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Of Mojave milkweed and mirrors: The population genomic structure of a species impacted by solar energy development

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Abstract

A rapid renewable energy transition has facilitated the development of large, ground-mounted solar energy facilities worldwide. Deserts, and other sensitive aridland ecosystems, are the second most common land-cover type for solar energy development globally. Thus, it is necessary to understand existing diversity within environmentally sensitive desert plant populations to understand spatiotemporal effects of solar energy siting and design. Overall, few population genomic studies of desert plants exist, and much of their biology is unknown. To help fill this knowledge gap, we sampled Mojave milkweed (*Asclepias nyctaginifolia*) in and around the Ivanpah Solar Electric Generating Station (ISEGS) in the Mojave Desert of California to understand the species' population structure, standing genetic variation, and how that intersects with solar development. We performed Restriction-site Associated Sequencing (RADseq) and discovered 9942 single nucleotide polymorphisms (SNPs). Using these data, we found clear population structure over small spatial scales, suggesting each site sampled comprised a genetically distinct population of Mojave milkweed. While mowing, in lieu of blading, the vegetation across the solar energy facility's footprint prevented the immediate loss of the ISEGS Mojave milkweed population, we show that the effects of land-cover change, especially those impacting desert washes, may impact long-term genetic diversity and persistence. Potential implications of this include a risk of overall loss of genetic diversity, or even hastened extirpation. These findings highlight the need to consider the genetic diversity of impacted species when predicting the

impact and necessary conservation measures of large-scale land-cover changes on species with small population sizes.

1 | INTRODUCTION

Desert ecosystems are areas of high solar energy potential, making them the second largest recipient environment (by area) globally for large, ground-mounted solar energy development (hereafter solar energy, >1 megawatts [MW_{DC}]; Kruitwagen et al., 2021; Prǎvǎlie et al., 2019). While solar energy facilities provide low-carbon, efficient energy, they can have substantial ecological impacts on aridland ecosystems, which are often already threatened (Grodsky & Hernandez, 2020; Hernandez et al., 2014; Stoms et al., 2013). Previous work illustrates that the effects of land-use and land-cover change on desert species are mostly negative (Sutherland et al., 2012) and include increased invasions by exotic annual grasses, higher fire risk, de-vegetation, extensive soil erosion, and reduced plant succession (Abatzoglou & Kolden, 2011; Abella, 2010; Cameron et al., 2012).

Land-use and land-cover changes associated with solar energy development may specifically alter patterns of wind, shade, hydrology (Armstrong et al., 2014; Suuronen et al., 2017; Tanner et al., 2020) plants (Grodsky & Hernandez, 2020; Hernandez et al., 2020; Tanner et al., 2021), and patterns of herbivory and pollination (Grodsky et al., 2021; Hernandez et al., 2014; Lovich & Ennen, 2011). Concentrating solar power (CSP) facilities, a type of solar energy, use large mirrors to reflect direct radiation to power towers and can increase local albedo by 30%–56%. The development of CSP may create localized drought conditions due to altered wind speeds, evapotranspiration, and excess heat (Lovich & Ennen, 2011). As many desert species live near their physiological water and heat limits, even small changes in their habitat, such as changes in patterns of hydrological flows supporting washes, can have large consequences (Archer & Predick, 2008; Grippo et al., 2015). Many desert species also struggle to recover from or adapt to rapid environmental changes, which can have long-term effects on population growth rates and individual fitness (Moore-O'Leary et al., 2017; Tanner et al., 2014).

Despite their economic importance and potential for large-scale habitat displacement, we have a limited understanding of the ecological impacts of solar energy development. Many desert plants have life history strategies that make them particularly vulnerable to impacts because they rely on conditions that only occur in a subset of climatic years for reproduction, dispersal, and gene-flow (Shryock et al., 2014). Additionally, due to their relatively large footprints and land transformation compared to fossil fuels and other renewables (Lovering et al., 2022), a single solar energy facility can encompass distributions of many plant species in a region. To increase the environmental sustainability of operating and planned solar energy facilities, an understanding of desert plant populations and their vulnerabilities to solar energy facility design is necessary. This need for an increased understanding of the impacts of solar energy development on plant populations is particularly pressing as development of renewable energy increases in aridlands globally (Hernandez, Hoffacker, & Field, 2015; Hernandez, Hoffacker, Murphy-Mariscal, et al., 2015; Kruitwagen et al., 2021).

Information about the spatial structure and genetic health of desert plant populations is needed to inform solar energy development. However, few population genetics studies of North American desert plants, especially genome-wide studies, exist. Therefore, there is not enough information currently to inform solar energy facility development, particularly siting and design, and to incorporate conservation actions that will protect geographically restricted plant species of conservation concern during development. Gaps in knowledge include a lack of understanding of how many unique populations exist in a given area and how much genetic diversity may be lost from anthropogenic disturbances, such as solar energy development (Allendorf, 2017; Fraser, 2017; Hoffmann et al., 2015). Genetic information can fill the information gaps regarding population structure, the existence of local adaptation, and presence of unique genetic diversity within populations (Charlesworth et al., 2003; Nadeau & Jiggins, 2010).

The southwestern United States is a hotspot for solar energy development (Lovich & Ennen, 2011). Within this region is the Mojave Desert, covering over 13 million hectares, many of which are ecologically intact due to the sparseness of city centers and large swathes of public land (Cameron et al., 2012). This region is also a hotspot for endemic, environmentally sensitive, and evolutionarily diverse plant life that is foundational to desert ecosystems (Vandergast et al., 2013). In the Mojave, desert

plants provide habitat and food resources to several charismatic invertebrates and vertebrates, including the federally listed desert tortoise (*Gopherus agassizii*, under the United States [US] federal Endangered Species Act [ESA]), black-tailed jackrabbit (*Lepus californicus*), the state listed Mojave ground squirrel (*Xerospermophilus mohavensis*, under the California ESA, US), the effectively listed monarch butterfly (*Danaus plexippus*, under the US federal ESA), queen butterfly (*Danaus gilippus*), and sphinx moth (Sphingidae) (Esque et al., 2003; Grodsky et al., 2017, 2019, 2020; Moore-O'Leary et al., 2017; Saul-Gershenz et al., 2020). Increasingly, the Mojave Desert is stressed by anthropogenic change (Randall et al., 2010) and impacts to desert plants are widespread (Agha et al., 2020; Lovich & Bainbridge, 1999; Tanner et al., 2021). As the Mojave Desert is progressively subjected to land-use and land-cover change, it is critical to understand and anticipate their impacts on plant species diversity (Smith et al., 2023).

The Ivanpah Solar Electric Generating System (ISEGS), a CSP facility located in the Mojave Desert of California, provides a model study system for determining how solar energy development affects rare plant populations. Located at the base of Clark Mountain, construction of ISEGS occurred between 2010 and 2014. At the time of its completion, ISEGS was the world's largest CSP facility, with an area of over 16 km^2 and a nameplate capacity of 392 megawatts (generating approximately 700,000 MWhy^{-1} of electricity annually from 2014 to 2020). Incorporated into the facility design were mitigation strategies to reduce impacts on the desert community by (1) mowing vegetation below and in between the heliostats (in lieu of blading, which removes all aboveground biomass and all soil surface microtopography, including washes) in all areas beyond the innermost heliostat loops (i.e., closest to the power tower); and, (2) the creation of undisturbed "halos" or micro-refugia where rare plants were identified prior to construction and left undisturbed (Grodsky & Hernandez, 2020). Importantly, it was not clear at the time if such an approach would have a conservation benefit.

