ARTICLE

Effects of solar energy development on ants in the Mojave Desert

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Abstract

Land-use change from solar energy development may affect desert ecosystems and the soils, plants, and animals therein, yet our understanding of these interactions is nascent. With their ubiquity, criticality as ecosystem constituents, and sensitivity to environmental variation, ants may be useful study organisms for elucidating ecological effects of solar energy development in deserts. Our objectives were to disentangle the response of a desert ant community to solar energy development decisions and test the efficacy of ants as bioindicators at a solar power facility (392 MW) in the Mojave Desert, USA. We used pitfall traps to collect ants in treatments representing different solar energy development decisions, including variably intense site preparation practices: blading (i.e., bulldozing) and mowing, and establishment of undeveloped patches in solar fields, replicated across three power blocks comprising the facility and in undeveloped control sites surrounding the facility. We determined that ant abundance, species richness, Shannon Diversity Index, and functional richness were lower in bladed treatments than in all other treatments and controls. For most taxonomic and functional ant responses, we detected no difference between nonbladed treatments and controls; these results suggest that less intensive site preparation and increased spatial heterogeneity (i.e., undeveloped patches in solar fields) can reduce the negative effects of solar energy development on desert ants. However, our results indicate that ants may serve as useful bioindicators of the severity of anthropogenic disturbance from solar energy development in deserts, and indicator analysis signifies that solar energy infrastructure may negatively affect some species with high ecological value (e.g., harvester ants). Negative effects of solar energy development on ants can have significant implications for desert ecosystem function and integrity, but conservation-minded solar facility design and construction may lead to avoidance of "bottom-up" ecological ramifications of increased solar production during the renewable energy transition.

KEYWORDS
anthropogenic disturbance, ants, Formicidae, functional diversity, Ivanpah Valley, land-use change, Mojave Desert, patches, site preparation, solar energy

INTRODUCTION

Solar energy is a central component of the energy transition to net-zero emissions, but its deployment creates challenges for biodiversity conservation and management (Agha et al., 2020; Grodsky, 2021; Jager et al., 2021). Empirical information pertinent to understanding ecological effects and environmental trade-offs of solar energy development generally is lacking (Murphy-Mariscal et al., 2018). Meanwhile, there exists great potential for complex exchanges among solar energy development, ecosystems, and species, such as species–species and species–process interactions (Grodsky et al., 2017; Moore-O'Leary et al., 2017). Large, ground-mounted solar energy facilities (e.g., >10 MW) often get sited away from urban centers on conservation lands (Grodsky, 2021), as has been described for solar energy development on previously undeveloped desert scrublands near protected areas in California (Hernandez et al., 2015). Indeed, land-use change from solar energy development in the Mojave Desert, for example, may result in decreased conservation values as defined by The Nature Conservancy's Mojave Desert Ecoregional Assessment (see Parker et al., 2018).

Deserts are prioritized as recipient environments for solar energy development, in part, because they have abundant solar resources and a sociopolitically perpetuated reputation for barrenness and durability (Mulvaney, 2017). In fact, deserts are biodiversity hotspots (Durant et al., 2012) susceptible to climate change (Copeland et al., 2017) and sensitive to increased intensity and rates of anthropogenic disturbance (Lovich & Bainbridge, 1999). Whereas solar energy development in deserts may mitigate climate change for society at large, it can have negative, local effects on ecosystems and people (Grodsky & Hernandez, 2020; Nilson & Stedman, 2023). For example, site preparation for solar energy development resulting in altered soils and vegetation in the Mojave Desert negatively affected flower-visiting beetles and flies, with potential cascading effects on globally imperiled cacti populations and ecosystem services (Grodsky et al., 2021). Limited empirical elucidation of ecological interactions involving solar energy development may currently restrict conservation-minded management of rapid, solar energy buildout in deserts globally (Grodsky, 2021).

The omnipresence of invertebrates in arid lands may catalyze applications for bioindication across resource-limited and expansive desert environments; invertebrates can simultaneously respond to local environmental changes and employ advanced mobility to distribute throughout desert landscapes (Gerlach et al., 2013). One square meter of soil in the Mojave Desert may be inhabited by ~12,400 individual arthropods (Franco et al., 1979),

whereas a desert kit fox (*Vulpes macrotis arsipus*) may occupy a home range of up to 18 km^2 in the same desert ecosystem (Randel & Silvy, 2015). A study at a concentrating solar power facility in arid rangelands found significant differences in invertebrate community composition inside solar facilities relative to undeveloped controls (Jeal et al., 2019). Similarly, Grodsky et al. (2021) detected significant differences in the abundance and diversity of flower-visiting beetles and flies inside a concentrating solar power facility relative to undeveloped controls in the Mojave Desert. Taken together, these studies indicate potential for invertebrate bioindicators to detect solar facility-level environmental changes in deserts.

From Africa to Mexico and from the Middle East to Australia, ants are ubiquitous and exhibit great abundances and trophic diversities in deserts of the world (Gibb et al., 2019; Kaspari et al., 2019; Marsh, 1986; Paknia & Pfeffer, 2011; Rojas & Fragoso, 2000; Sanders & Gordon, 2003). Ants are especially useful bioindicators for conservation monitoring because they are numerous, relatively easy to sample, sensitive and quick to respond to environmental variables, critical ecosystem constituents, and functionally important at multiple trophic levels (Anderson, 1997; Del Toro et al., 2012; King et al., 1998; Majer, 1983). Further, ants have a demonstrated capacity to test the effects of land management actions and inform management-based monitoring (Grodsky et al., 2015; Underwood & Fisher, 2006). For example, ant response to fuel reduction methods in forests can inform forest-management activities in the Appalachian Mountains, USA (Campbell et al., 2019), and ant response to grazing has guided rangeland management in Australia (Anderson & Majer, 2004; Read & Anderson, 2000). Ants have been used, albeit sparingly, as bioindicators in studies of anthropogenic disturbance from renewable energy development, such as forest bioenergy (Grodsky et al., 2018) and biofuel cropping systems (Helms et al., 2020, 2021; Kim et al., 2017).

Based on available scientific literature, there is currently a lack of understanding of ant responses to anthropogenic disturbances in desert ecosystems, including solar energy development, especially in the creosote bush scrub vegetation community where ant diversity is particularly high and distinct (e.g., Bestelmeyer & Wiens, 2001; Chew, 1977). Indeed, creosote bush scrub is the primary recipient vegetation community for solar development in the Desert Southwest, USA (Grodsky & Hernandez, 2020). Whitford et al. (1999) noted a "remarkable resistance" of ant species to human-induced disturbances in desert rangelands. Similarly, disturbance from grazing had little effect on ant species richness, diversity, and composition in desert grasslands and the transitional zones from desert

grassland to shortgrass steppe in the Chihuahuan Desert (Bestelmeyer & Wiens, 2001). However, intensive site preparation for solar energy development such as blading (e.g., bulldozing vegetation and root biomass; see *Experimental design* section) causes significant soil disturbance and vegetation removal (Grodsky & Hernandez, 2020). Meanwhile, ant composition in desert grasslands, for example, may be best explained by soil texture and resultant effects of shrub density (Bestelmeyer & Wiens, 2001). Additionally, removal of extrafloral nectary-bearing desert plants (e.g., cacti) from solar energy development may negatively affect ant species that have coevolved to feed on their nectar (Pemberton, 1988).

Our objectives were to disentangle the response of a desert ant community to solar energy development decisions and test the efficacy of ants as bioindicators at a utility-scale solar facility in the Mojave Desert, USA. We hypothesized that ant abundance, richness, and diversity would be reduced by site preparation practices that disturb soils and vegetation (i.e., blading and mowing), thereby simultaneously reducing ant functional diversity. Based on the responses of nonbee insect flower visitors at the study site (see Grodsky et al., 2021), we additionally posited that undisturbed patches initially designed for rare plant conservation within the solar facility would harbor greater vegetation cover and thereby ant species richness than bladed and mowed sites. We further hypothesized that undisturbed patches within the solar facility would harbor a similar taxonomic and functional diversity of ants to that of undeveloped controls outside the solar facility.

