-
	Runoff Control vs. Runoff	Year	1	3.72	*0.062*
		Microhabitat	1	0.03	0.858
		Year*Microhabitat	1	0.50	0.485
		Residuals	36	-	-
E. wallacei	Control vs. Shade	Year	1	9.71	**0.004**
		Microhabitat	1	6.57	**0.015**
		Year*Microhabitat	1	0.61	0.439
		Residuals	36	-	-
	Runoff Control vs. Runoff	Year	1	8.57	*0.006*
		Microhabitat	1	0.15	0.699
		Year*Microhabitat	1	0.06	0.811
		Residuals	36	-	-
(b) Species richness					
E. mohavense	Control vs. Shade	Year	1	11.17	**0.002**
		Microhabitat	1	2.36	0.133
		Year*Microhabitat	1	7.84	**0.008**
		Residuals	36	-	-
	Runoff Control vs. Runoff	Year	1	1.06	0.310
		Microhabitat	1	0.22	0.643
		Year*Microhabitat	1	1.48	0.232
		Residuals	36	-	-
E. wallacei	Control vs. Shade	Year	1	63.65	**<0.001**
		Microhabitat	1	6.52	**0.015**
		Year*Microhabitat	1	0.23	0.635
		Residuals	36	-	-
		Year	1	24.39	**<0.001**

Microhabitats		Predictor	Df	*F*-value	*P*-value
	Runoff Control vs. Runoff	Microhabitat	1	0.28	0.598
		Year*Microhabitat	1	0.05	0.821
		Residuals	36	-	-

Results from ANOVA models of (a) Shannon diversity index by site, and (b) species richness by site.

Source: UC Davis

Table B-11: Native and Exotic Abundance by Site

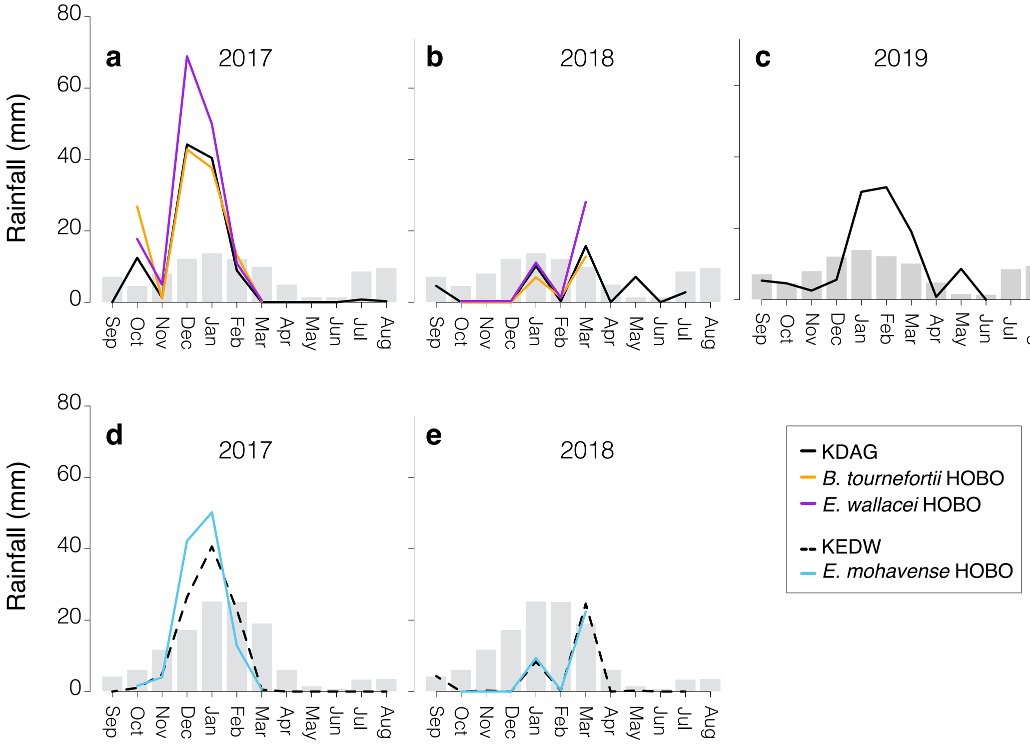
Species	Microhabitats	Predictor	Df	Deviance	Resid. Df	Resid. Dev	*P*-value
