

Solar energy development impacts flower-visiting beetles and flies in the Mojave Desert

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ABSTRACT

Deserts support a high diversity of insect pollinators and vascular plants with which pollinators have coevolved. Deserts are increasingly prioritized as recipient environments for ground-mounted solar energy development, which represents a novel, anthropogenic disturbance in desert ecosystems and drives land-use change across desert landscapes. Pollinators confer ecosystem services, yet anthropogenically driven land-use change has played a large role in their decline globally. Our objective was to elucidate relationships between solar energy development and non-bee insect flower visitors (i.e., beetles, flies, moths, and wasps) at Ivanpah Solar Electric Generating System (ISEGS, 392 MW) in the Ivanpah Valley of the Mojave Desert. We used blue vane traps to collect non-bee insect flower visitors in treatments that represent different solar energy development decisions, including two types of site preparation practices (blading and mowing) and establishment of habitat patches in solar fields, replicated across three power blocks in ISEGS and in undeveloped control sites surrounding ISEGS. We determined that count and taxa richness of non-bee insect flower visitors and counts of individual non-bee insect flower visitor taxa were greater in undeveloped controls than in ISEGS. Our results indicate that disturbance from solar energy development negatively affected non-bee insect flower visitors, including beetles and flies, and that small habitat patches within solar fields in ISEGS largely did not support non-bee insect flower visitors. Disruption of non-bee insect flower visitor communities from solar energy development in deserts may lead to cascading effects on biodiversity, including potential decreases in globally imperiled and highly valuable cacti populations dependent on insect pollination. Losses in biodiversity from solar energy development in deserts may be eliminated by alternative siting (e.g., contaminated lands, rooftops), while gains can be achieved by sustainable decision making guided by solutions-oriented, collaborative research and techno-ecological synergies.

1. Introduction

Renewable energy facilitates emissions reductions and plays a key role in the energy transition, but its deployment presents pressing challenges for biodiversity conservation (Grodsky, 2021). We know little about the broader ecological effects and environmental tradeoffs of solar energy development, yet potential for complex interactions with ecosystems is high (Moore-O'Leary et al., 2017). In this paper, we address relationships between solar energy development and non-bee insect flower visitor abundance and taxa richness in the Mojave Desert.

The decline of pollinator populations has elicited significant

conservation concerns motivated by impending and actualized damages to ecosystem services, intricate plant-pollinator networks, and biodiversity at large (Potts et al., 2010; Goulson et al., 2015). A growing body of literature now frames the value of pollinators through the lens of anthropocentrism, illuminating the role they play in supporting global food security for and cultural values of humans (Potts et al., 2016; Reilly et al., 2020). In addition to the benefits of pollination traditionally linked to humans, pollinators also play critical roles in the persistence of plant populations for biodiversity conservation and ecosystem services. Recent research indicates that decreased pollinator diversity leads to decreased plant diversity (Ramos-Jiliberto et al., 2020). Additionally,

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reduced native pollinator abundance coincides with declines in threatened and endangered plant species (Mathiasson and Rehan, 2020). Research also indicates that ecologically and functionally specialized plants risk pollen limitation when plant-pollinator networks are disrupted (Bennett et al., 2020). Land-use change and climate change are primary drivers of pollinator declines globally (Potts et al., 2016; Lazaro and Tur, 2018; Durant and Otto, 2019). However, conservation policies and actions targeting pollinator declines remain few and nascent (Hall and Steiner, 2019). Further, the ecological extent and ramifications of pollinator declines may be muddled by geographic biases in research effort (e.g., Archer et al., 2014) and taxonomic biases favoring bees over other insect pollinators (e.g., Rader et al., 2020), as well as a lack of transdisciplinary research approaches (Bartomeus and Dicks, 2019).

Renewable energy development is a contemporary driver of land-use change that may rapidly induce novel and complex interactions among plants, animals, and people (e.g., Hernandez et al., 2014a, 2014b, Grodsky et al., 2019, Grodsky and Hernandez, 2020). Most large, ground-mounted solar energy facilities (>10 MW) in California, for example, are sited in natural desert scrublands near protected natural areas (Hernandez et al., 2015), potentially resulting in decreased overall conservation value (e.g., The Nature Conservancy's Mojave Desert Ecoregional Assessment; Parker et al., 2018). Grodsky and Hernandez (2020) assessed the response of the desert plant community to solar energy development in the Ivanpah Valley of the Mojave Desert; they determined that solar energy development decisions profoundly reduced desert plant cover, including that of cacti, and delivery of ecosystem services, including habitat for species and cultural services valued by indigenous groups. Furthermore, deserts and the plant-pollinator networks therein are especially vulnerable to climate change (e.g., Copeland et al., 2017), which can act in conjunction with land-use change from solar energy development to negatively affect pollinators (Potts et al., 2016).

Ground-mounted solar energy development often embodies large-scale, anthropogenic disturbance that alters soils and vegetation in deserts serving as global hotspots for bee diversity and likely strongholds for unstudied non-bee insect flower visitors (i.e., beetle, fly, moth, and wasp) (Griswold et al., 2006; Moore-O'Leary et al., 2017; Murphy-Mariscal et al., 2018). A recent study of invertebrate response to solar development in an arid environment, albeit rangeland, indicated that community composition of flying invertebrates significantly differed between a concentrating solar power (CSP) trough facility and surrounding undeveloped controls (Jeal et al., 2019). Additionally, Saul-Gershenz et al. (2018a) detected a greater abundance of wild bees in undeveloped areas of the Sonoran Desert relative to plots near solar facilities, and they found no relationship between native bee abundance and increasing distance of control plots in undeveloped desert from solar facilities.