MATERIALS AND METHODS

Study area

We conducted the study at a concentrating solar power facility (Ivanpah Solar Electric Generating System) and surrounding undeveloped desert scrubland. The facility has a gross capacity of 392 MW; it consists of 173,500 heliostats (347,000 individual mirrors) and three power towers, comprising ~1289 heliostat-covered hectares. The facility is located at the base of Clark Mountain, San Bernardino County (35°33′8.5″ N, 115°27′30.97″ W) on a bajada at elevations ranging from 855 to 1075 m in the Mojave Desert of California, United States. The facility was constructed in 2011 on a 1400-ha tract of previously undeveloped Mojave Desert creosote bush scrub on Bureau of Land Management lands in the Ivanpah Valley near the Mojave River corridor, the Mojave National Preserve, and Mesquite and Stateline Wildernesses, with joint private and U.S. Department of Energy funding. The Ivanpah Valley is geologically characterized by piedmonts, intersecting active and inactive alluvial fans and channels, and terminal playas (House et al., 2010). The climate in the Ivanpah Valley is BWh under the Köppen classification, a hot desert climate.

Experimental design

We designated each of the three power blocks (i.e., tower and associated heliostats; Figure 1) comprising the facility as replicated blocks. The area of each block is 3.66, 4.33, and 4.90 km^2, respectively. Developers sited each block along the bajada; therefore, blocks shared similar attributes to one another and surrounding undeveloped desert. We defined treatments in each block representing three unique solar energy development decisions as follows: (1) bladed, intensive site preparation via blading (bulldozing) with above- and belowground biomass removed; (2) mowed, moderate site preparation intensity via mowing, aboveground biomass retained up to a height of ~0.30 m; and (3) "halo," a pre-construction, plant-conservation decision that designated buffer zones around rare desert plants within the solar fields, which were roped off and left undisturbed (i.e., no site preparation, no heliostats), creating isolated habitat patches (average area = 22 m^2) (Figure 2). We established 15 plots in each of the three treatment units in blocks (five plots per treatment per block, treatment plots = 45, Figure 1). We designated 15 replicated control plots in undeveloped creosote bush scrub immediately surrounding the blocks that comprised the facility, creating a total of 60 plots (Figure 1); two plots in mowed treatments and one plot in controls were compromised (e.g., uprooted by an animal) and thereby excluded from the study. We situated control plots along five transects randomly selected from a set of superimposed grid points laid over a map of the facility in Geographic Information Software (QGIS, https://www.qgis.org/). Each transect contained three plots located at 250 m, 500 m, and 1 km from the boundary of the nearest block (Figure 1). We chose the upper limit of plot distances from landscape features based on the visual analysis of satellite imagery, coupled with distance measurements (taken with the "distance matrix" tool in QGIS). Our assessment indicated that plots established at a distance greater than 1 km from the facility would be confounded by other landscape features potentially affecting the distribution of ants, including Clark Mountain to the north (e.g., elevational plant community shift) and a golf course and highway to the south.
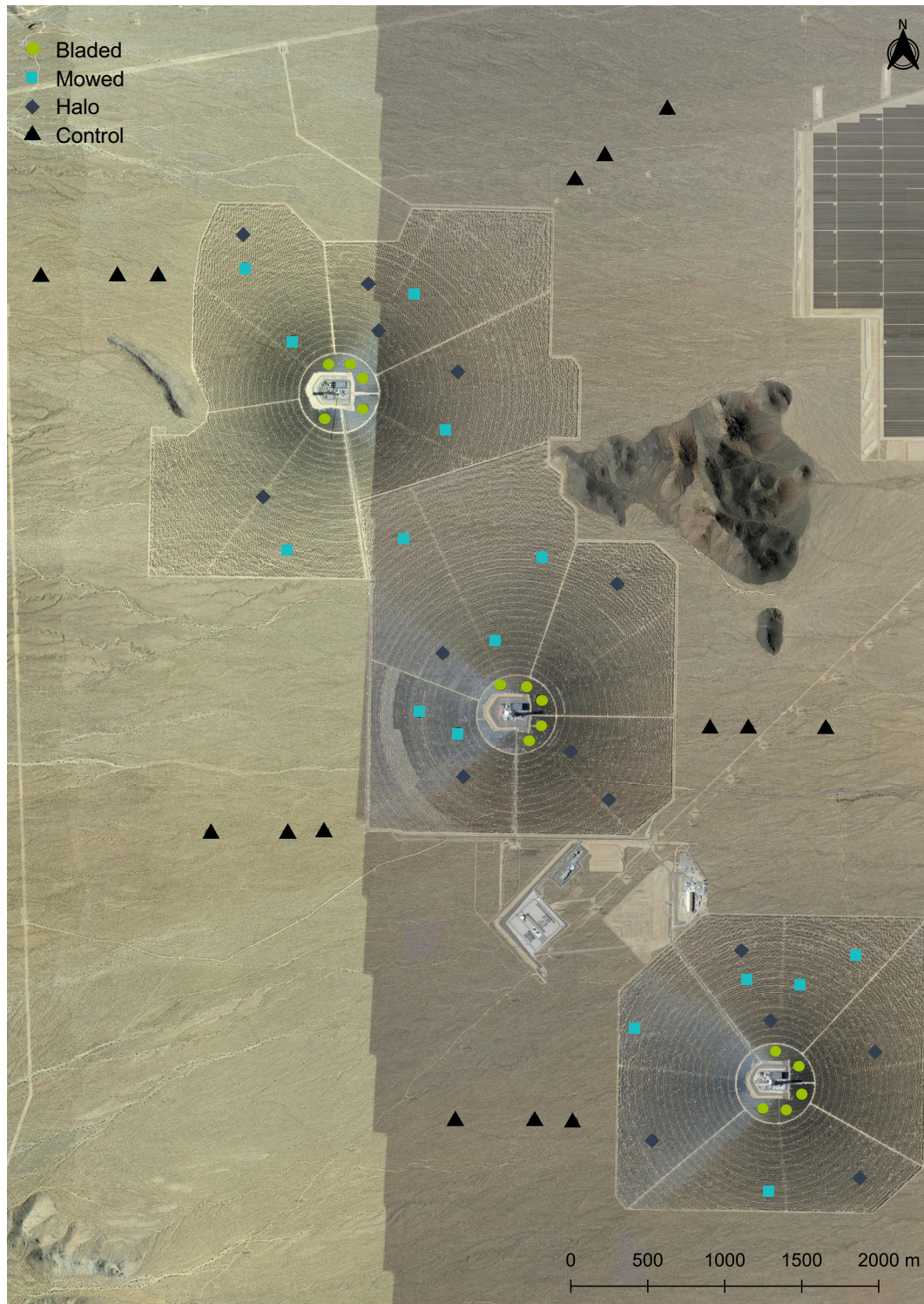
FIGURE 1 Concentrating solar power facility consisting of three, concentrating solar power blocks (i.e., tower and associated heliostats = replicated block) in the Ivanpah Valley, Mojave Desert, California, USA. Different shapes and colors show the spatial orientation of 60 ant sampling plots in treatments and controls (see also *Materials and methods*). Specific geographic location is not provided for security purposes.

