



Reduced ecosystem services of desert plants from ground-mounted solar energy development

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Deserts are prioritized as recipient environments for solar energy development; however, the impacts of this development on desert plant communities are unknown. Desert plants represent long-standing ecological, economic and cultural resources for humans, especially indigenous peoples, but their role in supplying ecosystem services (ESs) remains understudied. We measured the effect of solar energy development decisions on desert plants at one of the world's largest concentrating solar power plants (Ivanpah, California; capacity of 392 MW). We documented the negative effects of solar energy development on the desert scrub plant community. Perennial plant cover and structure are lower in bladed treatments than mowed treatments, which are, in turn, lower than the perennial plant cover and structure recorded in undeveloped controls. We determined that cacti species and Mojave yucca (*Yucca schidigera*) are particularly vulnerable to solar development (that is, blading, mowing), whereas *Schismus* spp.—invasive annual grasses—are facilitated by blading. The desert scrub community confers 188 instances of ESs, including cultural services to 18 Native American ethnic groups. Cultural, provisioning and regulating ESs of desert plants are lower in bladed and mowed treatments than in undeveloped controls. Our study demonstrates the potential for solar energy development in deserts to reduce biodiversity and socioecological resources, as well as the role that ESs play in informing energy transitions that are sustainable and just.

Throughout human history, desert plant species and the communities they comprise have supplied resources to peoples^{1,2}. In the Middle Stone Age (approximately 60,000 years ago), resident hunter-gatherer populations in the southern Namib Desert relied on edible desert plants as predictable food resources to supplement their diet of scarce meat³. People in North American deserts gathered fruits, roots and seeds for consumption dating back to 8,000 BC and human settlements in deserts greatly expanded following the adaptive use of native seeds for agriculture⁴. Native plant species are still ingrained in the cultural heritages and landscapes of indigenous desert peoples globally; desert plants provide elements and backdrops of creation stories, traditional foods and medicines, and habitats for spiritually important animals^{2,5,6}. Some of the same plants cultivated by indigenous desert peoples centuries ago are modern crops grown in arid regions today. For example, over 800,000 t of nopalitos (cladodes) and nearly 2.5 Mt of tunas (fruits) from cacti in the genus *Opuntia* are produced annually for commercial distribution in Mexico⁷.

The persistence of desert plants in both natural and modified environments may be a function of their perceived value rather than their empirical value. Humans select and permit the establishment of certain plants over others, which may or may not incorporate consideration of a plant's capacity to support ecosystem services (ESs) that humans depend on. For example, home-owner preferred lawns have locally displaced native desert plant species in urban landscapes of the southwestern United States, despite their higher water costs for landscape maintenance and lack of adaptive traits for an arid climate⁸.

Values are standards that rationalize human beliefs, behaviours and decisions and often encompass biological and socio-economic needs^{9,10}. Historically, social scientists have applied value systems to study behavioural phenomena, ranging from charity contributions to drug addiction¹¹. Value systems may provide a conceptual

bridge to link ecology and sociology; thus, they may be useful for identifying unintended consequences of anthropogenic activity and quantifying socioecological effects of decisions related to coupled human–natural systems and just energy transition goals^{12–15}. The application of value systems may further illuminate cultural and social services not yet adequately integrated into the current ESs framework (Fig. 1; see refs. ^{16,17}). Value systems may also enable assessments of emotional and societal risks taken by under-represented stakeholders (for example, indigenous peoples) to elucidate the effects of development decisions on their cultural heritages⁵. Furthermore, value systems can frame how people assign rights to activities such as resource management, thereby guiding practical objectives and judgments that have implications for human decisions and actions¹⁸.

The vulnerability of desert regions ($0.05 < \text{aridity index} < 0.20$) to climate change, combined with the increased intensity and rates of anthropogenic disturbance, may lead to diminished ESs supplied by natural resources in deserts^{19,20}. The potential for renewable energy development to mitigate climate change via reduced greenhouse gas emissions from the substitution of fossil fuels remains a powerful impetus for rapid build-out of solar energy in desert environments, where solar resources are relatively high globally. However, renewable energy development in relatively undisturbed desert environments may paradoxically elicit land-use and land-cover changes that can facilitate biodiversity loss, potentially diminishing ecosystem goods and services of societal value^{21,22}. For example, ground-mounted solar energy development in natural desert environments may negatively affect native desert plant species and thereby reduce the historically speciose plant communities that underpin primary production in desert ecosystems^{12,23}. Management and conservation of native desert plants have changed over time with the colonization of indigenously held lands (for example, post-European settlement in the United States). For example,

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modern land-use and land-cover modifications (such as mining and urbanization) have reduced plant species abundance and diversity in deserts²⁴.