Solar energy development decisions in deserts may alter resource availability for flower-visiting insects via novel manipulations to desert ecosystems historically maladapted to frequent, large-scale disturbance (Lovich and Bainbridge, 1999; Brooks and Matchett, 2006; Grodsky et al., 2017). Current industry standards are characterized by site preparation practices for solar energy development that remove vegetation either by bulldozing or mowing, both of which may reduce floral resources for flower-visiting insects (Grodsky and Hernandez, 2020). For example, bulldozing can promote invasive grasses (e.g., *Schismus* spp.) in the Mojave Desert (Grodsky and Hernandez, 2020). Invasive grasses in deserts readily spread via wind pollination, successfully compete with native plant species, and have the propensity to increase the frequency and intensity of fires (Brooks, 2000; Brooks, 2002). Therefore, competition and fire promotion by invasive grasses may diminish floral resource availability following intensive site preparation for solar energy development. Widespread and indiscriminate removal of native vegetation for solar energy development in deserts may also negatively affect insect flower-visitors. For example, specialist flower-visiting species may surpass generalist flower-visiting species in diversity, biomass,

and abundance in highly xeric environments like deserts (e.g., as seen with bees associated with *Larrea tridentata* (Minckley et al., 2000)). To date, post-construction retention of floral resources for flower-visiting insect conservation within desert (or any) solar facilities has yet to be empirically evaluated in the peer-reviewed literature.

The physical presence of solar energy infrastructure in desert landscapes may affect flower-visiting insects via a diversity of potential mechanisms. Heliostats (i.e., mirrors) at CSP facilities constitute novel sources of shade in desert environments, potentially altering soil temperatures, vegetation growth, and wildlife site use (Grodsky et al., 2017). For example, shade from solar panels may increase species richness, diversity, and abundance of desert annuals in caliche pan habitat (Tanner et al., 2020) but may decrease projected growth of rare desert annuals like *Eriophyllum mohavense* in wet years integral to seed bank replenishment (Tanner et al., 2021). Shade from heliostats in deserts may reduce insect flower-visitor activity via reduced floral resources and physiological effects of shade on the insects themselves. On the other hand, floral resources available to insect flower visitors may increase due to potential increases in plant densities from climate amelioration (e.g., nurse plant effect; Valiente-Banuet and Ezcurra, 1991).

While bees in agricultural settings dominantly constitute "pollinators" in some scientific circles and the public eye (e.g., Smith and Saunders, 2016), increasing scientific evidence suggests that "non-bee insect pollinators" also are important provisioners of pollination services and integral constituents of plant-pollinator networks (Langridge and Goodman, 1975, Orford et al., 2015, Doyle et al., 2020, Rader et al., 2020, Raguso, 2020). Although the Mojave and Sonoran Deserts of the southwestern United States harbor a great diversity of wild bees (e.g., Minckley et al., 1999; Griswold et al., 2006), little information on the distribution and conservation status of non-bee insect flower visitors in desert regions exists. Non-bee insect flower visitors, including beetles, flies, butterflies, moths, and wasps, may provide specific pollination services and fill distinct ecological niches in desert ecosystems. Additionally, non-bee insect flower visitors may exhibit responses to solar energy development in deserts separate from and in direct interrelation with bees. For example, many non-bee insect flower visitors in desert ecosystems spend their larval stages in various ecological roles, such as predators, herbivores and nest parasites and parasitoids of native bees (Saul-Gershenz et al., 2018b).

Considering current knowledge gaps pertaining to solar energy development and insect conservation in deserts, our objective was to elucidate relationships between solar energy development decisions, including site preparation practices and retention of undisturbed habitat patches in solar fields, and non-bee insect flower visitors at Ivanpah Solar Electric Generating System (ISEGS). We hypothesize that non-bee insect flower visitors in a desert scrubland ecosystem negatively respond to solar energy development decisions that disturb soils and remove vegetation, including blading and mowing. Secondly, we hypothesize that non-bee insect flower visitors negatively respond to increasing heliostat density in ISEGS due to increased shading, which may lead to decreased floral resources and physiological effects on the insects that overpower potential "nurse plant" effects of heliostat shading. Last, we hypothesize that non-bee insect flower visitors increase in abundance and diversity at increasing distances from ISEGS into surrounding undeveloped desert.

2. Methods

2.1. Study area

We conducted the study in ISEGS and surrounding undeveloped desert scrubland. Ivanpah Solar Electric Generating System is a CSP facility with a gross capacity of 392 MW. Ivanpah Solar Electric Generating System consists of 173,500 heliostats (347,000 individual mirrors) and three power towers, comprising ~1289 heliostat-covered

hectares; heliostat density averages 6.6 heliostats per 314.16 m² (see [Experimental design](#) section below). It 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 m to 1075 m in the Mojave Desert of California, United States. Ivanpah Solar Electric Generating System was constructed in 2011 on a 1400-ha tract of previously undeveloped Mojave Desert creosote scrubland in the Ivanpah Valley near the Mojave River corridor, the Mojave National Preserve, and Mesquite and Stateline Wildernesses. 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. Summer midday temperatures often exceed 40 °C. Annual precipitation averaged ~135 mm from 2011 to 2017, mostly occurring during the winter and summer seasons, and included several wet years

(2013 and 2016).

2.2. Experimental design

Within ISEGS, we designated each of the three power blocks (i.e., tower and associated heliostats; [Fig. 1](#)) as replicated blocks. The area of each block is 3.66 km², 4.33 km², and 4.90 km², respectively. Each block contains ~116,000 individual mirrors and is surrounded by 3.05-m-tall chain linked fencing. 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