The construction plans of ISEGS specifically attempted to limit the impact of construction on endemic desert plants. One such plant is Mojave milkweed (*Ascelpias nyctaginifolia*, Apocynaceae), an iteroparous perennial plant common throughout Arizona, Nevada, and New Mexico, but considered seriously threatened in California (Schmid & Tibor, 2001). In the Western Mojave, it is rare, found in the sandy soils of ephemeral and intermittent washes and slopes, and restricted to small microclimates in eastern California (Baldwin et al., 2002). Like many milkweed species, Mojave milkweed can propagate clonally and utilizes both wind and water for seed dispersal. This clonal propagation, coupled with the ability of the milkweed to die back vegetatively and exist in the soil as rhizomes, may help preserve genetic diversity during times of non-ideal conditions and disturbance.

To avoid mowing sensitive desert plants, ISEGS biologists mapped 202 Mojave milkweed individuals across 59 sites in 2008 and protected them within halos. Most were found in small- to medium sizes washes with sandy to gravelly soil. No information on individual plant traits (e.g., size), location, and population structure of Mojave milkweed was made publicly available (CEC, 2010). While the halos allowed milkweed to persist within ISEGS, the mowing and construction of concentric heliostats significantly altered the vegetation community within the ISEGS footprint (Grodsky & Hernandez, 2020). Understanding the population structure of Mojave milkweed both within and around the solar installation will be imperative in determining the best strategy to conserve this rare plant. Here, we aimed to address key information gaps related to the conservation of Mojave milkweed by determining the population structure and diversity of Mojave milkweed in the Ivanpah Valley, and its overlay with ISEGS. Our questions included:

1. Is there distinct population structure within the Ivanpah Valley Mojave milkweed or is it a continuous, panmictic population?
2. How does the spatial layout of the ISEGS facility overlay with any potential population structure, that is, how many unique populations does the ISEGS facility affect?
3. Is there unique genetic diversity found within ISEGS that could be lost due to disturbance?

2 | METHODS

2.1 | Sample collection

In 2015, we sampled leaf tissue of all vegetative Mojave milkweed plants at four locations: three sites undisturbed by facility construction and throughout ISEGS. The first of these sites ("Excelsior") is approximately 21 km west of ISEGS. The other two locations are approximately 5 km north ("Umberci")," and 60 km south ("Bobcat") of the solar facility (Figure 1). We cut small sections of green leaf tissue from mature plants and stored them in individually labeled coin envelopes with desiccant packets to promote drying. When present, we collected seeds for subsequent growth in a greenhouse, where leaves were cut and similarly stored once the plants reached sufficient maturity. It is important to note that while we collected all the plants present at the time, there is the possibility that some plants died back prior to our ability to collect them or remained dormant as rhizomes that season.
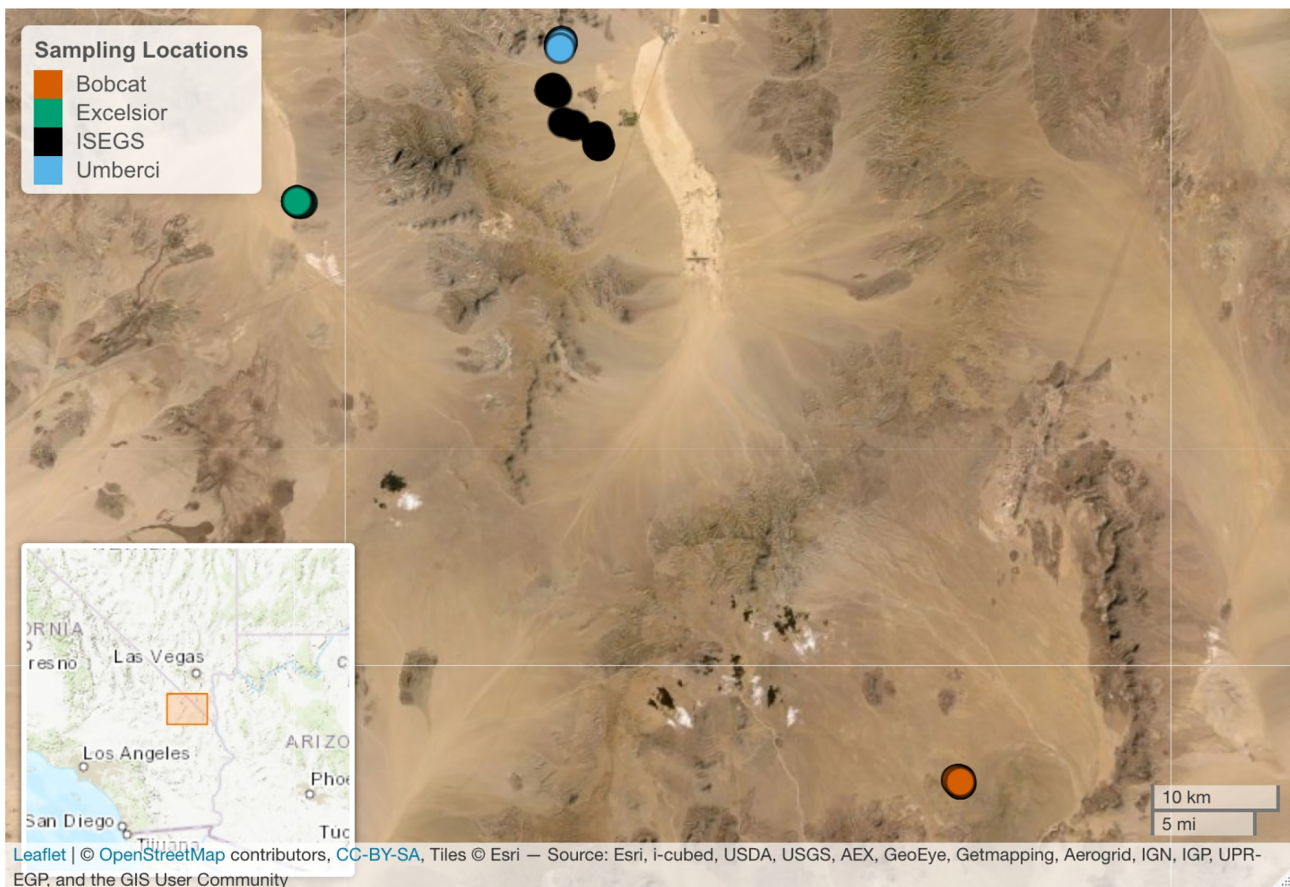
FIGURE 1 Map of the Mojave milkweed sampling sites. Note the spread of the sampling sites in the Ivanpah Solar Electricity Generating Station (ISEGS) facility compared to the natural populations. Samples from both 2015 and 2018 are included on the map.

We collected additional samples in the fall of 2018 from plants previously identified within the ISEGS halos ($n = 8$) as well as plants that emerged in halos after the 2015 sampling ($n = 30$). We also collected any previously unidentified plants that grew within the facility's footprint but outside of designated halo areas ($n = 51$). We acquired additional samples from the Umberci site of previously identified but unsampled plants ($n = 32$) and newly emerged plants ($n = 16$). We designated individuals (genets) based on the distance from other plants and sampled multiple ramets per genet if possible. We collected leaves from juvenile or adult individuals. For both years, we recorded the location of all plants present (Figure 1), even if they were too small to sample, to establish a census size (Table 1).