Ant sampling, identification, and measurements

We used pitfall traps to sample ants at plots in both the facility and control sites during a single, continuous sampling period from April 5 to May 5, 2018, encompassing a large portion of peak spring growing season for the year (Grodsky, 2023). We sampled ants seven years after the construction of the facility. Pitfall trapping has been deemed a reliable approach for sampling ants in a variety of
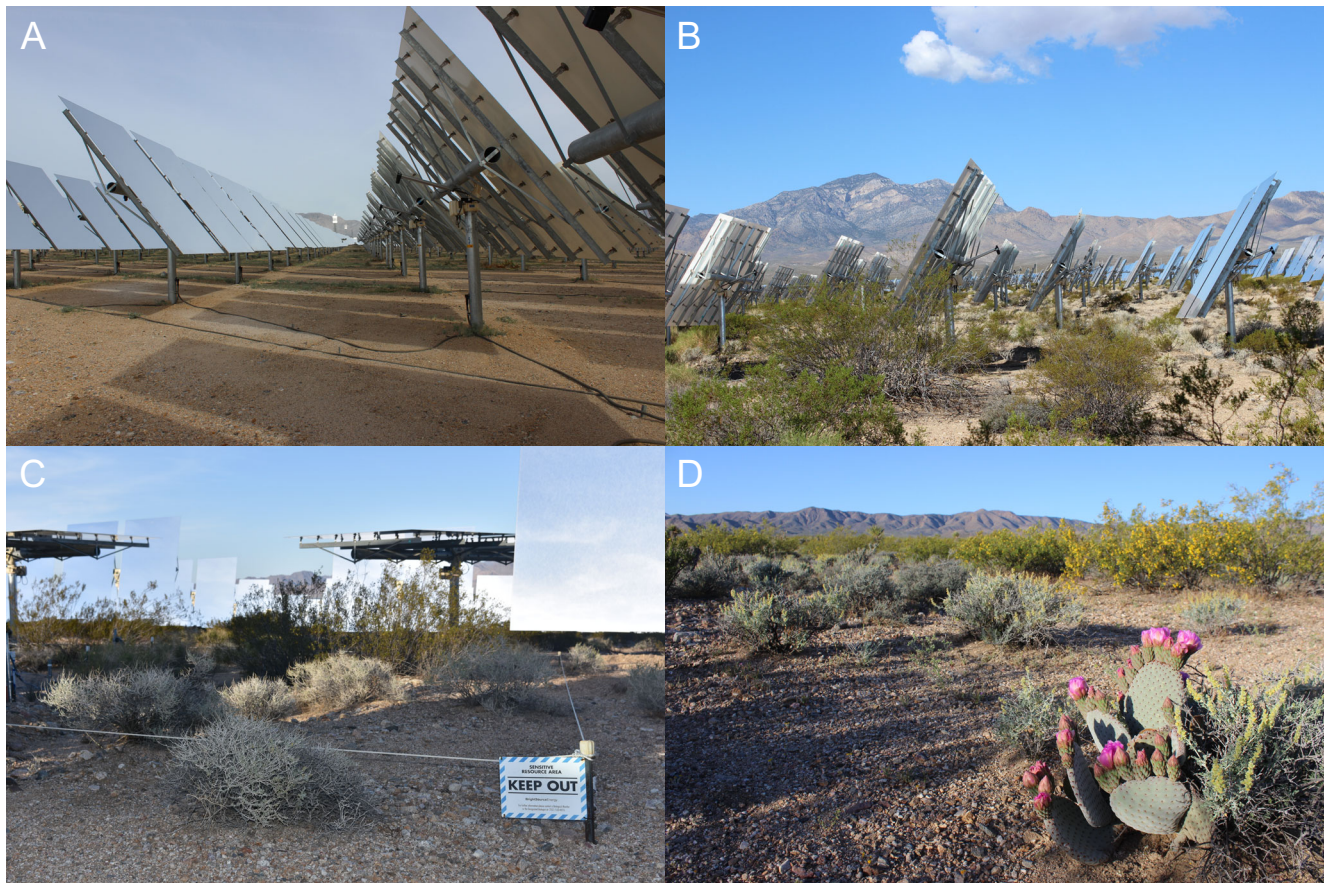
FIGURE 2 Photographs of solar energy development decision treatments: (A) bladed (bulldozed), (B) mowed, (C) "halo"; small (average area ~22 m^2) habitat patches within solar fields, and (D) control; undeveloped creosote scrub shrub outside of the solar power facility. Photo credit: Steven M. Grodsky.

environments (Agosti & Alonso, 2000; Roeder & Harmon-Threatt, 2022; Schultheiss et al., 2022; Sheikh et al., 2018). To avoid biases from any colony proximity to pitfall traps, we established pitfall traps >50 m from visible ant mounds in the surrounding area. Pitfall traps consisted of 0.47-L plastic containers with a diameter of ~8.5 cm filled with equal amounts of propylene glycol and water plus a drop of liquid dish soap to reduce surface tension (Spence & Niemelä, 1994). We placed the lip of each container at or slightly below ground level (e.g., Ausden, 1996). We covered each pitfall trap with a 5-cm^2 roof constructed from corrugated plastic and staked 5 cm into the ground with 14-gauge baling wire to prevent rain from flooding the pitfalls and to minimize evaporation of the liquid within the pitfalls.

Our sampling plots consisted of four pitfall traps situated at each corner (cardinal directions) of a 2 × 2-m^2 centered on each plot. At the conclusion of the sampling period, we strained and combined ants from each pitfall trap and stored specimens in 60-mL (Nalgene) bottles filled with 70% ethanol and labeled with trap locality data. We identified ants using taxonomic keys and checklists from the region (Creighton, 1950; Ikeda & des Lauriers, 2011).

We submitted voucher specimens of identified ant species to the collection at the USDA Northern Great Plains Agricultural Research Laboratory.

Following identification of ant species, we measured seven morphological traits for a subset of ant specimens from each species. We selected specimens from multiple plots (36 of 57 plots) and from each treatment (when possible); for species with low abundances, we measured all available individuals. We measured the following traits: Weber's length (WL), head width (HW), mandible length (ML), femur length (FL), scape length (SL), pronotum width (PW), and maximum eye width (MEW). Each of these traits is suggested to variably affect ant performance and is commonly used for calculating functional diversity indices (Table 1; Kaspari & Weiser, 1999; Silva & Brandão, 2010; Weiser & Kaspari, 2006). Following guidelines from the Global Ants Database (globalants.org; Parr et al., 2017), we measured traits for 6 specimens for monomorphic species and 10 specimens for polymorphic species; one exception to this procedure was *Camponotus fragilis* because we only collected eight individuals of the species. For the four dimorphic

TABLE 1 Morphological traits of ants that are hypothesized to affect ant performance.

cTrait	Acronym	Relation to ant performance
Weber's length	WL	Diagonal measurement across the length of the mesosoma. Body size indicator linked with many other life history and physiological traits.
Head width	HW	Restricts movement though gaps and limits the no. mandibular muscles.
Mandible length	ML	Linked to diet with longer mandibles being correlated with more predatory behavior.
Femur length	FL	Hind leg measurement linked to running speed and possibly thermoregulation.
Scape length	SL	Linked to sensory ability with length associated with ability to follow pheremone trails.
Pronotum width	PW	Limits movement through gaps and volume of muscle for load bearing.
Maximum eye width	MEW	Determines navigation ability, food searching ability, and activity periods. May be associated with predatory behavior.

Note: See Weiser and Kaspari (2006), Silva and Brandão (2010), Parr et al. (2017), and Wong et al. (2020) for full trait descriptions and their importance.

Pheidole species, we measured six minor workers but did not measure major workers because they comprised <1% of collected individuals from the genus.

Prior to the analysis, we applied a body-size correction to six of the morphological traits (i.e., HW, ML, FL, SL, PW, and MEW) by dividing each trait value by the individual's WL—an often-used proxy for ant body size (Wong et al., 2020). We averaged traits per species—standardized traits to have a mean of zero and unit variance—and then used these values to compute four functional diversity indices (in the R package "FD") (Laliberté et al., 2014; Laliberté & Legendre, 2010; Villéger et al., 2008). Functional diversity can be useful for understanding surface-active insect community assemblages in disturbed environments (Perry et al., 2020). We calculated the following functional diversity indices: (1) functional richness (FRic), the volume of functional space occupied by a community; (2) functional evenness (FEve), the regularity of the distribution of abundance in functional space; (3) functional divergence (FDiv), the divergence in the distribution of abundance in functional space; and (4) functional dispersion (FDis), the mean distance in multidimensional trait space of individual species to the centroid of all species. We could not calculate functional diversity indices for four bladed plots because each plot had less than three species; the software package we used requires three or more species to compute functional diversity indices. Additionally, we calculated community-weighted means (CWMs) for WL and each size-corrected trait.

Statistical analyses

We evaluated whether ant abundance, species richness, Shannon Diversity Index (i.e., the exponential of Shannon entropy), functional diversity indices, and CWMs for each morphological trait differed across treatments using generalized linear models (GLMs). We included treatment and block as fixed effects in the GLMs. We used a negative binomial distribution for ant abundance data that were overdispersed, a Poisson distribution for ant species richness, and a Gaussian distribution for ant diversity, functional diversity, and CWMs of morphological traits. We performed pairwise contrasts among treatments with Tukey *p*-value adjustment (using the "emmeans" package) (Lenth, 2020).

We tested whether ant community composition differed among treatments by conducting a nonparametric multivariate analysis of variance (i.e., PERMANOVA) with a Bray–Curtis index of similarity and 1000 permutations; PERMANOVA tests the null hypotheses of no difference among groups, using random permutations of the data with a pseudo *F*-statistic (Anderson, 2001). We visualized significant relationships with nonmetric multidimensional scaling ordinations; however, we used three dimensions ($k = 3$) to keep stress levels below 0.2. We performed pairwise contrasts among treatments (in the "pairwiseAdonis" package) (Arbizu, 2017). We calculated multivariate dispersion, a metric of beta diversity (Anderson et al., 2006), using group centroids and analyzed the treatment effects on multivariate dispersion with ANOVA (in the "vegan" package) (Oksanen et al., 2019).

We used indicator analysis (Dufrêne & Legendre, 1997) to identify whether specific ant species were associated with treatments. We determined statistical significance based on the multipatt function (in the "indicspecies" package), with 999 permutations (De Cáceres & Legendre, 2009). We ran all analyses in R, version 4.0.1, and set α = 0.05.