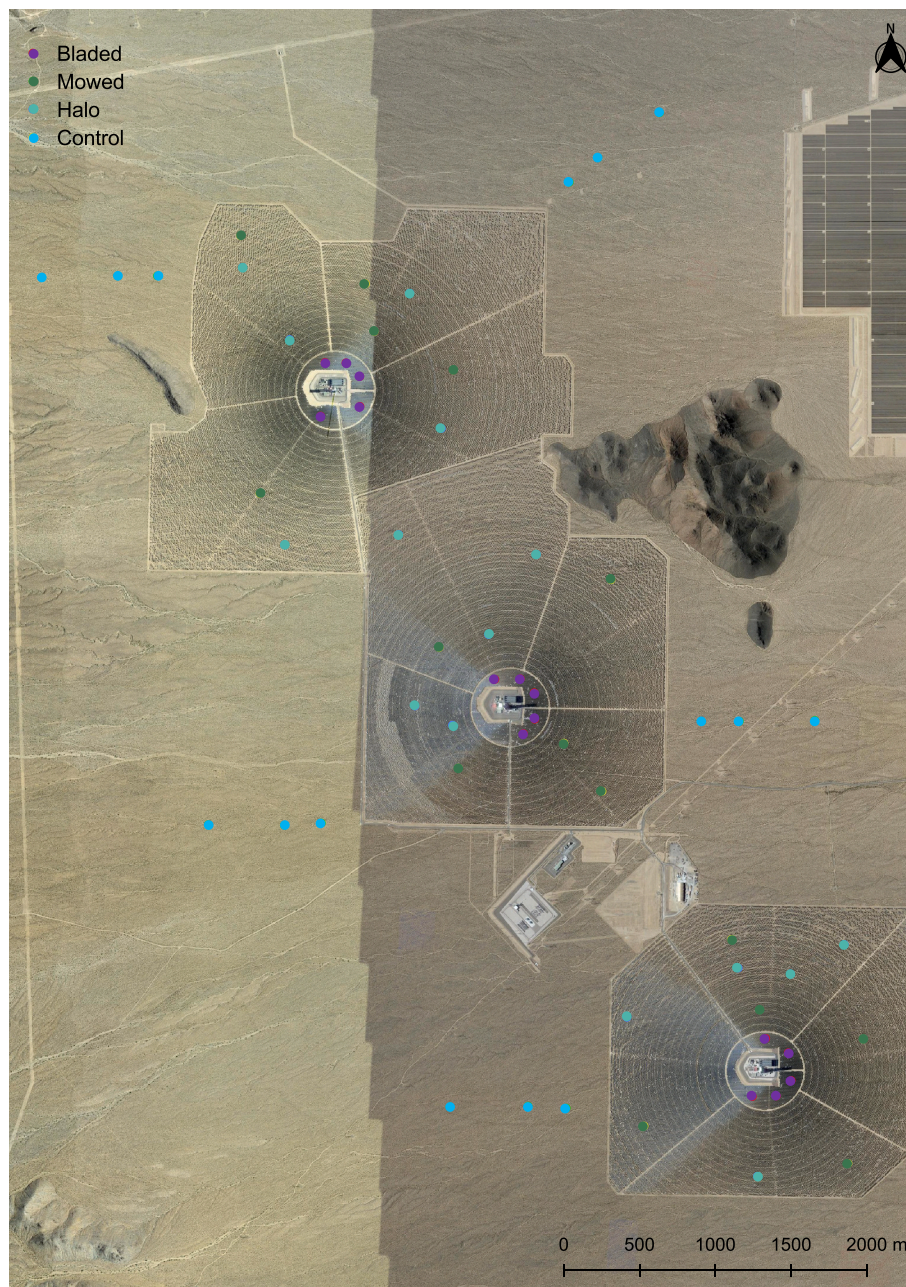


Fig. 1. Ivanpah Solar Electric Generating System (ISEGS, 392 MW), consisting of three concentrating solar power blocks (i.e., tower and associated heliostats; replicated block) in the Ivanpah Valley, Mojave Desert, California, USA. Different colored dots show the spatial orientation of 60 non-bee insect flower visitor sampling plots in treatments and controls (see also [Methods](#) section).

fields at ISEGS, which were roped off and left undisturbed (i.e., no site preparation, no heliostats), creating isolated habitat patches (average area = 22 m², Fig. 2). We replicated treatments five times in each block. We established 15 plots in each of the three treatment units in blocks (five plots per treatment per block, treatment plots = 45) (Fig. 1). We used the ‘distance matrix’ function in QGIS (QGIS.org, 2021) to measure the distance from each plot to the power tower in each block. We calculated heliostat density for each plot as the number of heliostats (any portion of either mirror on heliostat) contained within a 10-m buffer centered around each plot using QGIS (Grodsky and Hernandez, 2020).

We designated 15, replicated control plots in natural desert scrub immediately surrounding the blocks that comprised ISEGS, making a total of 60 plots (Fig. 2). We situated control plots along five transects randomly selected from a set of superimposed grid points laid over a map of ISEGS in QGIS. Each transect contained three plots located at 250 m, 500 m, and 1 km from the boundary of the nearest block (Fig. 1). We chose the upper limit of plot distances from landscape features based on 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 ISEGS would be confounded by other landscape features potentially affecting the distribution of non-bee insect flower visitors, including Clark Mountain to the north (e.g., elevational plant community shift) and a golf course and highway to the south.

2.3. Vegetation sampling

We sampled the desert plant community at all 60 plots from 5 April through 5 May 2018. We determined effects of solar energy development decisions and heliostat density on all desert plants, perennials, annuals, plants undergoing Crassulacean acid metabolism, and the invasive grass genus *Schismus*. Vegetation sampling methods are summarized in the Supplementary Information of Grodsky and Hernandez (2020).

2.4. Non-bee insect flower visitor sampling, sorting and identification

We used blue vane traps to sample non-bee insect flower visitors at plots in ISEGS and control sites during one, continuous sampling period from April 5th to May 5th, encompassing a large portion of the peak spring growing season, in 2018 and 2019. Blue vane traps specifically target flower-visiting insects by design and have been proven as an effective means by which to capture non-bee insect flower visitors in open landscapes like deserts (Hall and Rebound, 2019). In 2018, we sampled pollinators at all 60 plots. In 2019, we sampled pollinators at 45 plots due to reduced project personnel. We mounted each blue vane trap to a PVC pole at the height of the tallest shrub within a 10-m radius of the trap. We filled each blue vane trap with ~2 L of a solution comprised of equal parts soapy water and propylene glycol. At the end of each one-month sampling period, we extracted all specimens from each blue vane trap and stored them in vials with 70% ethanol. We labelled each vial with a collection date and a unique trap identifier. We sorted specimens into groups of known non-bee insect flower visitors based on the peer-reviewed literature: 1) coleopterans (beetles), 2) dipterans (flies), 3) hymenopterans (wasps), and 4) lepidopterans (butterflies and moths). We pinned and labelled all potential non-bee insect flower visitors. An expert entomologist and taxonomist [Dr. Josh Campbell of the USDA Northern Plains Agricultural Research Laboratory] identified non-bee insect flower visitors to family, and when possible, to genus and species, using appropriate taxonomic keys (e.g., Cole and Schlinger, 1969; Bohart and Menke, 1976; Goulet and Huber, 1993). Following identification of specimens to the lowest possible taxonomic level, we excluded all non-flower visiting insects from the analyses.