2.2 | Sequencing

For both the 2015 and 2018 samples, we disrupted the dried plant tissue with steel beads using a bead mill prior to extracting DNA. We performed DNA extractions using the DNeasy Plant Mini kit (QIAGEN Inc., Valencia, CA), and quantified the resulting concentrations of DNA using a Qubit fluorometer (Invitrogen, Carlsbad, CA). We diluted the purified DNA to a concentration of 10.0 ng/uL using low TE in preparation for Restriction site Associated DNA Sequencing (RADSeq) using the Best-RAD method (Ali et al., 2016). A modification to Ali et al. (2016) is that we used the restriction endonuclease *pstI* to digest the DNA due to the more favorable number of cut sites given the GC content and size of the *Asclepias syriaca* reference genome (Weitemier et al., 2019; Genbank accession GFXT01000000). We sonicated samples to a fragment length of 200 base pairs for the 2015 samples and 300 base pairs for the 2018 samples using a Covaris m220 (Covaris, Woburn, MA). Following library preparation with the NEBnext Ultra DNA kit for Illumina (New England Biolabs, Inc., Ipswich, MA), we performed library trace analysis using a Bioanalyzer 2100 (Agilent, Santa Clara, CA). We sequenced the 2015 samples on the Illumina HiSeq3000 platform at the University of California Davis DNA Technologies Core (PE-2 × 100 bp). For the 2018 samples, we sequenced on the Illumina HiSeq X platform (PE-2 × 150 bp) at the UC Davis Sequencing Center

TABLE 1 Measurements of diversity for Mojave milkweed populations of the Ivanpah Valley.

Site name	Samples collected 2015/2018	Samples analyzed 2015/combined years	Census size (total)	Allelic richness (rarefied)	Ho	He	Fis (95% CI)	Ne (95% CI)	Av. φ
Bobcat	27/0	20/20	30	1.47	0.138	0.138	0.001 (−0.013 to 0.003)	33.0 (15.7–212.0)	0.01
Excelsior	12/0	11/11	23	1.45	0.135	0.136	−0.001 (−0.008 to 0.011)	71.5 (25.5–infinite)	0.001
ISEGS	23/90	17/84	226	1.5	0.142	0.144	0.007* (0.005 to 0.018)	27.6 (12.2–421.4)	0.003
Umberci	34/47	42/60	79	1.47	0.142*	0.140*	−0.004* (−0.016 to −0.004)	23.8 (14.1–46.5)	0.002

Note: Some samples were collected from the same plant across sampling years. All values were calculated using a dataset with clonal ramets removed. Ho = observed heterozygosity, He = expected heterozygosity, Fis = inbreeding coefficient, Ne = effective population size, Av. Φ = within-population relatedness coefficient. There were no significant differences between observed and expected heterozygosity following Bartlett's test for the homogeneity of variances ($p \ll 0.001$) and a paired t-test (95% confidence intervals [CI]) in any of the populations except Umberci (denoted with an asterisk). Fis 95% CI were calculated by bootstrapping using boot.ppfis in hierfstat (significant intervals denoted with an asterisk). Reported CI for Ne were calculated using the pseudo-jackknife method outlined in (Jones et al., 2016).

(Novogene Corporation Inc.). The longer read length for the 2018 samples was due to the technical specifications of the sequencing platform. Prior to analyzing data from both sampling years, we trimmed the 2018 samples to the same length as the 2015 samples (100 bp) using trimmomatic v0.38 (Bolger et al., 2014).

2.3 | SNP discovery

Following sequencing, we demultiplexed data for all individuals from both sampling years ($n = 233$) using -process_radtags in STACKS v2.4 (Catchen et al., 2011, 2013) and the following tags: --bestrad, -c, -r, -D. We aligned the files to the *A. syriaca* reference genome (Weitemier et al., 2019) (Genbank accession GFXT01000000) using the --very-sensitive-local wrapper in Bowtie2 v2.3.4 (Langmead & Salzberg, 2012). We used the -ref_map.pl pipeline in STACKS v2.4 to call random SNPs (--write_random_snp) in the dataset. We retained loci that were present in at least 30% of individuals per population within a single population and proceeded with quality filtration on the resulting VCF file.

We quality filtered the resulting file using VCFtools v0.1.15 (Danecek et al., 2011). Initially, we identified and removed individuals that were not genotyped at greater than 95% of loci and genotypes with a minimum read depth of less than 5. We then filtered out all genotypes with a gene quality score of less than 20. We subsequently removed loci with a minor allele count (MAC) of less than three (see O'Leary et al., 2018), followed by filtering out SNPs with a call rate of less than 90%. The final filtration step again identified and removed individuals with less than 85% of loci genotyped. We performed the SNP discovery on all samples combined to ensure the same loci were called across all samples and later separated out individual sampling years for downstream analysis. We removed any remaining monomorphic and uninformative loci using informloci in the R (R Core Team, 2020) package poppr (Kamvar et al., 2014, 2015) prior to proceeding with further analyses.

2.4 | Genetic diversity

We analyzed our SNP dataset to determine genetic diversity using allelic richness, effective population size (Ne), inbreeding coefficients (Fis), population differentiation, and observed/expected heterozygosity. We calculated heterozygosity, Fis, and allelic richness using the basic.stats and allelic.richness functions of hierfstat (Goudet, 2005). Private alleles were determined using the private_alleles function in the R package poppr (Kamvar et al., 2014,

2015). In the private allele calculations, we used datasets from 2015 and a combined 2015 and 2018 dataset that excluded clones. We calculated the effective population size using NeEstimator v2.1 (Do et al., 2014) under the linkage disequilibrium model with an allele frequency of 0.05 using our clone-free dataset from 2015 (see below).

2.5 | Population structure

When determining population structure, we removed clonal ramets from the 2015 dataset according to their multilocus genotypes, using the mlg.filter function with a genetic distance threshold of 0.04 as calculated by the bitwise.dist function in poppr (Kamvar et al., 2014). We incorporated relatedness by calculating pairwise φ among all samples using the relatedness2 estimator in VCFtools (Danecek et al., 2011; Manichaikul et al., 2010). We removed individuals with pairwise φ values greater than 0.177, which corresponds with first-degree relatives such as full siblings and parent-offspring pairs, as clustering algorithms can be influenced by close relatives (Rodríguez-Ramilo et al., 2014; Rodríguez-Ramilo & Wang, 2012). For each dataset, we evaluated the population structure of the plants using discriminant analysis of principle components via the R package adegenet (Jombart, 2008; Jombart et al., 2010). We cross-referenced these results using the program *STRUCTURE* (Falush et al., 2003, 2007; Hubisz et al., 2009; Pritchard et al., 2000) and visualized the data using Structure Harvester (Earl & vonHoldt, 2011). We also assessed population differentiation (Fst) using the method outlined by Weir and Cockerham (1984) using the package hierfstat (Goudet, 2005). To further investigate the relationships between individuals, we calculated Minimum Spanning Networks (MSN) in poppr using the bitwise.dist and poppr.msn functions. Finally, we tested for isolation by distance in the samples using the R package conStruct (Bradburd et al., 2018).

3 | RESULTS

3.1 | Sequencing and SNP discovery

We averaged 229,029,275 raw sequences per library, 4,306,523.6 mapped reads per individual, and an average coverage across loci of 30.5×. After filtering, we discovered 9942 SNPs with <3% missingness in the combined dataset of 175 samples. For the dataset comprised of individuals identified in 2015, we discovered 9503 SNPs across 90 individuals with an average missingness of

3.23%. For the dataset comprised of individuals identified in 2018, we found 9643 polymorphic SNPs across 113 individuals with an average missingness of 2.46%. The discrepancy in the number of SNPs between the dataset is due to the removal of monomorphic loci from the dataset following the separation by sampling year.