(a) Native abundance							
E. mohavense	Control vs. Shade	Null	-	-	39	51.82	-
		Year	1	3.97	38	47.85	**0.046**
		Microhabitat	1	3.03	37	44.82	*0.082*
		Year*Microhabitat	1	1.65	36	43.17	0.199
	Runoff Control vs. Runoff	Null	-	-	39	50.34	-
		Year	1	0.04	38	50.30	0.842
		Microhabitat	1	0.01	37	50.29	0.933
		Year*Microhabitat	1	7.53	36	42.76	**0.006**
E. wallacei	Control vs. Shade	Null	-	-	39	230.69	-
		Year	1	159.12	38	71.57	**<0.001**
		Microhabitat	1	20.74	37	50.83	**<0.001**
		Year*Microhabitat	1	7.93	36	42.90	**0.005**
	Runoff Control vs. Runoff	Null	-	-	39	108.42	-
		Year	1	53.02	38	55.40	**<0.001**
		Microhabitat	1	6.80	37	48.60	**0.009**
		Year*Microhabitat	1	3.19	36	45.41	*0.074*
(b) Exotic abundance							
E. mohavense	Control vs. Shade	Null	-	-	39	75.15	-
		Year	1	6.12	38	69.03	**0.013**
		Microhabitat	1	25.86	37	43.17	**<0.001**
		Year*Microhabitat	1	0.35	36	42.82	0.554
	Runoff Control vs. Runoff	Null	-	-	39	58.35	-
		Year	1	11.73	38	46.61	**0.001**
		Microhabitat	1	0.74	37	45.88	0.391
		Year*Microhabitat	1	0.61	36	45.26	0.434
E. wallacei	Control vs. Shade	Null	-	-	39	47.17	-
		Year	1	0.03	38	47.14	0.871
		Microhabitat	1	4.18	37	42.96	**0.041**
		Year*Microhabitat	1	0.01	36	42.95	0.917
		Null	-	-	39	47.02	-