2.5. Statistical framework and analysis

Given the reduced sampling effort in 2019 relative to 2018, we analyzed non-bee insect flower visitor datasets separately for each year of the study. We plotted counts of non-bee flower visiting taxa and visually binned them into one of the following three levels: 1) super-abundant; 2) abundant; and 3) rare (Grodsky et al., 2018a, b). We set the

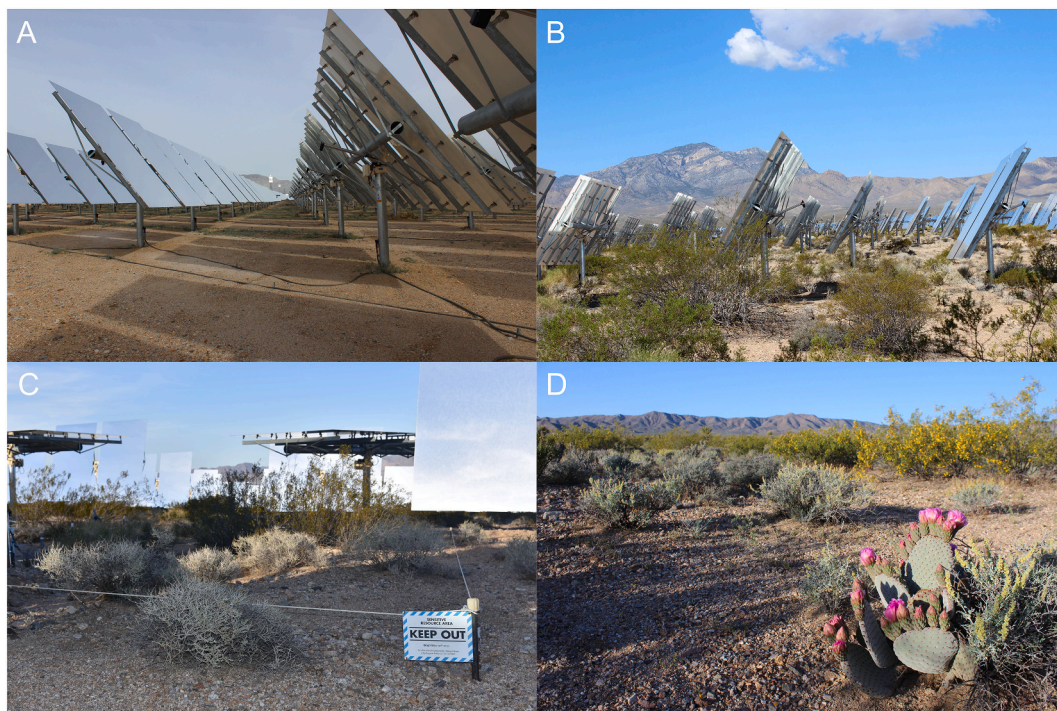


Fig. 2. Photographs of solar energy development decision treatments: A) bladed, B) mowed, C) establishment of habitat patches (“halos”), and D) a control plots in undeveloped desert scrubland.

cutoff for inclusion of individual non-bee flower visiting taxon in analyses at the break between abundant and rare levels, thereby excluding non-bee flower visitors with relatively low counts from analyses. For example, the cutoff between abundant and rare non-bee insect flower visitors in 2018 was $n = 13$ because counts of non-bee insect flower visiting insects dropped from $n = 13$ to $n \leq 5$ at that transition point on the plot of non-bee insect flower visitor counts. In 2019, the cutoff between relatively abundant and rare non-bee flower visiting insects was $n = 14$. We calculated non-bee insect flower visitor taxa richness as the number of individual non-bee insect flower visitor taxa identified down to the lowest taxonomic level available. We computed Simpson and Shannon diversity indices for all non-bee flower visiting taxa (i.e., both common and rare taxa) in the R package ‘vegan’ (Oksanen et al., 2013).

We developed a series of Poisson generalized linear models (GLMs) to elucidate relationships between solar energy development and non-bee insect flower visitors in ISEGS and surrounding desert scrub. For all Poisson GLMs, we assessed overdispersion by dividing the residual deviance by the residual degrees of freedom to determine if the quotient was ≤ 1.2 (Payne et al., 2018). If we detected overdispersion, we instead developed quasi-Poisson GLMs.

First, we ran Poisson GLMs with non-bee insect flower taxa richness, count of all non-bee insect flower visitors, and count of each individual non-bee insect flower visitor taxon (i.e., order, family, genus, and species down to lowest taxonomic level) that met criteria for inclusion in analyses in each treatment in each block per year as dependent variables; we used solar energy development decision and block as independent variables. For the next series of models, we first used a Pearson product-moment correlation test to determine if a relationship existed between heliostat density and distance from power towers in blocks. We then developed Poisson GLMs with non-bee insect flower visitor taxa richness and count of all non-bee insect flower visitors in each treatment in each block per year as dependent variables and heliostat density and block as independent variables. For the last series of models, we isolated non-bee insect flower visitor taxa richness and counts of non-bee insect flower visitors in control plots categorized by their distance from ISEGS (i.e., 250 m, 500 m, and 1 km). We then developed Poisson GLMs with non-bee insect flower visitor diversity and taxa richness and count of all non-bee insect flower visitors in each distance class in controls surrounding each block per year as dependent variables and distance class from ISEGS and block as independent variables. We followed the same modeling procedure for non-bee insect flower visitor diversity indices as each of three modeling exercises above, using the Simpson and Shannon diversity index, respectively, as the response variable and a Gaussian rather than Poisson distribution.