3.2 | Genetic diversity

Overall, genetic diversity was similar across sites (Table 1). All sites had similar values for allelic richness, with ISEGS having the highest allelic richness (1.5) and Excelsior the lowest (1.45; Table 1). The values of observed heterozygosity (Ho) were also similar across sites, with ISEGS and Umberci have the highest observed value (Ho = 1.42) and Excelsior the lowest (Ho = 1.35; Table 1). Umberci and ISEGS were also the only sites with a significant difference in expected versus observed heterozygosity. However, in ISEGS, the observed heterozygosity was less than expected, and in Umberci, we saw the opposite trend, where observed heterozygosity was greater than expected. Both ISEGS and Umberci had significant inbreeding coefficients, with ISEGS having a slightly positive value (0.007) and Umberci a slightly negative measurement (−0.004; Table 1). Bobcat had the highest average coefficient of relatedness (φ) of 0.01. Clonal ramets were confirmed in all sites but Excelsior. The effective population sizes (Ne) of each population ranged from 24 to 72 (Table 1). The calculated Ne is smaller than the census size in both Umberci and ISEGS. The Ne estimate of Bobcat is closest to the census number, and the estimate for Excelsior is roughly five times greater than the census size, even though it had the smallest values for diversity metrics such as observed heterozygosity and allelic richness.

We found alleles private to each population, with more unique diversity discovered in ISEGS in the additional year of sampling (Table 1; Figure 2). For the 2015 dataset, 1896 out of the 9503 loci had alleles private to a single site, with a portion of the private alleles present in only a single individual (Table 2; Figure 2). The number of private alleles per site ranged from 186 in Excelsior to 841 in Umberci, representing 1%–5% of total allelic diversity per site (Table 2; Figure 2). The site with the largest proportion of private alleles in 2015 was Umberci (0.050) and the site with the lowest was Excelsior (0.013). For the dataset comprising both 2015 and 2018 samples, 1059 out of the 9942 alleles were private to a single sampling site, and all private alleles were present in at least two individuals in each population. Excelsior again contained the
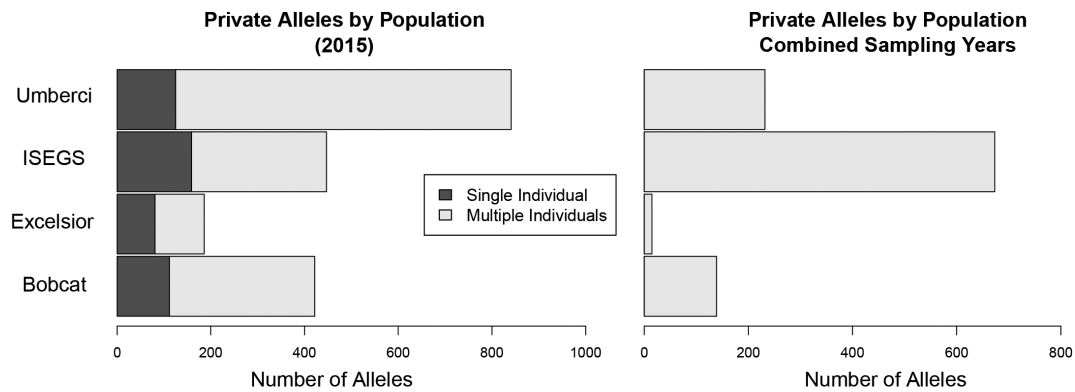
FIGURE 2 Private alleles of Mojave milkweed from the 2015 sampling year and a combination of individuals from sampling years. As the additional sampling year included many individuals from both ISEGS and Umberci, an overall decrease in private alleles is not unexpected as the populations are geographically close to one another and would reasonably share many alleles. No private alleles were found in a single genet in the combined years, while there were many cases of a single genet containing alleles in 2015.

TABLE 2 Proportion of private alleles in Mojave milkweed populations across sampling years.

Population	2015			Combined years		
	Total alleles in population	Total private alleles	Relative proportion of alleles	Total alleles in population	Total private alleles	Relative proportion of alleles
Bobcat	15,860	422	0.027	16,304	139	0.009
Excelsior	14,749	186	0.013	15,182	15	0.001
Ivanpah Solar Electric Generating Station (ISEGS)	16,050	447	0.028	19,212	673	0.035
Umberci	16,785	841	0.050	17,861	232	0.013

Note: Allele counts were calculated using the mk.counts function in the R package PopGenReport.

fewest private alleles (15) and ISEGS contained the greatest (673), representing between <1 and 4% of the allelic diversity (Table 2). Like the original dataset, the combined-year samples had the lowest proportion of private alleles in Excelsior (0.001), but the population with the largest proportion of private alleles was ISEGS (0.035; Table 2).
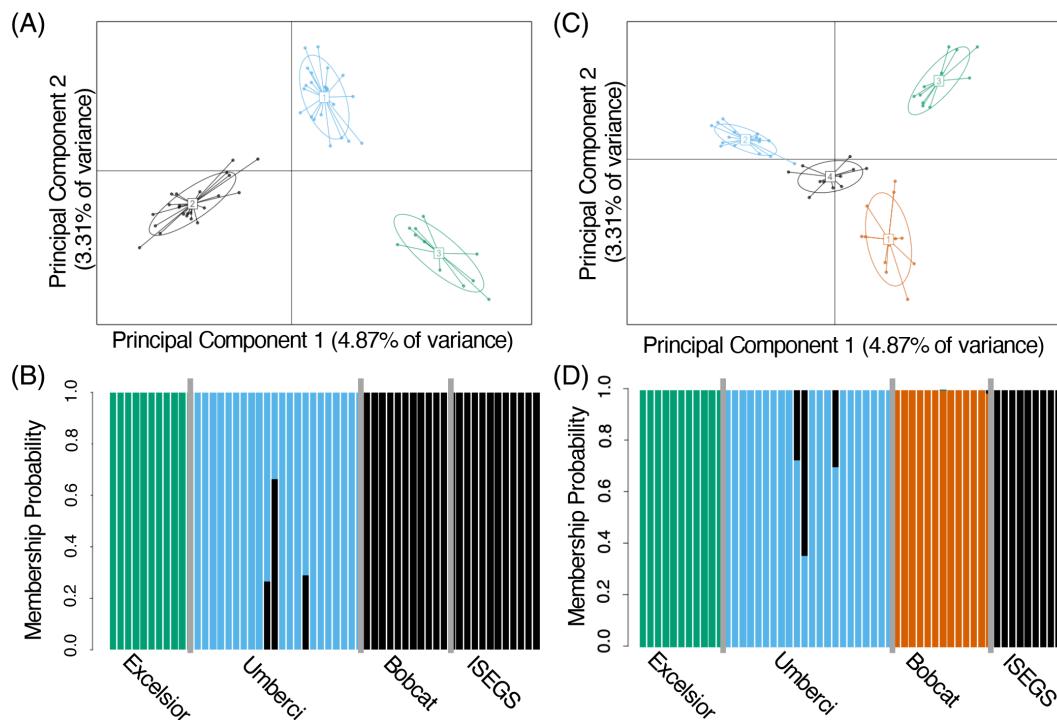
3.3 | Population structure

Using the samples from 2015, we confirmed distinct populations of Mojave milkweed across the Ivanpah Valley. Principal components analysis (PCA) and K-means clustering prior to discriminant analysis of principal components (DAPC) indicated that two to five groups had the best fit (Figures S1–S3 and S5), with the Umberci site consistently separating out first, followed by ISEGS, Bobcat, and Excelsior (Figure 3). At $K = 5$, the Umberci population began subdividing (Figure S4). During cross-validation, STRUCTURE analysis indicated four populations (Figure S5). The MSN analysis revealed a similar

pattern of genetic distances that corresponded with this population structure, placing ISEGS as the center of the network with a few individuals from the surrounding sites clustering with the ISEGS samples (Figure 4). As the ISEGS Mojave milkweed individuals are located centrally in the network, this suggests that they contain variation that is ancestral to the other populations. ISEGS also had the lowest genetic differentiation (Fst) from the surrounding populations (0.036 [pairwise with Bobcat], 0.038 [pairwise with Excelsior], and 0.040 [pairwise with Umberci], Table 3); however, all Fst values were statistically significant, indicating that each population is well-differentiated (Table 3). The isolation by distance model was not significant, indicating that isolation by distance does not appear to drive the population structure in our system.