Species	**Microhabitats**	**Predictor**	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev**	***P*-value**
	Runoff Control vs. Runoff	Year	1	1.08	38	45.94	0.298
		Microhabitat	1	0.16	37	45.77	0.685
		Year*Microhabitat	1	2.12	36	43.65	0.145

Results from GLM models of (a) native abundance, and (b) exotic abundance by site.

Source: UC Davis

Figure B-1: Rainfall Across Years and Sites



Rainfall recorded at permanent weather stations closest to each site (< 45 km distant in all cases). Rainfall recorded at KDAG in the 2017 - 2019 hydrologic years is shown in (a – c); this station was closest to the *B. tournefortii* and *E. wallacei* sites. Rainfall recorded at KEDW in the 2017 – 2018 hydrologic years is shown in (d, e); this station was closest to the *E. mohavense* site. Black lines show volumes recorded at KDAG or KEDW; colored lines show rainfall recorded by onsite HOBO rain gauges. Monthly rainfall averages from 1944 – 2018 are shown as gray bars for each weather station.

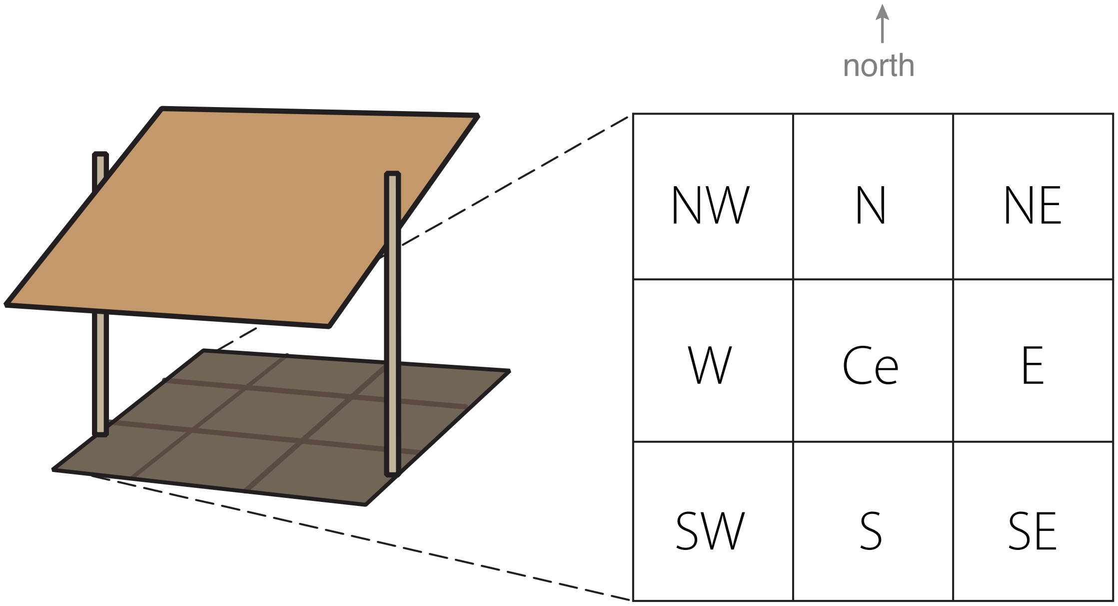
Source: UC Davis

Figure B-2: Panel Construction

Panel frames were welded from rebar, with brackets to hold plywood solar shields in place. Panel legs were pounding into the ground until the bottom edge was ~20 cm from the ground (this distance sometimes varied due to local topography). Plastic sheeting (4 mm Coroplast, corrugatedplastics.net) was affixed to plywood shields to improve rainfall runoff. Weathered shields and sheeting were replaced as needed.

Source: UC Davis, photos by Karen Tanner

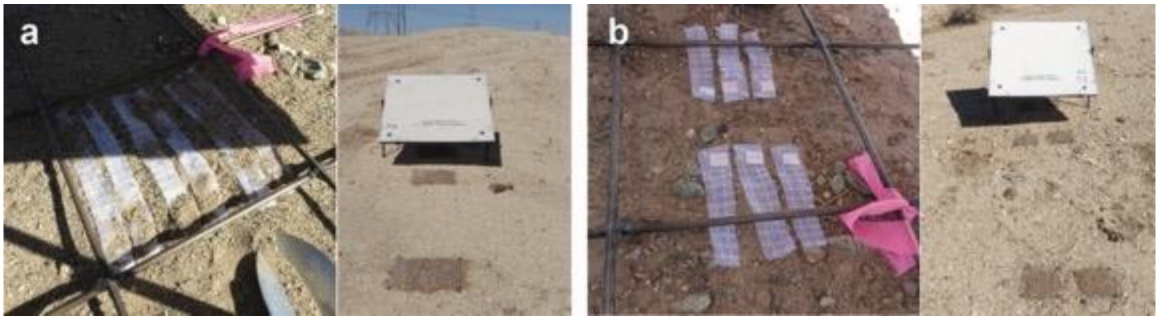
Figure B-3: Panel Light Environment Sampling Design



Measurements of photosynthetically active radiation were taken in full sun and across the shade footprint, defined by the shadow cast under panels near solar noon. This footprint was divided into 9 subplots named for the cardinal and ordinal directions; the central subplot is labeled Ce, where light should be most restricted.

Source: UC Davis

Figure B-4: Artificial Seed Bank Packets



Artificial seed bank packets were buried and secured with hardware cloth in the Shade, Runoff, and Control microhabitats at each plot. a) Arrangement of packets exposed to ambient conditions, shown here in the Shade microhabitat; b) arrangement of packets at the fungicidal treatment plots, again shown for the Shade microhabitat; the spatial separation shown permits isolation of fungicidal treatment to one 3-packet group in each microhabitat.