We performed likelihood-ratio tests on all Poisson GLMs using the ‘drop1’ function in R to determine significant effects of solar energy development decisions, heliostat density, and distance from ISEGS, respectively, on non-bee insect flower visitors. For the categorical variables (i.e., solar energy development decision, distance class from ISEGS), we conducted post hoc Tukey’s pairwise comparisons of means, using general linear hypothesis testing with a Holm adjustment (glht function; single-step method) in the R package ‘multcomp’. We set $\alpha = 0.05$ to determine statistical significance.

3. Results

Species richness and Shannon diversity indices of all desert plants and desert perennials were lower in bladed treatments than in all other treatment and controls (Table S1). Height per individual, percent cover of perennial plants, and percent cover of flowering perennials were lower in bladed treatments than all other treatments and controls, and lower in mowed treatments than in halo treatments and controls (Table S1). Percent cover of CAM plants was lower in bladed and mowed treatments than in halo treatments and controls (Table S1). Conversely, percent cover of *Schismus* spp., a genus of invasive grass, was higher in bladed treatments than all other treatments and controls (Table S1).

Percent cover of desert perennials, CAM plants, *L. tridentata*, and *Am-brosia dumosa* decreased with increasing heliostat density, whereas percent cover of *Schismus* spp. increased with increasing heliostat density (Table S2).

We collected 990 non-bee insect flower visitors, comprising 21 families and at least 37 genera in 2018 (Table S3) and 734 non-bee insect flower visitors, comprising 15 families and at least 26 genera in 2019 (Table S4). In both years, we captured fewer flower-visiting wasps and moths than flower-visiting dipterans and coleopterans (Table S3, Table S4). We analyzed counts of 13 and eight individual non-bee insect flower visitor taxon in 2018 and 2019, respectively (Table 1).

We detected negative effects of solar energy development on the non-bee insect flower visitor community relative to undeveloped controls surrounding ISEGS (Table 1, Table S5). We documented significantly lower non-bee insect flower visitor taxa richness, counts of non-bee insect flower visitors, counts of flower-visiting coleopterans, and counts of *Trichodes ornatus* (Cleridae: Coleoptera) in ISEGS than outside of it in both years (Fig. 3). We documented the same trend for flower visiting dipterans, Bombyliids (Diptera), and *Malachius* sp. (Melyridae: Coleoptera) in 2018 and *Lordotus* spp. (Bombyliidae: Diptera) in 2019. We did not detect a significant relationship between counts of crabronid, pompilid, and sphecid wasps nor count of the moth species *Hyles lineata* and ISEGS in either year.

We also detected some differences in non-bee flower visitor response to solar energy development decisions within ISEGS and some similarities in non-bee insect flower abundance between the halo treatments in ISEGS and undeveloped controls outside of ISEGS (Table 1, Table S5). In 2018, count of *Lordotus* spp. was greater in controls than in bladed and mowed treatments, but not statistically different from those in halo treatments. In 2019, the Simpson diversity index was greater in controls and halo treatments than in bladed treatments, whereas the Shannon diversity index was greater in controls and mowed treatments than in bladed treatments. Non-bee insect taxa richness was greater in controls than in bladed treatments, but similar among mowed and halo treatments within ISEGS in 2019. In 2019, count of flower-visiting dipterans and Bombyliids was greater in controls than in halo treatments, but not statistically different from those recorded in mowed and bladed treatments.

We documented some relationships between heliostat density in ISEGS and the count and diversity of non-bee insect flower visitors (Table S6). In 2018, count of all non-bee insect flower visitors decreased with increasing heliostat density. In 2019, Simpson and Shannon diversity indices decreased with increasing heliostat density. We did not detect any relationship between non-bee insect flower visitors and distance from ISEGS at control sites in either year (Table S7).

4. Discussion

The generally negative response of the non-bee insect flower visitor community to development of ISEGS seven and eight years after its construction exemplifies potential for proliferation of long-term ecological ramifications stemming from industrial-scale solar energy development in deserts. While anecdotal evidence points to direct mortality of flying invertebrates in the ‘‘solar flux’’ zone of the airspace around solar towers at ISEGS specifically (Diehl et al., 2016), our empirical results indicate that displacement of non-bee insect flower visitors via indirect effects of habitat loss from solar energy development is a valid conservation concern. The fact that non-bee insect flower visitor measurements typically did not differ between bladed and mowed treatments in ISEGS suggests that any form of site preparation for solar energy development in deserts, regardless of its intensity, may represent anthropogenic disturbance sufficient to displace non-bee insect flower visitors. Further, establishment of relatively small habitat patches (average = 22 m²) within ISEGS largely failed to conserve non-bee insect flower visitors in the solar facility.

The physical disturbance of habitat following site preparation at

Table 1

Mean (95% CI) non-bee insect flower visitor diversity, taxa richness, and counts in solar energy development decision treatments, including blading ($n = 3$), mowing ($n = 3$), and establishment of habitat patches (“halos”; $n = 3$), within Ivanpah Solar Electric Generating System and in surrounding undeveloped desert scrub ($n = 3$), 5 April–5 May 2018 and 2019, Ivanpah Valley, Mojave Desert, California, USA. Significant treatment effects are indicated in bold; letters a and b indicate significant differences among treatments [bladed, mowed, and habitat patches (“halo”)] and controls. We reported results of likelihood ratio tests for Poisson GLMs (indicated by § symbol) and scaled deviance for quasi-Poisson GLMs. We set the statistical significance level (α) to 0.05.