4 | DISCUSSION

Our study shows that Mojave milkweed is highly structured throughout the Ivanpah Valley, and the footprint of the ISEGS facility supports an entire, genetically distinct

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FIGURE 3 Discriminant analysis of principal components (DAPC) and membership probability plots of the Mojave milkweed individuals identified in 2015. There is clear population structure present in the Mojave milkweed populations of the Ivanpah Valley. Shown are scatterplots of individuals under $K = 3$ (a) and $K = 4$ (c) genetic groups and their corresponding membership probabilities (b and d, respectively) from the DAPC analysis. The analysis also suggests past gene flow between ISEGS and Umberci, as there are individuals clustered in Umberci that have membership probability in ISEGS.
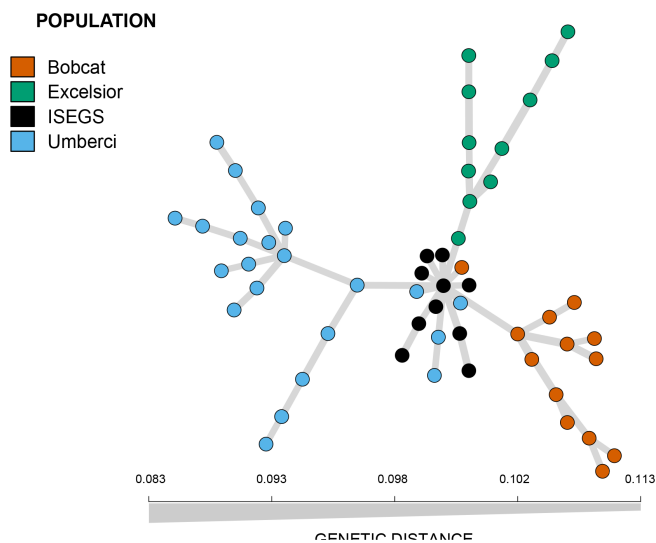
FIGURE 4 Minimum Spanning Network of the 2015 samples. Horizontal axis indicates pairwise Euclidean distance of each sample, which has no underlying biological assumptions. The ISEGS Mojave milkweed individuals are located centrally in the network, suggesting that they contain variation that is ancestral to the other populations. The populations' ancestral position is further supported by some individuals that were sampled from other populations clustering closer, based on genetic distance, to ISEGS samples than their putative populations.

population of this rare plant species. We found that each sampled population of Mojave milkweed contained unique genetic variation. The DAPC analysis shows that populations throughout the Ivanpah Valley are highly structured; however, there is evidence of some recent gene flow between the ISEGS and Umberci populations (Figure 3). This is most likely due to the relatively closer proximity between these populations compared to others and facilitated by the ability of the milkweed seeds to be dispersed by wind (Wyatt & Broyles, 1994). Interestingly, the MSN based on genetic distance placed some individuals from other sites within the ISEGS cluster (Figure 4). This finding, coupled with the central location of the ISEGS cluster in the network, the number of private alleles, and the lowest pairwise Fst values associated with ISEGS, strengthens the idea that ISEGS plants serve as a source of rare genetic diversity for Mojave milkweed in the Ivanpah Valley. This finding coincides with other studies of endemic plants of narrow geographic range (Radosavljević et al., 2015; Surina et al., 2014) where the central populations tend to have higher genetic diversity than other populations across the range.

The distinct population structure of Mojave milkweed in the Ivanpah Valley, coupled with the small effective population size of each individual population, may lead to

TABLE 3 Pairwise differentiation among the Mojave milkweed populations.

	Bobcat	Excelsior	ISEGS	Umberci
Bobcat		0.045	0.036	0.053
Excelsior	(0.042–0.049)		0.038	0.056
Ivanpah Solar Electric Generating Station (ISEGS)	(0.034–0.038)	(0.035–0.040)		0.040
Umberci	(0.050–0.055)	(0.053–0.060)	(0.038–0.042)	

Note: Upper diagonal is Fst calculated according to Weir and Cockerham (1984). Lower diagonal shows 95% confidence intervals following 999 permutations.

eventual genetic erosion (Aguilar et al., 2008). This is especially true given the small Ne values (Table 1), leaving these populations susceptible to reduced population viability (Frankham et al., 2014). The calculated Ne values as well as most of the confidence intervals of the Mojave milkweed populations were less than the 50/500 rule, where in the short term an Ne ≥ 50 reduces inbreeding depression and a long-term Ne ≥ 500 maintains evolutionary potential (Jamieson & Allendorf, 2012). For one of the populations, Excelsior, the pseudo-jackknifed upper-bound confidence interval returned a value of "infinite" (Table 1). This finding may be interpreted as an insignificant interval as the genetic results may be explained entirely by the sample size being too small rather than the effects of genetic drift (Waples & Do, 2010). As Excelsior was the population with the smallest census and sampling sizes, this is not altogether unsurprising. However, given that the Excelsior population had the smallest observed and expected heterozygosity values, the least allelic richness, and the lowest proportion of private alleles, there are likely impacts to the population's long-term evolutionary capacity regardless of the insignificant Ne upper bound (Allendorf, 1986; Lesica & Allendorf, 1992). Finally, while the sampled populations of Mojave milkweed have similar overall genetic diversity, the extremely small size of each population and high proportion of private alleles within each population means the loss of a single individual could result in the loss of a significant amount of the genetic diversity within that population.

Genetic diversity is essential for the persistence of populations of rare species. When populations have extremely small numbers of individuals, they are at increased risk of inbreeding depression, loss of genetic diversity, and fixation of maladaptive traits (Lande, 1998). These are important considerations in mitigation and management strategies (Clarke et al., 2012; Coates et al., 2018), especially in plants (Oostermeijer et al., 2003). Overall genetic diversity, one of the pillars of biodiversity (DeWoody et al., 2021), is critical in maintaining population longevity because increased diversity is linked to increased fitness (Frankham, 1995; Willis, 1993) and adaptive potential (Fernandez-Fournier et al., 2021). This is especially prescient in an age of unprecedented anthropogenic change (Foley et al., 2013).

The distinct population structure of Mojave milkweed in the Ivanpah Valley, coupled with the small effective population size of each individual population, may lead to eventual genetic erosion (Aguilar et al., 2008). This is especially true given the small Ne values (Table 1), leaving these populations susceptible to reduced population viability (Frankham et al., 2014). The observed Ne values of each of the Mojave milkweed populations were much less than the 50/500 rule, where in the short term, an Ne of 50 reduces inbreeding depression and a long-term Ne of 500 maintains evolutionary potential (Jamieson & Allendorf, 2012). Coupled with these consequences, populations with consistently small Ne values are at a greater risk for the loss of important genetic variation due to the process of genetic drift (Ellstrand & Elam, 1993).