Photos by Karen Tanner

Figure B-5: Animal Disturbance of Artificial Seed Banks

Apparent rabbit disturbance to artificial seed bank packets. Occasionally an entire packet was found lying on the soil surface; more often, packets were partially pulled through hardware cloth covers (both scenarios are shown above).

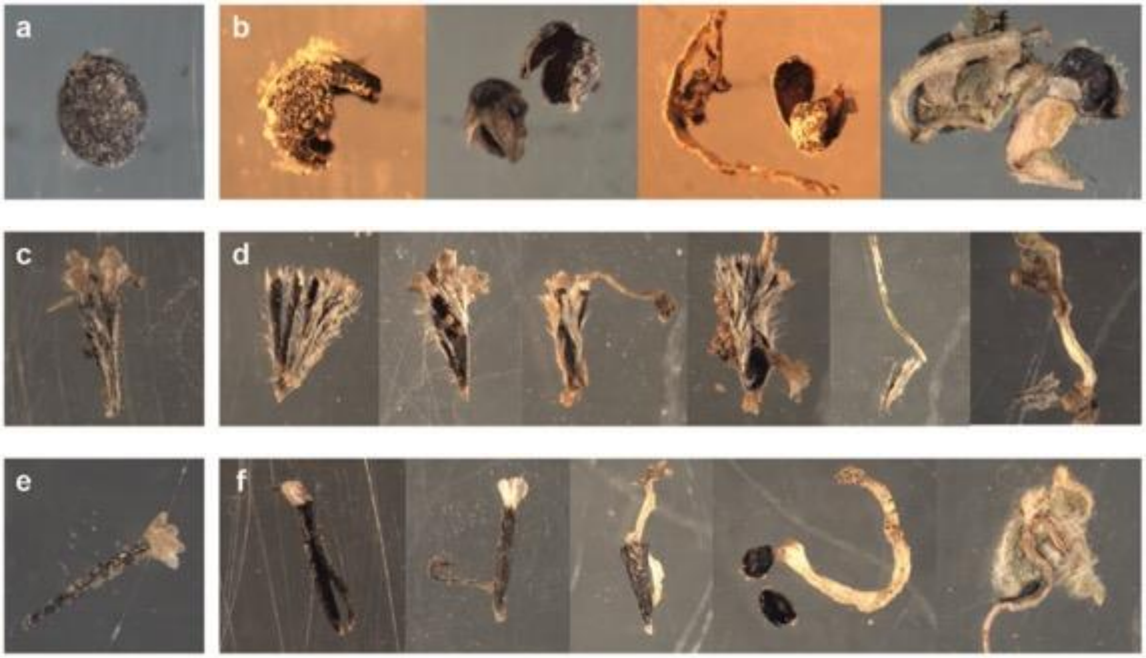
Photo by Karen Tanner

Figure B-6: Fungicide Experimental Design

A fungicidal soil drench was applied to half of the packets installed in each microhabitat (Shade, Runoff, Control); an aluminum barrier box contained the liquid until it soaked into the soil, preventing runoff and exposure of packets in adjacent untreated locations. An equivalent volume of water was applied to the untreated packets.

Source: UC Davis, photos by Karen Tanner

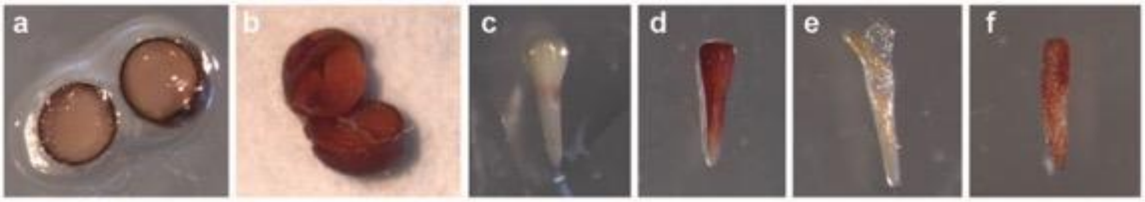
Figure B-7: Representative Images of Intact and Compromised Seed



Representative images of seed recovered from artificial seed bank packets. a) An intact, apparently dormant *B. tournefortii* seed; b) compromised *B. tournefortii* seeds; c) an intact *E. mohavense* seed; d) compromised *E. mohavense* seeds; e) an intact *E. wallacei* seed; f) compromised *E. wallacei* seeds. Compromised seeds may result from either germination or decay; in some cases shown, plant remnants are associated with the seeds, indicating successful germination.