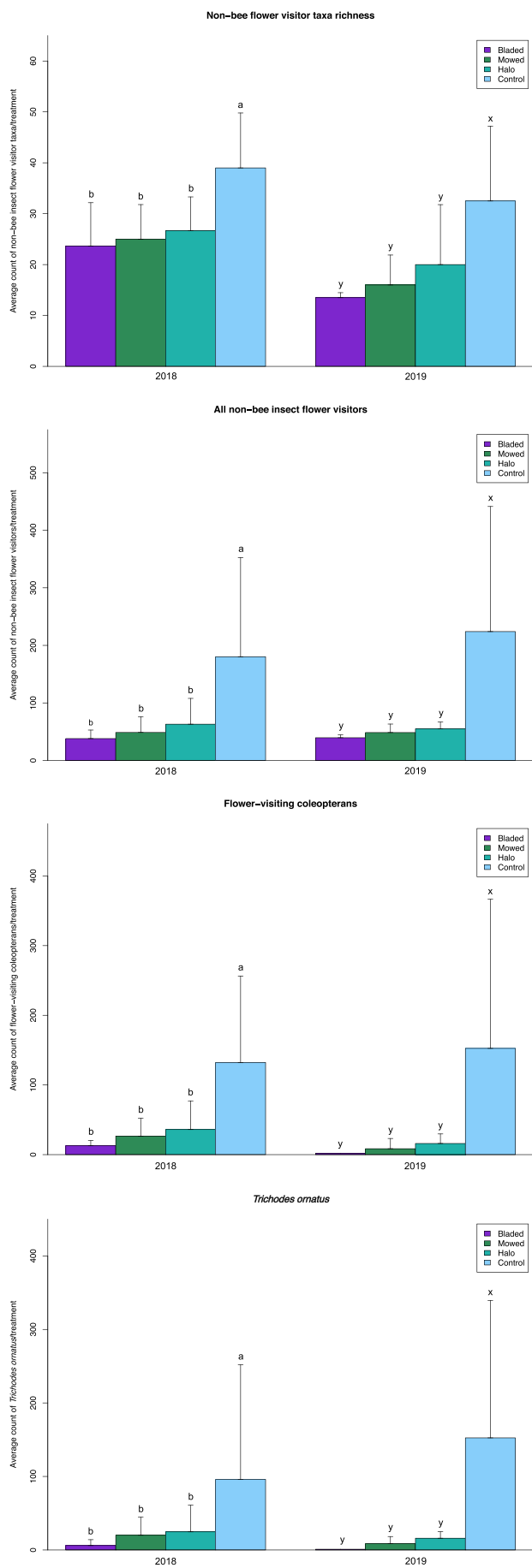
Non-bee insect flower visitors	Treatment effect		Treatments			
	LRT/scaled dev	Pr(χ^2)	Bladed	Mowed	Halo	Control
2018						
Simpson's Diversity Index	0.58	0.90	0.63 ± 0.14	0.63 ± 0.15	0.67 ± 0.03	0.64 ± 0.15
Shannon-Weaver Diversity Index	1.33	0.72	1.22 ± 0.38	1.27 ± 0.41	1.35 ± 0.14	1.47 ± 0.33
Taxa richness [§]	15.33	<0.01	23.67 ^b ± 8.49	25.00 ^b ± 6.79	26.67 ^b ± 6.63	39.00 ^a ± 10.79
All taxa	56.62	<0.01	38.00 ^b ± 14.80	48.67 ^b ± 27.36	63.00 ^b ± 44.84	180.33 ^a ± 172.36
Coleoptera (beetles)	40.80	<0.01	12.67 ^b ± 7.70	26.67 ^b ± 25.46	36.00 ^b ± 41.16	132.33 ^a ± 124.01
Buprestidae: <i>Acmaeodera</i> sp.	1.65	0.64	1.67 ± 0.65	2.67 ± 1.31	3.67 ± 7.19	2.00 ± 1.13
Cleridae: <i>Trichodes ornatus</i>	24.06	<0.01	6.00 ^b ± 8.16	20.00 ^b ± 24.48	24.67 ^b ± 36.15	96.67 ^a ± 156.28
Melyridae: <i>Malachius</i> sp.	27.55	<0.01	5.00 ^b ± 3.92	1.67 ^b ± 0.65	3.67 ^b ± 3.46	24.67 ^a ± 3.46
Diptera (flies)	19.01	<0.01	12.33 ^b ± 1.73	13.33 ^b ± 5.23	15.33 ^b ± 7.95	28.33 ^a ± 15.36
Bombyliidae spp.	24.64	<0.01	5.33 ^b ± 2.36	8.33 ^b ± 4.28	10.00 ^b ± 4.53	19.67 ^a ± 15.41
Bombyliidae: <i>Lordotus</i> spp. [§]	21.10	<0.01	3.00 ^b ± 2.99	3.00 ^b ± 0	5.67 ^{ab} ± 3.27	11.00 ^a ± 13.91
Bombyliidae: <i>Oligodranes</i> spp. [§]	4.54	0.21	1.67 ± 3.27	1.33 ± 1.73	1.00 ± 1.96	3.67 ± 3.46
Syrphidae spp.	1.96	0.58	3.67 ± 1.73	2.33 ± 0.65	2.00 ± 1.13	3.33 ± 0.65
Hymenoptera (wasps)	15.74	<0.01	5.00 ^{ab} ± 2.99	1.67 ^b ± 1.73	5.67 ^{ab} ± 5.23	11.67 ^a ± 2.85
Crabronidae spp. [§]	10.33	0.02	1.67 ± 1.73	0.33 ± 0.65	2.67 ± 5.23	0.33 ± 0.65
Pompilidae spp. [§]	4.52	0.21	1.33 ± 0.65	0.67 ± 1.31	2.00 ± 1.13	0.33 ± 0.65
Lepidoptera: Sphingidae: <i>Hyles lineata</i>	2.12	0.55	8.00 ± 5.88	6.67 ± 8.64	6.00 ± 5.19	8.00 ± 1.96
2019						
Simpson Diversity Index	11.77	0.01	0.29 ^b ± 0.14	0.48 ^{ab} ± 0.30	0.52 ^a ± 0.34	0.58 ^a ± 0.08
Shannon-Weaver Diversity Index	12.96	<0.01	0.55 ^b ± 0.76	0.85 ^a ± 1.18	1.02 ^{ab} ± 1.41	1.14 ^a ± 1.58
Taxa richness [§]	11.81	0.01	13.50 ^b ± 0.98	16.00 ^{ab} ± 5.88	20.00 ^{ab} ± 11.78	32.50 ^a ± 14.70
All taxa	35.27	<0.01	39.50 ^b ± 4.90	48.50 ^b ± 14.70	55.00 ^b ± 11.76	224.00 ^a ± 217.36
Coleoptera (beetles)	62.83	<0.01	2.00 ^b ± 0	8.50 ^b ± 14.70	16.00 ^b ± 13.72	152.50 ^a ± 214.62
Cleridae: <i>Trichodes ornatus</i>	57.16	<0.01	1.00 ^b ± 0	5.00 ^b ± 9.80	7.50 ^b ± 8.82	126.50 ^a ± 187.18
Diptera (flies)	11.30	0.02	35.00 ^{ab} ± 5.88	33.50 ^{ab} ± 22.53	26.50 ^b ± 4.90	61.50 ^a ± 8.82
Bombyliidae spp.	10.28	0.02	30.50 ^{ab} ± 4.89	31.50 ^{ab} ± 14.84	25.00 ^b ± 3.92	59.50 ^a ± 8.82
Bombyliidae: <i>Lordotus</i> spp. [§]	77.87	<0.01	0 ^b	1.00 ^b ± 1.96	0 ^b	17.50 ^a ± 24.50
Bombyliidae: <i>Oligodranes</i> spp.	1.74	0.63	30.50 ± 4.90	30.50 ± 22.54	25.00 ± 3.92	42.00 ± 15.68
Syrphidae spp. [§]	1.06	0.79	2.50 ± 0.98	1.50 ± 0.98	1.50 ± 0.98	1.50 ± 0.98
Hymenoptera (wasps)	4.53	0.21	2.00 ± 1.96	5.00 ± 5.88	9.50 ± 0.98	10.00 ± 3.92
Sphecidae spp.	13.16	<0.01	0.50 ± 0.98	4.00 ± 5.88	8.00 ± 1.96	0.50 ± 0.98