Another concern for these populations of rare plants lies in one of its life history strategies, clonality, as excessive clonal propagation increases allelic diversity and heterozygosity at the expense of increased inbreeding (Balloux et al., 2003; Meloni et al., 2013). Additionally, as Mojave milkweed is self-incompatible, it is overall more susceptible to the loss of genetic variation following disturbance and habitat fragmentation (Honnay & Jacquemyn, 2007), which may impact the ISEGS population due to the presence of the solar energy facility. The combined effects of clonality and self-incompatibility appear to reduce genetic diversity, potentially due to reduced mate availability (Honnay & Jacquemyn, 2008). Following disturbance in the form of urbanization, clonal, self-incompatible plants had decreased clonal diversity and reproductive success (Bartlewicz et al., 2015), which would further affect population viability, especially in populations with already low numbers (Honnay & Bossuyt, 2005). As our dataset included putative clones in all sites except for Excelsior, the potential effects of clonality on the reproductive strategy of Mojave milkweed and its population longevity should be investigated (Witte & Stöcklin, 2010).

The ISEGS facility clearly overlays an entire population of Mojave milkweed that contains considerable genetic distinctiveness, so local extirpation of the milkweed could result in the loss of crucial genetic diversity

for the persistence and adaptive potential of the species in this region (Ricklefs, 1987). This highlights the importance of protecting this population within ISEGS. It is also important to note that construction of the facility likely resulted in mortality of some individuals prior to this study (as Mojave milkweed can remain dormant belowground for greater than 1 year), thus resulting in the undetected loss of their genetic diversity. While mowing instead of blading within ISEGS preserved some plants, a recent study found that the mowed areas in ISEGS had less plant cover and structure of cacti and Mojave yucca (*Yucca schidigera*) than undeveloped areas (Grodsky & Hernandez, 2020), indicating an overall loss of biodiversity. The question of how the construction of USSE impacts long-term diversity is ripe for investigation. Of special interest would be if the construction and operation of the ISEGS facility significantly alters (1) hydrological patterns supporting intermittent and ephemeral washes that are preferred substrates for Mojave milkweed germination and establishment (Grippo et al., 2015), (2) patterns of herbivory owing to fencing that may impact animal movement within and outside the facility's footprint (Grodsky et al., 2020; Sawyer et al., 2022), and (3) habitat fragmentation. All effects individually or combined may lead to reduced genetic variation and loss of local genetic structure in plant populations (Young et al., 1996).

Our findings demonstrate the importance of understanding population structure and genetic composition of rare and imperiled plants when designing large, ground-mounted solar energy facilities. The insights gained from this study are useful for siting and designing future solar energy facilities sustainably, including the importance of multi-year species monitoring in deserts prior to construction. Our work shows that creating the halos was beneficial to the genetic health of the Mojave milkweed in the area, as it preserved an entire, genetically unique population. However, the impact of solar energy infrastructure on patterns of hydrological flow that create and sustain desert washes—washes that serve as critical substrates for Mojave milkweed—remains a critical research gap. Loss of the unique genetic diversity found in this population could be detrimental to the long-term persistence and adaptive capacity of this important plant. In the future, the siting of large, ground-mounted solar energy should consider the population structure of rare and imperiled species in the area as to ensure sites do not entirely overlay single populations. Understanding the population structure of species impacted by solar energy development can serve to align goals for a rapid, renewable energy transition and biological conservation.

DATA AVAILABILITY STATEMENT
Dataset available at https://doi.org/10.5061/dryad.59zw3r28c

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REFERENCES
Abatzoglou, J. T., & Kolden, C. A. (2011). Climate change in Western US deserts: Potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management*, *64*, 471–478.
Abella, S. R. (2010). Disturbance and plant succession in the Mojave and Sonoran deserts of the American southwest. *International*

Journal of Environmental Research and Public Health, 7, 1248–1284.

Agha, M., Lovich, J. E., Ennen, J. R., & Todd, B. D. (2020). Wind, sun, and wildlife: Do wind and solar energy development short-circuit conservation in the western United States? *Environmental Research Letters*, 15, 075004.

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y., & Lobo, J. (2008). Genetic consequences of habitat fragmentation in plant populations: Susceptible signals in plant traits and methodological approaches. *Molecular Ecology*, 17, 5177–5188.

Ali, O. A., O'Rourke, S. M., Amish, S. J., Meek, M. H., Luikart, G., Jeffres, C., & Miller, M. R. (2016). RAD capture (rapture): Flexible and efficient sequence-based genotyping. *Genetics*, 202, 389–400.

Allendorf, F. W. (1986). Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology*, 5, 181–190.

Allendorf, F. W. (2017). Genetics and the Conservation of Natural Populations: Allozymes to Genomes. *Molecular Ecology*, 26, 420–430.

Archer, S. R., & Predick, K. I. (2008). Climate change and ecosystems of the southwestern United States. *Rangelands*, 30, 23–28.

Armstrong, A., Waldron, S., Whitaker, J., & Ostle, N. J. (2014). Wind farm and solar park effects on plant–soil carbon cycling: Uncertain impacts of changes in ground-level microclimate. *Global Change Biology*, 20, 1699–1706.

Baldwin, B. G., Boyd, S., Ertter, B., Patterson, R., Rosatti, T. J., & Wilken, D. (Eds.). (2002). *The Jepson desert manual: Vascular plants of southeastern California*. University of California Press.

Balloux, F., Lehmann, L., & de Meeûs, T. (2003). The population genetics of clonal and partially clonal diploids. *Genetics*, 164, 1635–1644.

Bartlewicz, J., Vandepitte, K., Jacquemyn, H., & Honnay, O. (2015). Population genetic diversity of the clonal self-incompatible herbaceous plant *Linaria vulgaris* along an urbanization gradient. *Biological Journal of the Linnean Society*, 116, 603–613.

Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics*, 30, 2114–2120.

Bradburd, G. S., Coop, G. M., & Ralph, P. L. (2018). Inferring continuous and discrete population genetic structure across space. *Genetics*, 210, 33–52.

Cameron, D. R., Cohen, B. S., & Morrison, S. A. (2012). An approach to enhance the conservation-compatibility of solar energy development. *PLoS One*, 7, e38437.

Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An analysis tool set for population genomics. *Molecular Ecology*, 22, 3124–3140.

Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: building and genotyping loci de novo from short-read sequences. *G3 (Bethesda)*, 1, 171–182.

CEC, California Energy Commission. (2010). *Ivanpah solar electric generating system, commission decision*. CEC-800-2010-004 CMD Docket Number 07-AFC-5.

Charlesworth, B., Charlesworth, D., & Barton, N. H. (2003). The effects of genetic and geographic structure on neutral variation. *Annual Review of Ecology, Evolution, and Systematics*, 34, 99–125.

Clarke, L. J., Jardine, D. I., Byrne, M., Shepherd, K., & Lowe, A. J. (2012). Significant population genetic structure detected for a new and highly restricted species of Atriplex (Chenopodiaceae) from Western Australia, and implications for conservation management. *Australian Journal of Botany*, 60, 32–41.

Coates, D. J., Byrne, M., & Moritz, C. (2018). Genetic diversity and conservation units: Dealing with the species-population continuum in the age of genomics. *Frontiers in Ecology and Evolution*, 6, 165.

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., Durbin, R., & 1000 Genomes Project Analysis Group. (2011). The variant call format and VCFtools. *Bioinformatics*, 27, 2156–2158.