RESULTS

We collected 5885 individual ants representing 20 different ant species in the plots. Blading negatively affected the ant

community relative to other solar energy development decisions and undeveloped controls; we documented greater ant abundance ($\chi^2 = 35.99$, df = 3, $p < 0.001$), species richness ($\chi^2 = 34.89$, df = 3, $p < 0.001$), and Shannon Diversity Index ($\chi^2 = 43.11$, df = 3, $p < 0.001$) in mowed, halo, and control plots than in bladed plots. We found that ant abundance was ca. twofold greater in mowed and halo plots compared with control plots, and ant abundance in nonbladed treatment and control plots was greater than that in bladed plots (Figure 3A). We determined that ant species richness was similar in nonbladed treatments and controls, with plots supporting ca. 7.5 species—an approximate 2.3-fold increase compared with the average 3.3 ant species in bladed plots (Figure 3B). We determined differences in Shannon Diversity Index that paralleled those observed for ant species richness, with halo and control plots being statistically similar and ca. twofold greater Shannon values from nonbladed and control plots than from bladed plots (Figure 3C). Diversity in mowed plots, however, was similar to halo plots, but differed from control plots. We observed differences in ant community composition among treatments (Figure 4; pseudo $F_{3,53} = 2.51$, $p < 0.001$). Ant species composition differed in bladed plots relative to mowed, halo, and control plots (Appendix S1: Table S1). However, multivariate dispersion was not different across treatments ($F = 2.66$, df = 3, $p = 0.058$).

We found a core set of nine ant species present in each treatment and controls, including *Aphaenogaster megommata*, *Dorymyrmex insanus*, *Forelius mccooki*, *Myrmecocystus mexicanus*, *Pheidole gilvescens*, *Pheidole hyatti*, *Pheidole xerophila*, *Pogonomyrmex rugosus*, and

Solenopsis xyloni (Table 2). We determined that only two species were unique to a particular treatment: *Pheidole rugulosa* in bladed plots and *Monomorium ergatogyna* in halo plots. Based on indicator analyses, we determined that five species were statistically indicative of nonbladed treatments: *Crematogaster depilis*, *Dorymyrmex flavus*, *Forelius mccooki*, *Forelius pruinosus*, and *Pheidole xerophila* (Table 3). Only one species, *Pheidole hyatti*, was
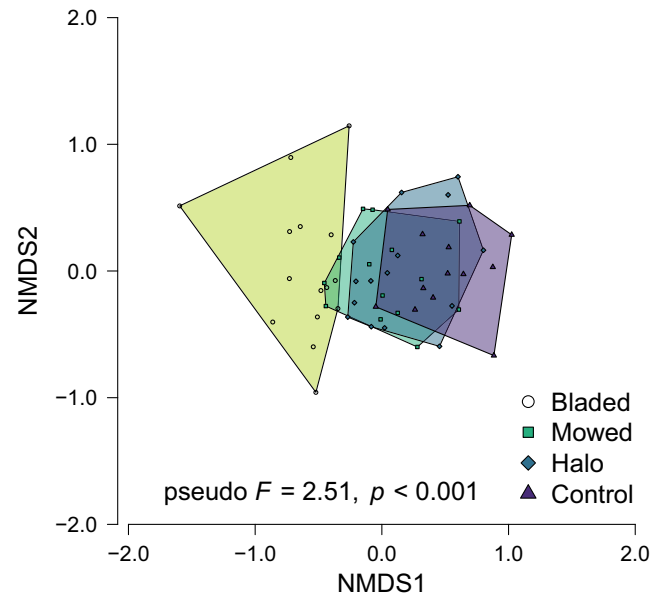
FIGURE 4 Nonmetric multidimensional scaling (NMDS) ordination of ant communities grouped in convex hulls for solar energy development decision treatments, Mojave Desert, USA. Points represent pooled data per plot.
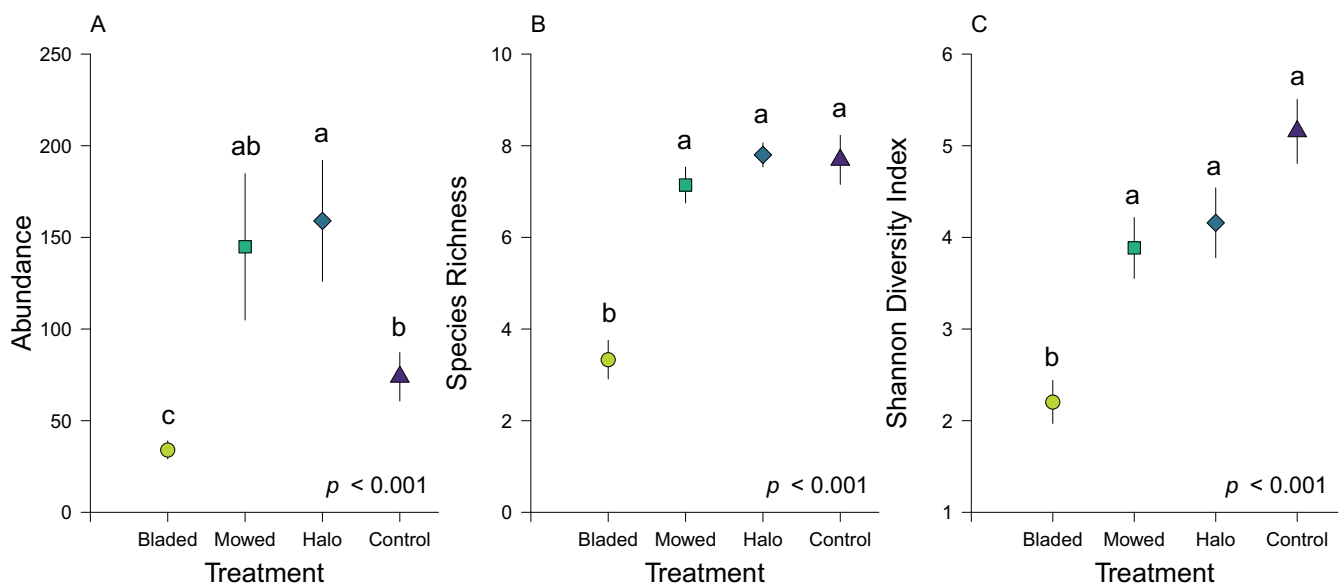
FIGURE 3 Abundance, species richness, and Shannon Diversity Index for ants in solar energy development decision treatments, Mojave Desert, USA. All points are means (±SE). Different letters indicate significant differences between treatments ($p < 0.05$).

TABLE 2 Mean pitfall trap captures per plot of ant species in solar energy development decision treatments, Mojave Desert, USA.

Species	Functional group	Foraging medium	Bladed	Mowed	Halo	Control
Aphaenogaster megommata	G	Soil	0.07	0.07	0.20	0.08
Camponotus fragilis	G	Soil	...	0.29	...	0.31
Crematogaster depilis	G	Plant/soil	...	7.29	9.07	13.92
Dorymyrmex flavus	HT	Plant	...	2.36	1.67	0.62
Dorymyrmex insanus	HT	Plant	0.80	4.29	2.60	2.15
Forelius mccooki	HT	Plant	1.80	11.21	10.47	7.92
Forelius pruinosus	HT	Plant	...	2.86	3.93	6.23
Monomorium ergatogyna	G	Plant/soil	...	...	0.53	...
Myrmecocystus flaviceps	LF	Plant	...	1.93	0.80	0.38
Myrmecocystus mexicanus	G	Plant	0.27	2.50	49.80	4.08
Novomessor cockerelli	G	Soil	...	1.14	1.40	4.46
Pheidole gilvescens	SH	Soil	0.6	5.57	0.67	2.23
Pheidole hyatti	SH	Soil	3.2	2.93	15.87	1.08
Pheidole rugulosa	SH	Soil	3.07	...	...	...
Pheidole xerophila	SH	Soil	8.27	46.50	30.87	20.62
Pogonomyrmex imberbiculus	SH	Soil	...	...	0.73	0.08
Pogonomyrmex rugosus	SH	Soil	0.07	1.14	4.53	2.23
Solenopsis xyloni	G	Plant/soil	13.00	17.00	12.27	7.08
Temnothorax neomexicanus	G	Soil	...	...	0.20	0.46
Veromessor pergandei	SH	Soil	2.93	37.79	13.40	...

Note: Ellipses indicate zero captures. Functional groups are denoted as follows: G, generalist; HT, hemipteran tender; LF, liquid feeder; SH, seed harvester (Ikeda & des Lauriers, 2011; Nash et al., 2004).