ISEGS may have affected non-bee insect flower visitors via several potential ecological mechanisms and in different magnitudes throughout their varied and often little-known life histories. Disturbance of desert soils such as compaction and erosion and removal of vegetation during site preparation affected the cover of desert plant species seven years postconstruction at ISEGS (Grodsky and Hernandez, 2020). Apart from Lepidoptera species and Buprestids, all the non-bee insect flower visitors collected in our study are predators in their larval stage. Given the potential for solar energy development to affect trophic interactions in the Mojave Desert (e.g., Moore-O'Leary et al., 2017; Grodsky et al., 2020a; Grodsky et al., 2020b; Saul-Gershenz et al., 2020), it is possible that site preparation at ISEGS altered host plants of phytophagous insects that served as a prey base for larval non-bee insect flower visitors. Pollinator abundance and species richness often are tightly linked with abundance and diversity of plants (Banasak, 1996). As adults, generalist non-bee insect flower visitors may have used abundant *L. tridentata*, which had largely recovered throughout most of ISEGS seven years postconstruction (Grodsky and Hernandez, 2020) and flowered during the sampling periods of both years (Grodsky, S.M., pers. obs.). In contrast, non-bee insect flower visitors specializing on insect prey that they feed their young may have decreased in abundance if host plants supporting their prey negatively responded to disturbance from solar energy development decisions.

The inability of long-lived cacti to rebound following disturbance from site preparation for solar energy development in deserts (see Grodsky and Hernandez, 2020) may have “bottom-up” ecological effects on non-bee insect flower visitors. Cacti support a diversity of wildlife species in deserts ecosystems, spanning from ants to birds (Polis, 1991;

Aranda-Rickert et al., 2014; Goettsch et al., 2015). For example, cacti provide pollen resources to a great diversity of wild bees throughout the Mojave and Sonoran Deserts of the United States (Grant and Hurd, 1979; Simpson and Neff, 1987; Janeba, 2009; Reyes-Agüero et al., 2006). It may stand to reason that if a vast array of wild bees coevolved with cacti in the Mojave Desert, then the same may be true for non-bee insect flower visitors. The obligate pollinator mutualisms between yucca moths (Lepidoptera: Prodoxidae) and yuccas (*Yucca* spp.) in North American deserts are a classic example of coevolution between plants and non-bee insect flower visitors in ecology (Pellmyr et al., 1996), as is the coevolved mutualism between fig wasps (Agaonidae) and their hosts (Moraceae: *Ficus* spp.) in the tropics (Weiblen, 2002). By this logic, abundance of non-bee insect flower visitors may have coincided, in part, with that of cacti, which were far more abundant in undeveloped desert controls than in the same solar energy development decision treatments in ISEGS (Grodsky and Hernandez, 2020).

Plant-pollinator relationships may interface with other ecosystem processes to shape responses of non-bee insect flower visitors to solar energy development. Wild bees are parasitized by at least two non-bee insect flower visitors that exhibited a strong, negative relationship with solar energy development. Bombyliids are possibly Batesian mimics and well-known parasitoids of bees; adults lay eggs in the vicinity of hosts (e.g., solitary bee burrow), and the bombyliid larvae eventually eat the host larvae (Hull, 1973; Yeates and Greathead, 1997). Larvae of *T. ornatus* are nest parasites of bees, especially those in the family Megachilidae (Linsley and MacSwain, 1943). Meanwhile, the Mojave Desert may support highly diverse assemblages of nectivorous bombyliids (Evenhuis, 1975). *T. ornatus* is considered a generalist flower



(caption on next column)

Fig. 3. Non-bee insect flower visitor responses to solar energy development decisions, including blading ($n = 3$), mowing ($n = 3$), and establishment of habitat patches (“halos”; $n = 3$), within Ivanpah Solar Electric Generating System and in surrounding undeveloped desert scrub ($n = 3$), 5 April–5 May 2018 and 2019, Ivanpah Valley, Mojave Desert, California, USA. Bars indicate upper 95% CI. Letters a and b and x and y indicate significant differences among treatments and controls in 2018 and 2019, respectively. We set the statistical significance level (α) to 0.05.

visitor consistent with its wide geographic range in the western United States (Linsley and MacSwain, 1943). Little information exists on the ecology of bombyliids (Toft, 1983) and the family Cleridae to which *T. ornatus* belongs (Opitz, 2002). Nevertheless, availability of bee hosts, in conjunction with that of floral resources, may have influenced the distribution and abundance of bombyliids and *T. ornatus* in and around ISEGS.