DeWoody, J. A., Harder, A. M., Mathur, S., & Willoughby, J. R. (2021). The long-standing significance of genetic diversity in conservation. *Molecular Ecology*, 30, 4147–4154.

Do, C., Waples, R. S., Peel, D., Macbeth, G. M., Tillett, B. J., & Ovenden, J. R. (2014). NeEstimator v2: Re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. *Molecular Ecology Resources*, 14, 209–214.

Earl, D. A., & vonHoldt, B. M. (2011). Structure Harvester: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, 4, 359–361.

Ellstrand, N. C., & Elam, D. R. (1993). Population genetic consequences of small population size: Implications for plant conservation. *Annual Review of Ecology and Systematics*, 24, 217–242.

Esque, T. C., Schwalbe, C. R., DeFalco, L. A., Duncan, R. B., & Hughes, T. J. (2003). Effects of desert wildfires on desert tortoise (*Gopherus agassizii*) and other small vertebrates. *The Southwestern Naturalist*, 48, 103–111.

Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, 164, 1567–1587.

Falush, D., Stephens, M., & Pritchard, J. K. (2007). Inference of population structure using multilocus genotype data: Dominant markers and null alleles. *Molecular Ecology Notes*, 7, 574–578.

Fernandez-Fournier, P., Lewthwaite, J. M. M., & Mooers, A. Ø. (2021). Do we need to identify adaptive genetic variation when prioritizing populations for conservation? *Conservation Genetics*, 22, 1–12.

Foley, S. F., Gronenborn, D., Andreae, M. O., Kadereit, J. W., Esper, J., Scholz, D., Pöschl, U., Jacob, D. E., Schöne, B. R., Schreg, R., Vött, A., Jordan, D., Lelieveld, J., Weller, C. G., Alt, K. W., Gaudzinski-Windheuser, S., Bruhn, K.-C., Tost, H., Sirocko, F., & Crutzen, P. J. (2013). The Palaeoanthropocene—The beginnings of anthropogenic environmental change. *Anthropocene*, 3, 83–88.

Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: A review. *Genetical Research*, 66, 95–107.

Frankham, R., Bradshaw, C. J. A., & Brook, B. W. (2014). Genetics in conservation management: Revised recommendations for the 50/500 rules, red list criteria and population viability analyses. *Biological Conservation*, 170, 56–63.

Fraser, D. J. (2017). Genetic diversity of small populations: Not always "doom and gloom"? *Molecular Ecology*, 26, 6499–6501.

Goudet, J. (2005). HIERFSTAT, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes*, 5, 184–186.

Grippo, M., Hayse, J. W., & O'Connor, B. L. (2015). Solar energy development and aquatic ecosystems in the southwestern United States: Potential impacts, mitigation, and research needs. *Environmental Management*, 55, 244–256.

Grodsky, S., Moore-O'Leary, K., & Hernandez, R. (2017). From butterflies to bighorns: Multi-dimensional species-species and species-process interactions may inform sustainable solar energy development in desert ecosystems. In: Reynolds, R.L. (Ed.), *Proceedings of the 31st Annual Desert Symposium*. California State University Desert Studies Center, Zzyzx, CA, April 14–15, 2017.

Grodsky, S. M., Campbell, J. W., & Hernandez, R. R. (2021). Solar energy development impacts flower-visiting beetles and flies in the Mojave Desert. *Biological Conservation*, *263*, 109336.

Grodsky, S. M., & Hernandez, R. R. (2020). Reduced ecosystem services of desert plants from ground-mounted solar energy development. *Nature Sustainability*, *3*, 1036–1043.

Grodsky, S. M., Saul-Gershenz, L. S., Moore-O'Leary, K. A., & Hernandez, R. R. (2020). Her Majesty's desert throne: The ecology of queen butterfly oviposition on Mojave milkweed host plants. *Insects*, *11*, 257.

Grodsky, S. M., Saul-Gershenz, L. S., Moore-O'Leary, K. A., Whitney, J. P., & Hernandez, R. R. (2019). Hare don't care! Consumption of a rare, desert milkweed containing phytochemicals by the black-tailed jackrabbit. *Journal of Arid Environments*, *174*, 103991.

Hernandez, R. R., Easter, S. B., Murphy-Mariscal, M. L., Maestre, F. T., Tavassoli, M., Allen, E. B., Barrows, C. W., Belnap, J., Ochoa-Hueso, R., Ravi, S., & Allen, M. F. (2014). Environmental impacts of utility-scale solar energy. *Renewable and Sustainable Energy Reviews*, *29*, 766–779.

Hernandez, R. R., Hoffacker, M. K., & Field, C. B. (2015). Efficient use of land to meet sustainable energy needs. *Nature Climate Change*, *5*, 353–358.

Hernandez, R. R., Hoffacker, M. K., Murphy-Mariscal, M. L., Wu, G. C., & Allen, M. F. (2015). Solar energy development impacts on land cover change and protected areas. *Proceedings of the National Academy of Sciences*, *112*, 13579–13584.

Hernandez, R. R., Tanner, K. E., Haji, S., Parker, I. M., Pavlik, B. M., & Moore-O'Leary, K. A. (2020). Simulated photovoltaic solar panels alter the seed bank survival of two desert annual plant species. *Plants*, *9*, 1125.

Hoffmann, A., Griffin, P., Dillon, S., Catullo, R., Rane, R., Byrne, M., Jordan, R., Oakeshott, J., Weeks, A., Joseph, L., Lockhart, P., Borevitz, J., & Sgrò, C. (2015). A framework for incorporating evolutionary genomics into biodiversity conservation and management. *Climate Change Responses*, *2*, 1.

Honnay, O., & Bossuyt, B. (2005). Prolonged clonal growth: Escape route or route to extinction? *Oikos*, *108*, 427–432.

Honnay, O., & Jacquemyn, H. (2007). Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology*, *21*, 823–831.

Honnay, O., & Jacquemyn, H. (2008). A meta-analysis of the relation between mating system, growth form and genotypic diversity in clonal plant species. *Evolutionary Ecology*, *22*, 299–312.

Hubisz, M. J., Falush, D., Stephens, M., & Pritchard, J. K. (2009). Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources*, *9*, 1322–1332.

Jamieson, I. G., & Allendorf, F. W. (2012). How does the 50/500 rule apply to MVPs? *Trends in Ecology & Evolution*, *27*, 578–584.

Jombart, T. (2008). Adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405.

Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics*, *11*, 94.

Jones, A. T., Ovenden, J. R., & Wang, Y.-G. (2016). Improved confidence intervals for the linkage disequilibrium method for estimating effective population size. *Heredity*, *117*, 217–223.

Kamvar, Z. N., Brooks, J. C., & Grünwald, N. J. (2015). Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Frontiers in Genetics*, *6*, 208.

Kamvar, Z. N., Tabima, J. F., & Grünwald, N. J. (2014). Poppr: An R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ*, *2*, e281.

Kruitwagen, L., Story, K. T., Friedrich, J., Byers, L., Skillman, S., & Hepburn, C. (2021). A global inventory of photovoltaic solar energy generating units. *Nature*, *598*, 604–610.

Lande, R. (1998). Anthropogenic, ecological and genetic factors in extinction and conservation. *Population Ecology*, *40*, 259–269.

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with bowtie 2. *Nature Methods*, *9*, 357–359.

Lesica, P., & Allendorf, F. W. (1992). Are small populations of plants worth preserving? *Conservation Biology*, *6*, 135–139.