TABLE 3 Indicator analysis of ant species in solar energy development decision treatments, Mojave Desert, USA.

Species	Bladed	Mowed	Halo	Control	Specificity	Fidelity	IndVal	*p*
Crematogaster depilis	...	*	*	*	1.0000	0.6905	0.831	0.01
Dorymyrmex flavus	...	*	*	*	1.0000	0.3810	0.617	0.03
Forelius mccooki	...	*	*	*	0.9427	0.7857	0.861	0.01
Forelius pruinosus	...	*	*	*	1.0000	0.5714	0.756	0.01
Myrmecocystus mexicanus	...	...	*	*	0.9512	0.8571	0.903	0.01
Novomessor cockerelli	...	...	...	*	0.6370	0.5385	0.586	0.04
Pheidole hyatti	*	*	*	...	0.9533	0.6364	0.779	0.01
Pheidole xerophila	...	*	*	*	0.9222	0.9048	0.913	0.01

Note: An asterisk (*) indicates a taxon that was significantly associated with a particular treatment, whereas (...) indicates no significant association. Specificity is the sample estimate of the probability that the surveyed site belongs to the target site group given that the species has been found. Fidelity is the sample estimate of the probability of finding an ant species in sites belonging to the site group. Indicator analysis results are shown as the IndVal index test statistic and *p* value from permutational tests.

indicative of noncontrol plots, whereas *Myrmecocystus mexicanus* and *Novomessor cockerelli* were indicative of halo and control plots or just control plots, respectively (Table 3).

We found that bladed, mowed, and halo treatments all had lower FRic than control plots; however, the levels of difference varied (Figure 5A; $\chi^2 = 38.31$, df = 3, $p < 0.001$). Specifically, FRic in control plots was 3.3-fold greater than bladed plots and 1.4-fold greater than mowed and halo plots (Figure 5A). FEve and FDiv values—metrics that describe the shape of the distribution of abundances in functional space—were not different across
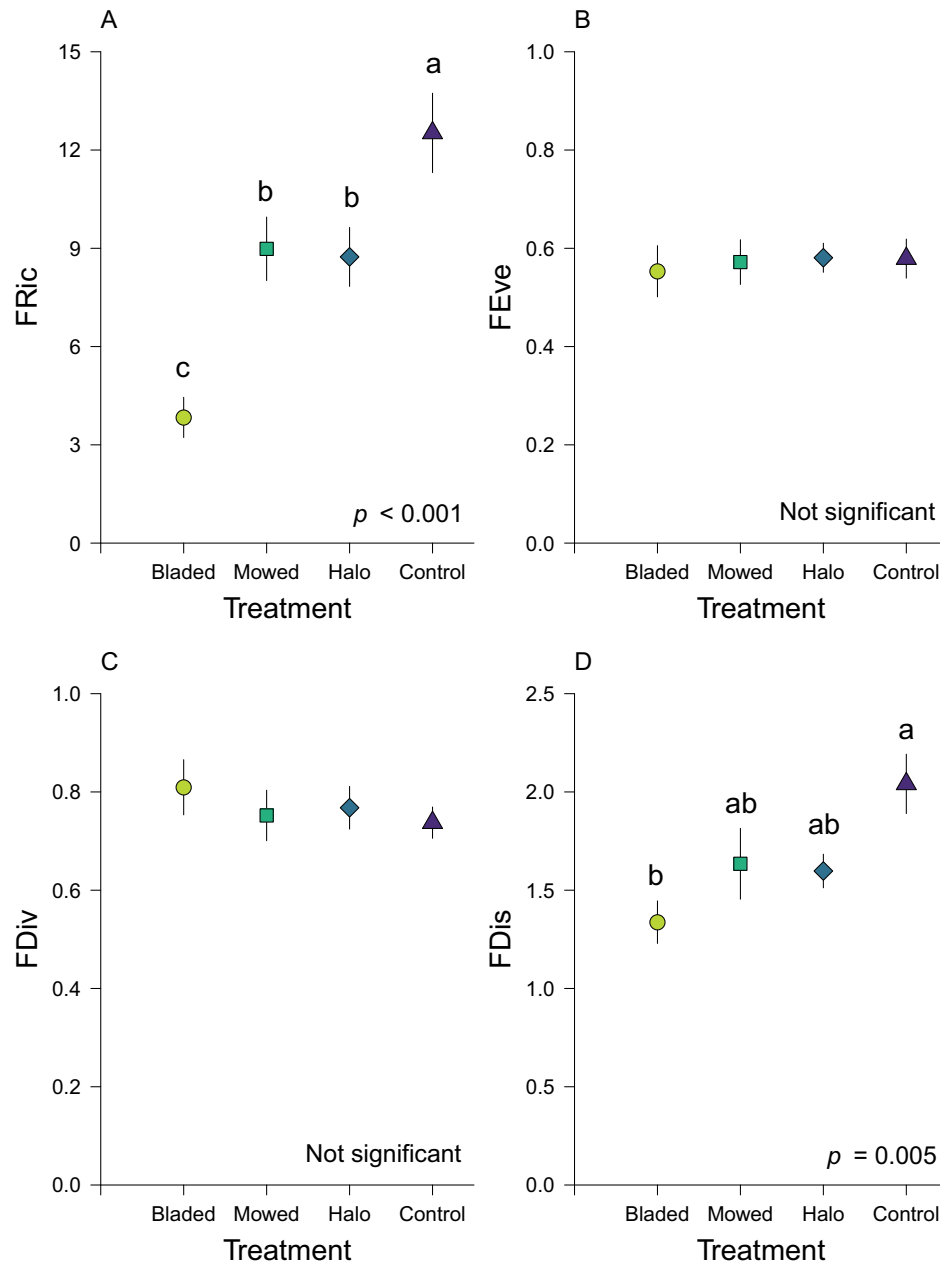
FIGURE 5 Functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) of ants in solar energy development decision treatments, Mojave Desert, USA. All points are means (±SE). Different letters indicate significant differences between treatments ($p < 0.05$).

treatments (Figure 5B,C; FEve: $\chi^2 = 0.38$, df = 3, $p = 0.944$; FDiv: $\chi^2 = 1.13$, df = 3, $p = 0.769$). In contrast, FDis was significantly different across treatments ($\chi^2 = 12.94$, df = 3, $p = 0.005$), but the only real dissimilarity occurred between bladed and control plots (Figure 5D). CWMs for all morphological traits except FL ($\chi^2 = 8.64$, df = 3, $p = 0.035$) were similar across treatments (Appendix S1: Table S2). FL was significantly greater in halo plots than in bladed, mowed, and control plots due to the high abundance of *Myrmecocystus mexicanus*, the species with the longest relative leg length.

DISCUSSION

Taxonomic and functional responses of the desert ant community to solar energy development decisions at the facility seven years post-construction suggest that blading (i.e., bulldozing) can lead to long-term, negative effects on ants in deserts. However, ant FRic varied across a gradient of solar energy development decision intensities, suggesting that desert ants may adapt to local conditions following some site preparation practices at solar facilities. Ant community composition in treatments

relative to controls demonstrates that less intense solar energy development decisions like mowing and conservation measures like preservation of habitat patches in solar fields show early promise to conserve desert ants after construction of solar facilities. Similarly, species indicator analyses often indicated high ant-species site specificity and fidelity among nonbladed treatments and controls alike, pointing toward bioindication that transcends solar facility boundaries and rejection of our hypothesis that mowing would negatively affect the ant community alongside blading.

Solar energy development decisions created variably severe disturbances to which desert ants responded with some apparent flexibility book-ended by definite thresholds. While blading is universally bad for ants and undeveloped desert may be the most ant-species rich and functionally diverse based on our results, ants largely were unaffected by intermediate disturbances such as mowing and undeveloped patches in solar fields. Contrastingly, nonbee insect flower visitors were more abundant and speciose in surrounding, undeveloped desert relative to all treatments at the same facility (Grodsky et al., 2021). Jeal et al. (2019) found no difference in ant abundance along a disturbance gradient (power block vs. solar field) in a concentrating solar power trough facility and surrounding, grazed arid rangeland in South Africa; however, they did not assess species-specific ant responses to variable site preparation intensities and conservation measures.