Photos by Sophia Haji

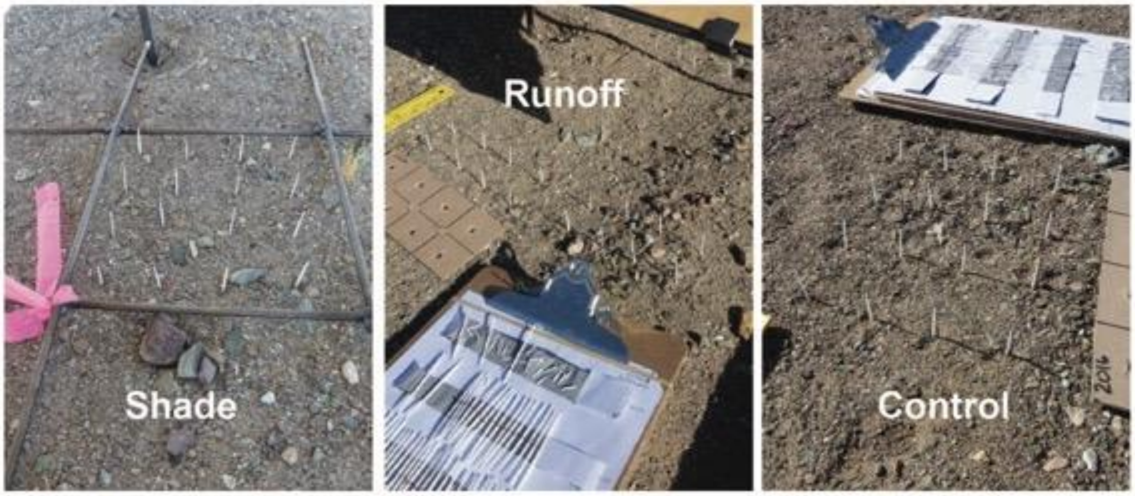
Figure B-8: Representative Images of Seed Staining



Seed embryo tissue following imbibition, cutting, and staining with 1% tetrazolium chloride solution. Dead seed embryo tissue remains white after staining, while live seed embryo tissue turns red. a) Dead *B. tournefortii;* b) live *B. tournefortii*; c) dead *E. mohavense;* d) live *E. mohavense*; e) dead *E. wallacei;* f) live *E. wallacei*.

Photos by Sophia Haji

Figure B-9: Seedling Emergence Experimental Design



Seedling toothpick arrays installed in the Shade, Runoff, and Control microhabitats.

Photos by Karen Tanner

Figure B-10: Aboveground Life Stages of Annual Plants

Aboveground life stages for *B. tournefortii* (top row), (b) *E. mohavense* (center), and (c) *E. wallacei* (bottom).