Apart from site preparation for solar energy development, non-bee insect flower visitors also may respond to the physical characteristics of solar facilities, including heliostats, electromagnetic fields, and sounds. Concentrating solar power facilities like ISEGS deploy hundreds of thousands of mirrors on desert landscapes. We hereby coin the “house of mirrors” effect as a possible explanation for reduced abundance of non-bee insect flower visitors in ISEGS. We posit that foraging flights of non-bee insect flower visitors and their ability to act on visual cues for identification of floral resources may be hindered by heliostats, which act as physical barriers in and of themselves and engender a myriad of potentially distorting image reflections at and above the heights of perennial and annual flowering desert plants, respectively. Although our treatment-level analyses suggest that this potential effect should be further evaluated, the fact that non-bee insect flower visitors did not respond to heliostat density may demonstrate that other factors could have stronger influences on their abundance and distribution in solar facilities (or that mirror densities were all above a threshold of manifested impact). Studies that track foraging insect flower visitors in both CSP and photovoltaic (PV) solar facilities may shed light on effects of solar energy infrastructure on the foraging behavior of non-bee insect flower visitors. Transformers and inverters at solar facilities, as well as the power lines connecting them to the grid, generate electromagnetic fields (Tell et al., 2015); low frequency electromagnetic fields have been shown to impair the cognitive and motor abilities of honey bees (e.g., Shepard et al., 2018) and may have similar effects on non-bee insect flower visitors. Both acoustically and non-acoustically oriented insects have been shown to be negatively affected by noise pollution (Senzaki et al., 2020), although studies specific to solar facilities are still nonexistent.

Our results are applicable to PV solar energy development in deserts. Historically, most PV facilities in deserts have been prepared by blading and mowing to heights lower than at CSP facilities like ISEGS, and they typically are devoid of habitat patches. These trends may suggest that increased intensity of disturbance at PV facilities relative CSP facilities might lead to even greater displacement of non-bee insect flower visitors. Additionally, heliostat density at CSP facilities inherently decreases with distance from the power towers (Grodsky and Hernandez, 2020), whereas PV facilities are comprised of uniformly dense panels that may shade and thereby reduce more floral resources relative to heliostats at CSP facilities. Several sites for PV facilities in the Sonoran Desert are set to be prepared by mowing at heights similar to or lower than that at ISEGS; similar displacement of non-bee insect flower visitors demonstrated by our study is likely to occur at these PV facilities. Unlike CSP facilities, photovoltaic solar facilities create polarized light pollution by reflecting horizontally polarized light, which, in turn, negatively affects some aquatic insects (Szaz et al., 2016) and may similarly impact non-bee insect flower visitors.

Displacement of non-bee insect flowers visitors at solar facilities in deserts may have cascading effects on insect-dependent plant

populations and ecosystem services, the latter of which are critical factors that shape ecosystem resiliency in coupled human-natural energy systems (Liu et al., 2007). Reductions in non-bee insect flower visitors will likely lead to decreased pollination as a regulating service in arid lands of the southwestern United States. Cacti populations are globally imperiled and maintain high ecosystem-service based values in the Mojave Desert (Goetsch et al., 2015; Grodsky and Hernandez, 2020). Additionally, insect-pollinated cacti are valuable agricultural crops in deserts outside of the United States, such as commercially distributed *Opuntia* species in the Chihuahuan Desert of Mexico (Sáenz-Hernández et al., 2002). Given the fact that reduced native pollinator abundances can coincide with declines in threatened and endangered plant species (Mathiasson and Rehan, 2020), displacement of non-bee insect flower visitors from desert solar facilities may exacerbate declines of sensitive cacti populations already impacted by site preparation for solar energy development (Grodsky and Hernandez, 2020). A plethora of desert plants potentially pollinated by non-bee insect flower visitors, including cacti, play key roles in the cultural heritages and landscapes of indigenous peoples in deserts globally. For example, desert plants are part of the cultural heritages of approximately half a million members of Native American tribes in the southwestern United States, who have been subjected to increased environmental vulnerability by the Westernization of their native lands and the subsequent exploitation of natural resources (summarized in Grodsky and Hernandez, 2020).

Biodiversity loss from solar energy development in deserts may be eliminated by alternative siting and limited by sustainable decision making, although research on the latter is woefully lacking (Moorman et al., 2019). Siting solar energy facilities on ecologically marginalized lands like abandoned farmland and contaminated sites and in the built environment (e.g., distributed solar on residential/commercial rooftops) rather than in undeveloped desert environments will sustain non-bee insect flower visiting populations in desert ecosystems while potentially conveying techno-ecological synergies (Hoffacker et al., 2017; Hernandez et al., 2019). Solar energy development decisions that may reduce negative effects on non-bee insect flower visitors and warrant investigation include the following: 1) mowing vegetation at heights taller than 0.30 m; 2) site preparation that entails neither blading nor mowing, such as “drive and crush”; and 3) creation of large-scale habitat patches within the footprint of solar facilities where soils and floral resources are left completely undisturbed via avoidance of desert washes and increased PV panel spacing, for example. In summary, disruption of non-bee insect pollinator communities from solar energy development in deserts may lead to cascading, negative effects on biodiversity, ecosystems, and ecosystem resiliency. As collaborations among diverse stakeholders, including solar developers, land managers, and researchers, continue to evolve, we suggest that prioritization of timely, solutions-oriented applied research is required to inform the sustainability of solar energy development in deserts specifically and diverse land covers globally.

Declaration of competing interest

We declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109336>.

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