Response of ants to solar energy development decisions likely was driven by physical perturbations to soils and vegetation during site preparation and the resultant habitat conditions. Blading at the facility led to compacted and eroded soils and little vegetation cover, except for invasive grasses (e.g., *Schismus* spp.) (Grodsky & Hernandez, 2020), leaving potentially unsuitable conditions for the many desert ants that nest and forage in soil (Ikeda & des Lauriers, 2011; Nash et al., 2004). Indeed, soil texture is known to affect the distribution of desert ant species (Johnson, 1992), and soil compaction has been shown to negatively affect granivorous ants in an arid ecosystem of central Mexico (Rivas-Arancibia et al., 2014). Although cacti and Mojave yucca (*Yucca schidigera*) remained absent from mowed areas in the facility seven years post-construction, creosote (*Larrea tridentata*) and white bursage (*Amrbosia dumosa*) recovered to reach covers similar to those in controls (Grodsky & Hernandez, 2020). Desert harvester ants nest near and forage on creosote bush (*Pogonomyrmex rugosus*; Rissing, 1988), while several other desert ant species found in our study are known to associate with it (Bestelmeyer & Wiens, 2001; Rango, 2005). White bursage also is a common food of desert seed-harvester ants (e.g., *Veromessor pergandei*; Rissing, 1982).

Desert ant response to small, undeveloped patches in solar fields sheds light on the prospect of integrating concepts of landscape ecology such as spatial heterogeneity (e.g., patches, corridors) into the design of sustainable solar facilities globally. Ant abundance was greater in undeveloped patches than in controls, suggesting that halos may have served as resource islands for ants within otherwise more heavily disturbed areas of the solar field. As the only significant functional trait, FL was greater in halos than other treatments and controls, which may indicate that ants with enhanced locomotion (i.e., longer legs) may have more readily accessed halos typically separated by large tracks of disturbed areas (e.g., mowed, presence of heliostats) in solar fields. Soils and vegetation, including cacti and Mojave yucca, remained unaltered in halos (Grodsky & Hernandez, 2020), which may have provided suitable nesting and foraging conditions for desert ants. Since small, undeveloped patches appeared to support desert ants at levels similar to expansive controls, one might hypothesize that even larger patches in solar fields may promote further benefits to ants. However, ant response to patch size has been shown to vary in some ecosystems like forests (e.g., Mitchell et al., 2002). Apart from larger patches in solar facilities warranting further investigation, recent research suggests that the connectivity of patches can also influence ant-mediated seed dispersal (Burt et al., 2022).

Ants may prove to be effective indicators of severity of disturbance from solar energy development decisions more so than solar development itself, with a few exceptions. For example, several ant species were indicative of nonbladed treatments in the facility and controls outside of it; this suggests a break in ant response between blading and other less intensive site preparation practices and undeveloped areas. However, two desert ant species indicated possible effects of solar energy infrastructure on ant-species distributions. *Myrmecocystus mexicanus* was an indicator species for only halo treatments and controls with reduced shading from heliostats and no shade from heliostats, respectively; Chew (1995) determined that *M. mexicanus* nests that were experimentally shaded either died or moved nest entrances away from shade. While the species is known for nectar-storing repletes, *M. mexicanus* is a generalist and a nocturnal predator of insects (Morgan, 1991). *Novomessor cockerelli*, a species only indicative of undisturbed desert, is a diurnal forager of seeds and a nocturnal predator of insects (Whitford & Ettershank, 1975). The response of these nocturnal, desert predators may point toward possible interactive effects of solar energy development on insect prey availability, which tends to increase at night, and/or relationships with temperature and saturation deficits

that drive nocturnal foraging behavior in these desert ant species (Whitford, 1978). Further, *M. mexicanus* and *N. cockerelli* are two of the three largest ant species in the desert scrub community (Chew, 1987), potentially suggesting that solar energy development affects larger desert ants more than smaller desert ants.

The negative effects of solar energy development decisions on desert ants may alter desert ecosystem function and integrity. For example, the Mojave Desert of California is home to large populations of diverse species of seed-eating (harvester) ants (Bernstein, 1974); harvester ants can significantly influence community structure and ecosystem functioning via their nest densities, nest longevities, and seed harvesting and handling (MacMahon et al., 2000). Differential seed predation, seed dispersal, and competition with other granivores combine to shape the influence of harvester ants on desert ecosystems (summarized in MacMahon et al., 2000). Further, harvester ants are ecosystem engineers that may affect the distribution of desert plants via seed dispersal and nutrient cycling (Wagner & Jones, 2006). Many desert ant species maintain mutualistic relationships with desert plants bearing extrafloral nectaries, including endemic cacti species globally threatened with extinction (Aranda-Rickert et al., 2014; Goettsch et al., 2015). Deserts are inhabited by a diversity of myrmecophagous animals, spanning desert birds with a high proportion of ants in their diet relative to temperate environments (Dean & Williams, 2004) to ant-specialist horned lizards (*Phrynosoma*) (Whitford & Bryant, 1979). Additionally, ant nests host a diversity of myrmecophiles (e.g., socially parasitic invaders) (summarized in Hölldobler & Kwapich, 2022).

The results of this study are relevant to both concentrating solar power and photovoltaic (PV) solar development because each technology drives similar land-use change and employs the same site preparation practices (Grodsky et al., 2021). In fact, concentrating solar power facilities are more spatially heterogenous than PV facilities due to the physics of light refraction from mirrors (i.e., decreasing heliostat density with increasing distance from power towers). Developers of the facility also employed habitat patches, whereas this practice is uncommon in PV facilities (Grodsky & Hernandez, 2020). Therefore, the effects of more uniform solar arrays in PV facilities without patches could have even greater effects on some ants (e.g., shade-intolerant species), especially when considering interactions with intensive site preparations practices. However, we are unaware of any studies of ant response to PV solar energy development in any ecosystem to date. Solar energy development is constantly evolving in the Desert Southwest, for example, where utility-scale solar has the longest history in

the United States. Based on our results, less intensive site preparation practices can reduce the adverse effects of solar energy development on desert ants; however, adaptive approaches such as mowing of vegetation to greater remnant heights and "drive and crush" (where vegetation is run over rather than cut) remained to be tested for any taxa.

CONCLUSION

Variation in solar energy development decisions, coupled with species-level ant identification and an array of statistical analyses, have allowed us to generate novel and foundational insights into ant response to solar energy development in the Mojave Desert. Less intensive solar energy development decisions may reduce the negative effects of solar energy development on desert ants, but solar infrastructure may still negatively affect some ant species with high ecological value. Our results suggest that ants may serve as useful bioindicators of the severity of anthropogenic disturbance from solar energy development in deserts, potentially pointing toward effective bioindication with ants at solar facilities in other ecosystems. Continual, active engagement of researchers and solar developers to inform adaptive management for sustainable solar energy development is pivotal to inform biodiversity conservation during the energy transition (Grodsky, 2021).

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Grodsky, 2023) are available from USGS ScienceBase: https://doi.org/10.5066/P90NJ687.

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REFERENCES

Agha, M., J. E. Lovich, J. R. Ennen, and B. D. Todd. 2020. "Wind, Sun and Wildlife: Do Wind and Solar Energy Development 'Short-Circuit' Conservation in the Western United States?" *Environmental Research Letters* 15: 075004.

Agosti, D., and L. E. Alonso. 2000. "The ALL Protocol – A Standard Protocol for the Collection of Ground-Dwelling Ants." In *Ants – Standard Methods for Measuring and Monitoring Biodiversity*. Biological Diversity Handbook Series, edited by D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, 204–6. Washington, DC: Smithsonian Institution Press.

Anderson, A. N. 1997. "Using Ants as Bioindicators: Multi-Scale Issues in Ant Community Ecology." *Conservation Ecology* 1: 8.

Anderson, A. N., and J. D. Majer. 2004. "Ants Show the Way Down Under: Invertebrates as Bioindicators of Land Management." *Frontiers in Ecology and the Environment* 2: 291–98.

Anderson, M. J. 2001. "A New Method for Non-Parametric Multivariate Analysis of Variance." *Austral Ecology* 26: 32–46.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. "Multivariate Dispersion as a Measure of Beta Diversity." *Ecology Letters* 9: 683–693.

Aranda-Rickert, A., P. Diez, and B. Marazzi. 2014. "Extrafloral Nectar Fuels Ant Life in Deserts." *AoB Plants* 6: plu068.

Arbizu, P. M. 2017. "pairwiseAdonis: Pairwise Multilevel Comparison Using Adonis." R Package Version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis.

Ausden, M. 1996. "Invertebrates." In *Ecological Census Techniques: A Handbook*, edited by W. J. Sutherland, 139–177. Cambridge: Cambridge University Press.

Bernstein, R. A. 1974. "Seasonal Food Abundance and Foraging Activity in Some Desert Ants." *The American Naturalist* 108: 490–98.