Lovering, J., Swain, M., Blomqvist, L., & Hernandez, R. R. (2022). Land-use intensity of electricity production and tomorrow's energy landscape. *PLoS One*, *17*, e0270155.

Lovich, J. E., & Bainbridge, D. (1999). Anthropogenic degradation of the Southern California desert ecosystem and prospects for natural recovery and restoration. *Environmental Management*, *24*, 309–326.

Lovich, J. E., & Ennen, J. R. (2011). Wildlife conservation and solar energy development in the desert southwest, United States. *Bioscience*, *61*, 982–992.

Manichaikul, A., Mychaleckyj, J. C., Rich, S. S., Daly, K., Sale, M., & Chen, W.-M. (2010). Robust relationship inference in genome-wide association studies. *Bioinformatics*, *26*, 2867–2873.

Meloni, M., Reid, A., Caujapé-Castells, J., Marrero, Á., Fernández-Palacios, J. M., Mesa-Coelo, R. A., & Conti, E. (2013). Effects of clonality on the genetic variability of rare, insular species: The case of Ruta microcarpa from the Canary Islands. *Ecology and Evolution*, *3*, 1569–1579.

Moore-O'Leary, K. A., Hernandez, R. R., Johnston, D. S., Abella, S. R., Tanner, K. E., Swanson, A. C., Kreitler, J., & Lovich, J. E. (2017). Sustainability of utility-scale solar energy—Critical ecological concepts. *Frontiers in Ecology and the Environment*, *15*, 385–394.

Nadeau, N. J., & Jiggins, C. D. (2010). A golden age for evolutionary genetics? Genomic studies of adaptation in natural populations. *Trends in Genetics*, *26*, 484–492.

O'Leary, S. J., Puritz, J. B., Willis, S. C., Hollenbeck, C. M., & Portnoy, D. S. (2018). These aren't the loci you'e looking for: Principles of effective SNP filtering for molecular ecologists. *Molecular Ecology*, *27*, 3193–3206.

Oostermeijer, J. G. B., Luijten, S. H., & den Nijs, J. C. M. (2003). Integrating demographic and genetic approaches in plant conservation. *Biological Conservation*, *113*, 389–398.

Prăvălie, R., Patriche, C., & Bandoc, G. (2019). Spatial assessment of solar energy potential at global scale. A geographical approach. *Journal of Cleaner Production*, *209*, 692–721.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959.

Radosavljević, I., Satovic, Z., & Liber, Z. (2015). Causes and consequences of contrasting genetic structure in sympatrically growing and closely related species. *AoB PLANTS*, *7*, plv106.

Randall, J. M., Parker, S. S., Moore, J., Cohen, B., Crane, L., Christian, B., Cameron, D., MacKenzie, J., Klausmeyer, K., Morrison, S., & Morrison, S. (2010). *Mojave Desert ecoregional assessment* (pp. 1–210). The Nature Conservancy.

Ricklefs, R. E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, *235*, 167–171.

Rodríguez-Ramilo, S. T., Toro, M. A., Wang, J., & Fernández, J. (2014). Improving the inference of population genetic structure in the presence of related individuals. *Genetics Research*, *96*, e003.

Rodríguez-Ramilo, S. T., & Wang, J. (2012). The effect of close relatives on unsupervised Bayesian clustering algorithms in population genetic structure analysis. *Molecular Ecology Resources*, *12*, 873–884.

Saul-Gershenz, L., Grodsky, S. M., & Hernandez, R. R. (2020). Ecology of the Western queen butterfly *Danaus gilippus* thersippus (Lepidoptera: Nymphalidae) in the Mojave and Sonoran deserts. *Insects*, *11*, 315.

Sawyer, H., Korfanta, N. M., Kauffman, M. J., Robb, B. S., Telander, A. C., & Mattson, T. (2022). Trade-offs between utility-scale solar development and ungulates on western rangelands. *Frontiers in Ecology and the Environment*, *20*, 345–351.

Schmid, R., & Tibor, D. P. (2001). California native plant Society's inventory of rare and endangered plants of California. *Taxon*, *50*, 1296.

Shryock, D. F., DeFalco, L. A., & Esque, T. C. (2014). Life-history traits predict perennial species response to fire in a desert ecosystem. *Ecology and Evolution*, *4*, 3046–3059.

Smith, C. I., Sweet, L. C., Yoder, J., McKain, M. R., Heyduk, K., & Barrows, C. (2023). Dust storms ahead: Climate change, green energy development and endangered species in the Mojave Desert. *Biological Conservation*, *277*, 109819.

Stoms, D. M., Dashiell, S. L., & Davis, F. W. (2013). Siting solar energy development to minimize biological impacts. *Renewable Energy*, *57*, 289–298.

Surina, B., Schneeweiss, G. M., Glasnović, P., & Schönswetter, P. (2014). Testing the efficiency of nested barriers to dispersal in the Mediterranean high mountain plant Edraianthus graminifolius (Campanulaceae). *Molecular Ecology*, *23*, 2861–2875.

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., ... Wiegand, T. (2012). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*, 58–67.

Suuronen, A., Muñoz-Escobar, C., Lensu, A., Kuitunen, M., Celis, N. G., Astudillo, P. E., Ferrú, M., Taucare-Ríos, A., Miranda, M. D., Kukkonen, J. V. K., ... Kukkonen, J. V. K. (2017). The influence of solar power plants on microclimatic conditions and the biotic Community in Chilean Desert Environments. *Environmental Management*, *60*, 630–642.

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

Tanner, K. E., Moore-O'Leary, K. A., Parker, I. M., Pavlik, B. M., Haji, S., & Hernandez, R. R. (2021). Microhabitats associated with solar energy development alter demography of two desert annuals. *Ecological Applications*, *31*, e02349.

Tanner, K. E., Moore-O'Leary, K. A., Parker, I. M., Pavlik, B. M., & Hernandez, R. R. (2020). Simulated solar panels create altered microhabitats in desert landforms. *Ecosphere*, *11*, e03089.

Vandergast, A. G., Inman, R. D., Barr, K. R., Nussear, K. E., Esque, T. C., Hathaway, S. A., Wood, D. A., Medica, P. A., Breinholt, J. W., Stephen, C. L., Gottscho, A. D., Marks, S. B., Jennings, W. B., & Fisher, R. N. (2013). Evolutionary hotspots in the Mojave Desert. *Diversity*, *5*, 293–319.

Waples, R. S., & Do, C. (2010). Linkage disequilibrium estimates of contemporary Ne using highly variable genetic markers: A largely untapped resource for applied conservation and evolution. *Evolutionary Applications*, *3*, 244–262.

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*, 1358–1370.

Weitemier, K., Straub, S. C. K., Fishbein, M., Bailey, C. D., Cronn, R. C., & Liston, A. (2019). A draft genome and transcriptome of common milkweed (Asclepias syriaca) as resources for evolutionary, ecological, and molecular studies in milkweeds and Apocynaceae. *PeerJ*, *7*, e7649.

Willis, J. H. (1993). Effects of different levels of inbreeding on fitness components in Mimulus guttatus. *Evolution*, *47*, 864–876.

de Witte, L. C., & Stöcklin, J. (2010). Longevity of clonal plants: Why it matters and how to measure it. *Annals of Botany*, *106*, 859–870.

Wyatt, R., & Broyles, S. B. (1994). Ecology and evolution of reproduction in milkweeds. *Annual Review of Ecology and Systematics*, *25*, 423–441.

Young, A., Boyle, T., & Brown, T. (1996). The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, *11*, 413–418.

SUPPORTING INFORMATION

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