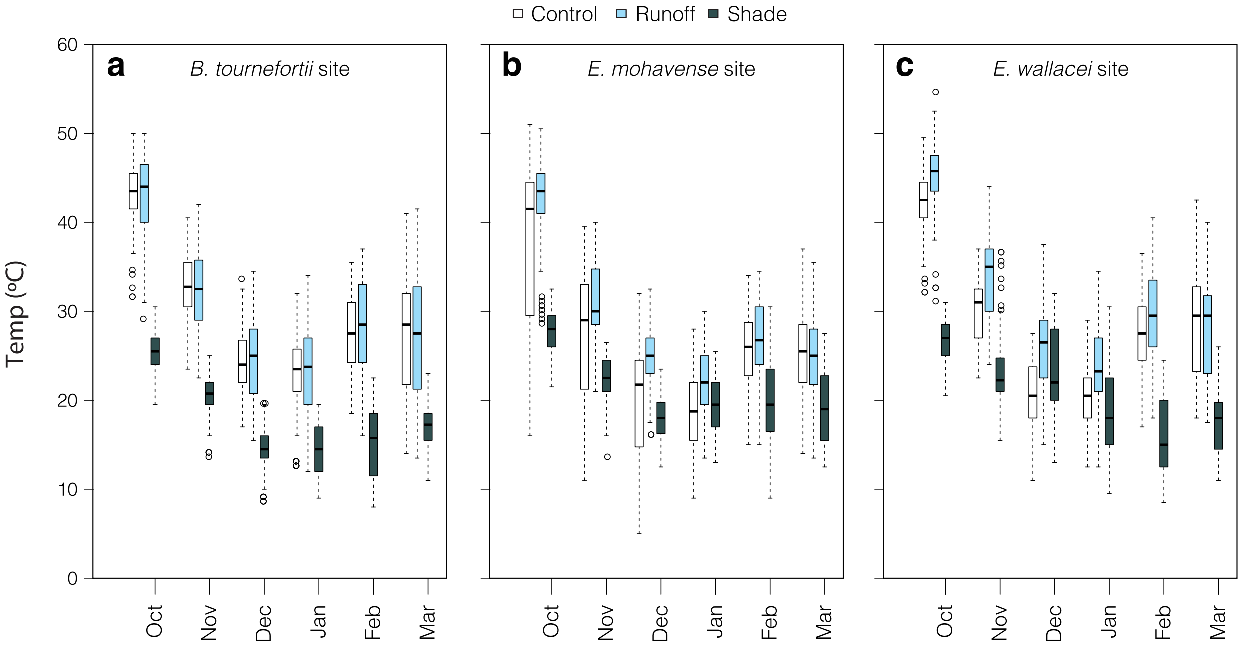
Photos by Karen Tanner

Figure B-11: Ant Disturbance of Toothpick Arrays

Toothpick arrays at the *B. tournefortii* site were frequently disturbed in 2017; toothpicks were often knocked over by ants, and seeds detached for harvest (personal observation, K. Tanner).

Photo by Karen Tanner

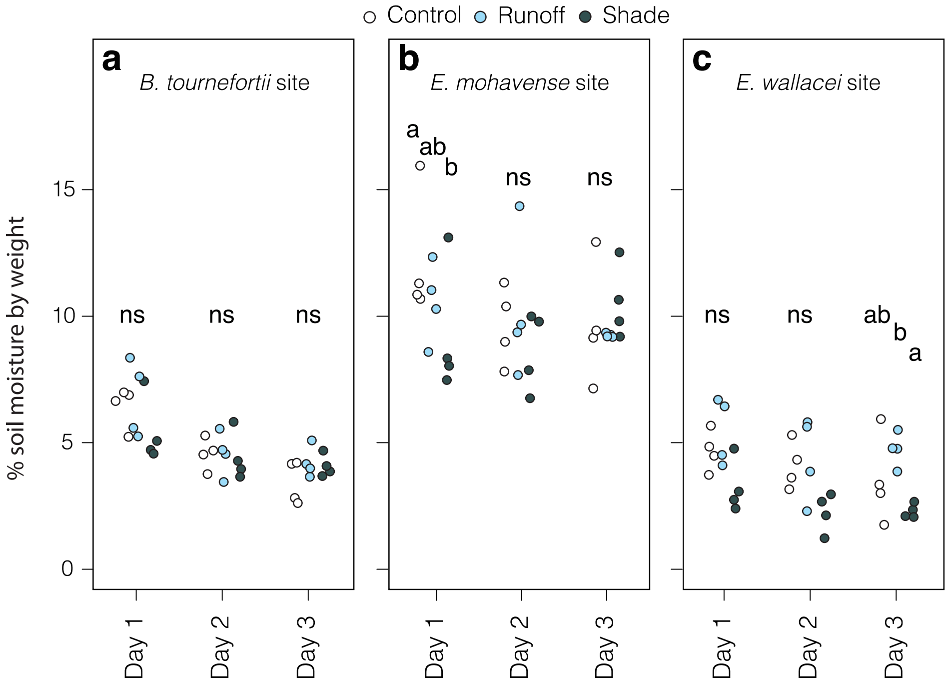
Figure B-12: Panel Soil Temperature Effects



Average soil temperature recorded by Thermochron iButtons in each microhabitat near solar noon, arranged by month. Data are shown for the 2017-2018 growing season at (a) the *B. tournefortii* site, (b) the *E. mohavense* site, and (c) the *E. wallacei* site.