Bestelmeyer, B. T., and J. A. Wiens. 2001. "Ant Biodiversity in Semiarid Landscape Mosaics: The Consequences of Grazing vs. Natural Heterogeneity." *Ecological Applications* 11: 1123–40.

Burt, M. A., J. Resasco, N. M. Haddad, and S. R. Whitehead. 2022. "Ants Disperse Seeds farther in Habitat Patches with Corridors." *Ecosphere* 13: e4324.

Campbell, J. W., S. M. Grodsky, D. A. Halbritter, P. A. Vigueira, C. C. Vigueira, O. Keller, and C. H. Greenberg. 2019. "Asian Needle Ant (*Brachyponera chinensis*) and Woodland Ant Responses to Repeated Applications of Fuel Reduction Treatments." *Ecosphere* 10: e02547.

Chew, R. M. 1977. "Some Ecological Characteristics of the Ants of a Desert-Shrub Community in Southeastern Arizona." *The American Midland Naturalist* 98: 33–49.

Chew, R. M. 1987. "Population Dynamics of Colonies of Three Species of Ants in Desertified Grassland, Southeastern Arizona, 1958-1981." *The American Midland Naturalist* 118: 177–188.

Chew, R. M. 1995. "Aspects of the Ecology of Three Species of Ants (*Myrmecocystus* spp., *Aphaenogaster* sp.) in Desertified Grassland in Southeastern Arizona, 1958–1993." *American Midland Naturalist* 134: 75–83.

Copeland, S. M., J. B. Bradford, M. C. Duniway, and R. M. Schuster. 2017. "Potential Impacts of Overlapping Land-Use and Climate in a Sensitive Dryland: A Case Study of the Colorado Plateau." *Ecosphere* 8: e01823.

Creighton, W. S. 1950. *The Ants of North America*, Vol. 104. Cambridge: Bulletin of the Museum of Comparative Zoology at Harvard University.

De Cáceres, M., and P. Legendre. 2009. "Associations between Species and Groups of Sites: Indices and Statistical Inference." *Ecology* 90: 3566–74.

Dean, W. R. J., and J. B. Williams. 2004. "Adaptations of Birds for Life in Deserts with Particular Reference to Larks (Alaudidae)." *Transactions of the Royal Society of South Africa* 59: 70–91.

Del Toro, I., R. R. Ribbons, and S. L. Pelini. 2012. "The Little Things that Run the World Revisited: A Review of Ant-Mediated Ecosystem Services and Disservices." *Myrmecological News* 17: 133–146.

Dufrêne, M., and P. Legendre. 1997. "Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach." *Ecological Monographs* 67: 345–366.

Durant, S. M., N. Pettorelli, S. Bashir, R. Woodroffe, T. Wacher, P. de Ornellas, C. Ransom, et al. 2012. "Forgotten Biodiversity in Desert Ecosystems." *Science* 336: 1379–80.

Franco, P. J., E. B. Edney, and J. F. McBrayer. 1979. "The Distribution and Abundance of Soil Arthropods in the Northern Mojave Desert." *Journal of Arid Environments* 2: 137–149.

Gerlach, J., M. Samways, and J. Pryke. 2013. "Terrestrial Invertebrates as Bioindicators: An Overview of Available Taxonomic Groups." *Journal of Insect Conservation* 17: 831–850.

Gibb, H., B. F. Grossman, C. R. Dickman, O. Decker, and G. M. Wardle. 2019. "Long-Term Responses of Desert Ant Assemblages to Climate." *Journal of Animal Ecology* 88: 1549–63.

Goettsch, B., C. Hilton-Taylor, G. Cruz-Piñón, J. P. Duffy, A. Frances, H. M. Hernández, R. Inger, et al. 2015. "High Proportion of Cacti Species Threatened with Extinction." *Nature Plants* 1: 15142.

Grodsky, S. M. 2021. "Matching Renewable Energy and Conservation Targets for a Sustainable Future." *One Earth* 4: 924–25.

Grodsky, S. M. 2023. "Mojave Desert Ants In and Around a Solar Facility, Derived from Pitfall Trap Sampling in 2018." Dataset. U.S. Geological Survey ScienceBase. https://doi.org/10.5066/P90NJ687.

Grodsky, S. M., J. W. Campbell, S. R. Fritts, T. B. Wigley, and C. E. Moorman. 2018. "Variable Responses of Non-Native and Native Ants to Coarse Woody Debris Removal Following Forest Bioenergy Harvests." *Forest Ecology and Management* 427: 414–422.

Grodsky, S. M., J. W. Campbell, and R. R. Hernandez. 2021. "Solar Energy Development Impacts Flower-Visiting Beetles and Flies in the Mojave Desert." *Biological Conservation* 263: 109336.

Grodsky, S. M., and R. R. Hernandez. 2020. "Reduced Ecosystem Services of Desert Plants from Ground-Mounted Solar Energy Development." *Nature Sustainability* 3: 1036–43.

Grodsky, S. M., K. A. Moore-O'Leary, and R. R. Hernandez. 2017. "From Butterflies to Bighorns: Multi-Dimensional

Species-Species and Species-Process Interactions May Inform Sustainable Solar Energy Development in Desert Ecosystems." In *Proceedings of the 31st Annual Desert Symposium*, edited by R. L. Reynolds. Zzyzx, CA: California State University Desert Studies Center.

Grodsky, S. M., R. B. Iglay, C. E. Sorenson, and C. E. Moorman. 2015. "Should Invertebrates Receive Greater Inclusion in Wildlife Research Journals?" *Journal of Wildlife Management* 79: 529–536.

Helms, J. A., S. E. Ijelu, B. D. Wills, D. A. Landis, and N. M. Haddad. 2020. "Ant Biodiversity and Ecosystem Services in Bioenergy Landscapes." *Agriculture, Ecosystems & Environment* 290: 106780.

Helms, J. A., K. A. Roeder, S. E. Ijelu, I. Ratcliff, and N. M. Haddad. 2021. "Bioenergy Landscapes Drive Trophic Shifts in Generalist Ants." *Journal of Animal Ecology* 90: 738–750.

Hernandez, R. R., M. K. Hoffaccker, M. Murphy-Mariscal, G. Wu, and M. F. Allen. 2015. "Solar Energy Impacts on Terrestrial Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 112: 13579–84.

Hölldobler, B., and C. L. Kwapich. 2022. *The Guests of Ants: How Myrmecophiles Interact with Their Hosts*. Cambridge: Harvard University Press.

House, P. K., B. J. Buck, and A. R. Ramelli. 2010. "Geological Assessment of Piedmont and Playa Flood Hazards in the Ivanpah Valley Area, Clark County, Nevada." Nevada Bureau of Mines and Geology Report 53.

Ikeda, M., and J. des Lauriers. 2011. "The Ant Fauna of the Mojave National Preserve." In *The Incredible Shrinking Pliocene, and Abstracts of Proceedings: The 2011 Desert Symposium*, edited by R. E. Reynolds, 104–113. Fullerton, CA: California State University Desert Studies Consortium. 136 pp.

Jager, H. I., R. A. Efroymson, and R. A. McManamay. 2021. "Renewable Energy and Biological Conservation in a Changing World." *Biological Conservation* 263: 109354.

Jeal, C., V. Perold, C. L. Seymour, S. Ralston-Paton, and P. G. Ryan. 2019. "Utility-Scale Solar Energy Facilities – Effects on Invertebrates in an Arid Environment." *Journal of Arid Environments* 168: 1–8.

Johnson, R. A. 1992. "Soil Texture as an Influence on the Distribution of the Desert-Seed Harvester Ants *Pogonomyrmex rugosus* and *Messor pergandei*." *Oecologia* 89: 118–124.

Kaspari, M., J. Bujan, K. A. Roeder, K. de Beurs, and M. D. Weiser. 2019. "Species Energy and Thermal Performance Theory Predict 20-Yr Changes in Ant Community Abundance and Richness." *Ecology* 100: e02888.

Kaspari, M., and M. D. Weiser. 1999. "The Size-Grain Hypothesis and Interspecific Scaling in Ants." *Functional Ecology* 13: 530–38.

Kim, T. N., A. F. Fox, B. D. Wills, T. D. Meehan, D. A. Landis, and C. Gratton. 2017. "Harvesting Biofuel Grasslands Has Mixed Effects on Natural Enemy Communities and no Effects on Biocontrol Services." *Journal of Applied Ecology* 54: 2011–21.

King, J. R., A. N. Anderson, and A. D. Cutter. 1998. "Ants as Bioindicators of Habitat Disturbance: Validation of the Functional Group Model for Australia's Humid Tropics." *Biodiversity and Conservation* 7: 1627–38.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91: 299–305.

Laliberté, E., P. Legendre, and B. Shipley. 2014. "FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology." R Package Version 1.0-12.

Lenth, R. 2020. "emmeans: Estimated Marginal Means, Aka Least-Square Means." R Package Version 1.4.8.

Lovich, J. E., and D. Bainbridge. 1999. "Anthropogenic Degradation of the Southern California Desert Ecosystem and Prospects for Natural Recovery and Restoration." *Environmental Management* 24: 309–326.

MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. "Harvester Ants (*Pogononmyrmex* spp.): Their Community and Ecosystem Influences." *Annual Review of Ecology and Systematics* 31: 265–291.

Majer, J. D. 1983. "Ants: Bio-Indicators of Minesite Rehabilitation, Land-Use, and Land Conservation." *Environmental Management* 7: 375–383.

Marsh, A. C. 1986. "Checklist, Biological Notes and Distribution of Ants in the Central Namib Desert." *Madoqua* 14: 333–344.

Mitchell, C. E., M. G. Turner, and S. M. Pearson. 2002. "Effects of Historical Land Use and Forest Patch Size on Myrmecochores and Ant Communities." *Ecological Applications* 12: 1364–77.

Moore-O'Leary, K. A., R. R. Hernandez, D. S. Johnson, S. R. Abella, K. E. Tanner, A. C. Swanson, J. Kreitler, and J. E. Lovich. 2017. "Sustainability of Utility-Scale Solar Energy – Critical Ecological Concepts." *Frontiers in Ecology and the Environment* 15: 385–394.

Morgan, R. C. 1991. "Natural History, Field Collection and Captive Management of Honey Ant." *International Zoo Yearbook* 30: 108–117.

Mulvaney, D. 2017. "Identifying the Roots of Green Civil War over Utility-Scale Solar Energy Projects on Public Lands across the American Southwest." *Journal of Land Use Science* 12: 493–515.

Murphy-Mariscal, M., S. M. Grodsky, and R. R. Hernandez. 2018. "Solar Energy Development and the Biosphere." In *A Comprehensive Guide to Solar Energy Systems*, edited by T. Letcher and V. Fthenakis, 391–405. London: Elsevier.

Nash, M. S., D. F. Bradford, S. E. Franson, A. C. Neale, W. G. Whitford, and D. T. Geggem. 2004. "Livestock Grazing Effects on Ant Communities in the Eastern Mojave Desert, USA." *Ecological Indicators* 4: 199–213.

Nilson, R. S., and R. C. Stedman. 2023. "Reacting to the Rural Burden: Understanding Opposition to Utility-Scale Solar Energy Development in Upstate New York." *Rural Sociology* 88: 578–605. https://doi.org/10.1111/ruso.12486.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. MacGlinn, P. R. Minchin, et al. 2019. "vegan: Community Ecology Package." R Package Version 2.5-6. https://CRAN.R-project.org/package=vegan.

Paknia, O., and M. Pfeffer. 2011. "Hierarchical Partitioning of Ant Diversity: Implications for Conservation of Biogeographical Diversity in Arid and Semi-Arid Areas." *Diversity and Distributions* 17: 122–131.

Parker, S. S., B. S. Cohen, and J. Moore. 2018. "Impact of Solar and Wind Development on Conservation in the Mojave Desert." *PLoS One* 13: e0207678.

Parr, C. L., R. R. Dunn, N. J. Sanders, M. D. Weiser, M. Photakis, T. R. Bishop, M. C. Fitzpatrick, et al. 2017. "*GlobalAnts*: A New Database on the Geography of Ant Traits (Hymenoptera: Formicidae)." *Insect Conservation and Diversity* 10: 5–20.

Pemberton, R. W. 1988. "The Abundance of Plants Bearing Extrafloral Nectaries in Colorado and Mojave Desert Communities of Southern California." *Madrono* 35: 238–246.

Perry, K. I., N. C. Hoekstra, Y. A. Delgado de la Flor, and M. M. Gardiner. 2020. "Disentangling Landscape and Local Drivers of Ground-Dwelling Community Assembly in an Urban Ecosystem." *Ecological Applications* 30: e02191.

Randel, C. J., and N. J. Silvy. 2015. "Desert Kit Fox Home Range – Southeastern California." *Israeli Journal of Ecology and Evolution* 61: 3–4.

Rango, J. J. 2005. "Arthropod Communities on Creosote Bush (*Larrea tridentata*) in Desert Patches of Varying Degrees of Urbanization." *Biodiversity and Conservation* 14: 2185–2206.

Read, J. L., and A. N. Anderson. 2000. "The Value of Ants as Early Warning Bioindicators: Responses to Pulsed Cattle Grazing at an Australian Arid Zone Locality." *Journal of Arid Environments* 45: 231–251.

Rissing, S. W. 1982. "Foraging Velocity of Seed-Harvester Ants, *Veromessor pergandei* (Hymeoptera: Formicidae)." *Environmental Entomology* 11: 905–7.

Rissing, S. W. 1988. "Seed-Harvester Ant Association with Shrubs: Competition for Water in the Mohave Desert?" *Ecology* 69: 809–813.

Rivas-Arancibia, S. P., H. Carrillo-Ruiz, A. B. Arce, D. M. Figueroa-Castro, and A. R. Andrés-Hernández. 2014. "Effect of Disturbance on the Ant Community in a Semiarid Region of Central Mexico." *Applied Ecology and Environmental Research* 12: 703–716.

Roeder, K. A., and A. N. Harmon-Threatt. 2022. "Woody Perennial Polycultures Increase Ant Diversity and Ant-Mediated Ecosystem Services Compared to Conventional Corn-Soybean Rotations." *Agriculture, Ecosystems and Environment* 336: 108025.

Rojas, P., and C. Fragoso. 2000. "Composition, Diversity, and Distribution of a Chihuahuan Desert Ant Community." *Journal of Arid Environments* 44: 213–227.

Sanders, N. J., and D. M. Gordon. 2003. "Resource-Dependent Interactions and the Organization of Desert any Communities." *Ecology* 84: 1024–31.

Schultheiss, P., S. S. Nooten, R. Wang, and B. Guénard. 2022. "The Abundance, Biomass, and Distribution of Ants on Earth." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2201550119.

Sheikh, A. H., G. A. Ganaie, M. Thomas, R. Bhandari, and Y. A. Rather. 2018. "Ant Pitfall Trapping: An Overview." *Journal of Entomological Research* 42: 421–436.

Silva, R. R., and C. R. Brandão. 2010. "Morphological Patterns and Community Organization in Leaf-Litter Ant Assemblages." *Ecological Monographs* 80: 107–124.

Spence, J. R., and J. K. Niemelä. 1994. "Sampling Carabid Assemblages with Pitfall Traps: The Madness and the Method." *The Canadian Entomologist* 126: 881–894.

Underwood, E. C., and B. L. Fisher. 2006. "The Role of Ants in Conservation Monitoring: If, When, and How." *Biological Conservation* 132: 166–182.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. "New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology." *Ecology* 89: 2290–2301.

Wagner, D., and J. B. Jones. 2006. "The Impact of Harvester Ants on Decomposition, N Mineralization, Litter Quality, and the Availability of N to Plants in the Mojave Desert." *Soil Biology and Biogeochemistry* 38: 2593–2601.

Weiser, M. D., and M. Kaspari. 2006. "Ecological Morphospace of New World Ants." *Ecological Entomology* 31: 131–142.

Whitford, W. G. 1978. "Structure and Seasonal Activity of Chihuahua Desert Ant Communities." *Insectes Sociaux* 25: 79–88.

Whitford, W. G., and M. Bryant. 1979. "Behavior of a Predator and Its Prey: The Horned Lizard (*Phrynosoma cornutum*) and Harvester Ants (*Pogomyrmex* spp.)." *Ecology* 60: 686–694.

Whitford, W. G., and G. Ettershank. 1975. "Factors Affecting Foraging Activity in Chihuahuan Desert Harvester Ants." *Environmental Entomology* 4: 689–696.

Whitford, W. G., J. Van Zee, M. S. Nash, W. E. Smith, and J. E. Herrick. 1999. "Ants as Indicators of Exposure to Environmental Stressors in North American Desert Grasslands." *Environmental Monitoring and Assessment* 54: 143–171.

Wong, M. K. L., B. Guénard, and O. T. Lewis. 2020. "The Cryptic Impacts of Invasion: Functional Homogenization of Tropical Ant Communities by Invasive Fire Ants." *Oikos* 129: 585–597.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.