Source: UC Davis

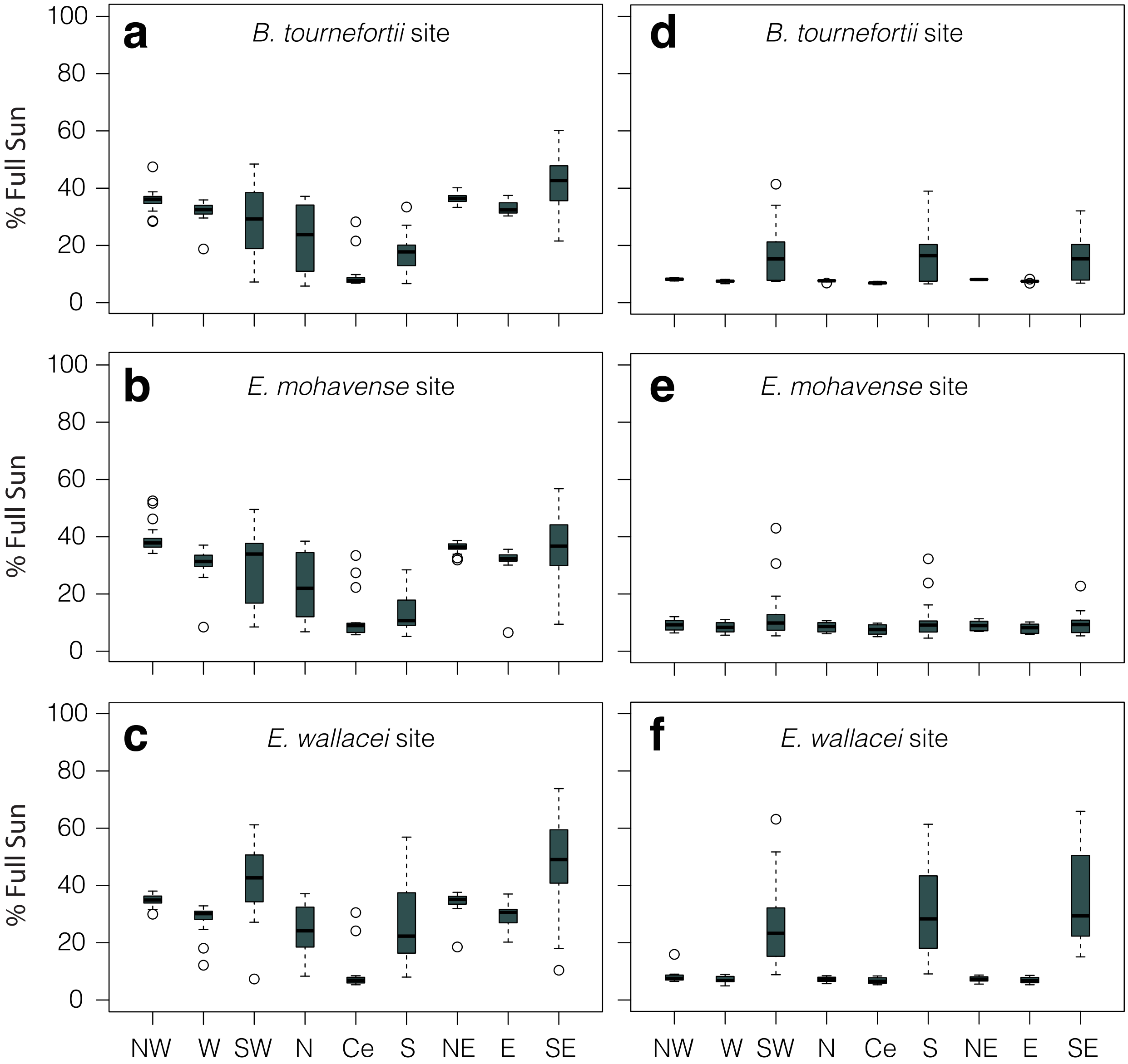
Figure B-13: Soil Moisture Effects



Results from gravimetric moisture analysis for soil cores collected over a three-day period at the (a) *B. tournefortii* site, (b) the *E. mohavense* site, and (c) the *E. wallacei* site. Letters above data points indicate significant differences.

Source: UC Davis

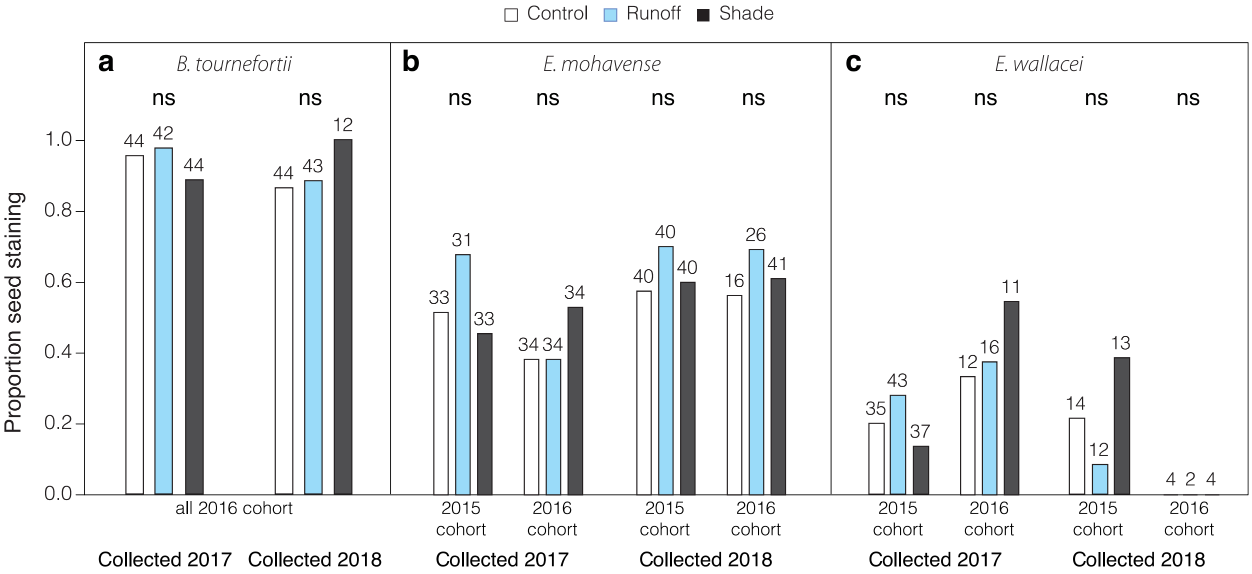
Figure B-14: Panel Light Environment Effects



Photosynthetically active radiation (PAR) receipts across subplots are expressed as a percentage of full sun in 2017 and 2018. Panels (a, b, c) show the average of measurements taken in each subplot during the morning, at solar noon, and in the afternoon at each site; panels (d, e, f) show the average of measurements taken at solar noon only. See Appendix B Figure 3 for a diagram of the subplot sampling locations (labels on the x-axis here show subplot locations named for cardinal and ordinal directions, plus "Ce" for the central subplot).

Source: UC Davis

Figure B-15: Seed Staining Rates



Seed staining rates in tetrazolium assays by species, seed cohort, microhabitat, and burial duration. Results are shown for (a) *B. tournefortii;* (b) *E. mohavense*; and (c) *E. wallacei*. Numbers above bars indicate sample sizes.

Source: UC Davis