Empirical evidence of the effects of solar energy development on native desert plants is lacking and ambiguous. For example, most utility-scale (>10 MW) solar energy facilities in California have been sited within desert scrublands and near protected natural areas, presumably leading to decreased plant biodiversity relative to alternative locations such as rooftops and degraded lands^{22,25}. However, this assumption contradicts an analysis of 30 consecutive years of Landsat satellite imagery across the Lower Colorado Desert that documented no effect of solar energy development on vegetation canopy cover based on normalized difference vegetation index (NDVI) values²⁶. Furthermore, a recent modelling study determined that solar and wind energy development in the Sahara could locally increase vegetation, but did not consider site preparation practices nor their consequences²⁷. In summary, field-based studies of the effects of solar energy development on desert plants are needed as a counterpoint to remote sensing and modelling studies to holistically draw informed conclusions that are meaningful to stakeholders. As studies of ESs often lack empirical validation of species–ESs relationships, field-based studies of plants as the bases of ecosystem functioning globally may be useful to validate the relative surfeit of theoretical ESs studies.

Results

We recorded the negative effects of solar energy development on the desert scrub plant community in the Ivanpah Valley, California, United States. We recorded the species richness and evenness of all desert scrub plants and perennials (68% of species composition; Supplementary Table 1) as being lower in the bladed treatments than in all other treatments and controls (Supplementary Table 2; see Fig. 2 and Fig. 3 for the spatial orientation and photographs of treatments, and Methods for a description of all treatments). We determined that both the structure and per cent cover (hereafter, ‘cover’) of perennials are lower in bladed treatments than in all other treatments, and lower in mowed treatments than in halo treatments and controls (Fig. 4a, Supplementary Table 3). Moreover, the combined cover of reproductive perennials, *Ambrosia dumosa* and *Larrea tridentata* is lower in bladed treatments than in all other treatments and in controls, and the cover of reproductive perennials and *Larrea tridentata* is lower in mowed treatments than in controls (Supplementary Table 3). See Supplementary Table 4 for the results for desert annuals.

Results from the analysis of desert plants grouped by photosynthetic pathway revealed that the cover of plants using the crassulacean acid metabolism (CAM) pathway is higher in controls and halo treatments than in mowed and bladed treatments (Fig. 4b). Meanwhile, the cover of the invasive grasses *Schismus* spp. (*S. arabicus* and *S. barbatus*, which are indistinguishable in

the field) is higher in bladed treatments than in all other treatments and controls (Fig. 4c). We found no biological soil crusts in bladed treatments.

Our results indicate that heliostat density decreases considerably with increasing distance from power towers in blocks (see inset in Fig. 2). We determined that the cover of perennials ($t = -4.78$, $P < 0.001$), CAM plants ($z = -2.32$, $P = 0.03$), *Ambrosia dumosa* ($z = -3.99$, $P < 0.001$) and *Larrea tridentata* ($z = -3.06$, $P = 0.004$) decreases with increasing heliostat density in ISEGS (Supplementary Table 5). See the Supplementary Information for the detailed results of the perennial and annual desert plant analyses.

We determined that the ES-based value (ESV; see Methods for definition) of desert plants differ among solar energy development decisions. We found that ESVs for provisioning, regulating and cultural services are lower in bladed and mowed treatments than in controls; ESVs for habitat services are lower in bladed treatments, which facilitate ecosystem disservices, than in controls (Fig. 5). On the basis of our assessment of the literature, we determined that CAM species (for example, cacti, *Yucca schidigera*) possess the highest ESVs and deliver over double the number of ESs per species than that of C_3 and C_4 plants (Fig. 1). Per species, CAM plants supply more provisioning, regulating and cultural services (2.00, 2.22 and 3.67, respectively) than C_3 plants (0.82, 1.04 and 1.52, respectively) and C_4 plants (0.66, 0.66 and 1.66, respectively). Desert scrub plants confer cultural services to 18 Native American ethnic groups included in the ESV system (Fig. 1). CAM plants confer more cultural services to a greater number of Native American ethnic groups (5.78 groups per species) than C_3 plants (2.57 groups per species) and C_4 plants (3 groups per species). *Yucca schidigera* and *Larrea tridentata* are the most valuable species in this ESV system; each species confers 94% of possible ESs outcomes. With the exception of a rare cactus species with limited representation in the literature and two invasive species, all desert plants in the ESV system provide wildlife habitat (Fig. 1).

Discussion

Deserts are inhabited by some of the most endangered species on Earth and harbour some of the poorest people, who increasingly rely on ESs in a changing climate²⁰. Nonetheless, deserts are largely neglected by governments and funding agencies and under-represented in scientific publications²⁰. Deserts are not considered ‘biodiversity hotspots’ in most heuristic frameworks for biodiversity conservation (for example, ref. 28), probably owing to the lack of development relative to their vastness and a relative dearth of ecological studies, but they often support high levels of biodiversity and endemism²⁰. Our results illustrate 188 instances of positive, plant species-specific ESs outcomes that span provisioning, regulating, habitat-based and cultural ESs in an ESV system comprising 16 possible ES–species pairings for 35 desert plant species. The goods and services of plants in deserts have been assessed in other global

Fig. 1 | ESV system of a desert scrub plant community in the Ivanpah Valley, Mojave Desert. ESs include first-tier ES categories and second-tier ES subcategories, incorporating ESs for societies in the Desert Southwest (United States). Plants include 33 native perennial and two invasive plant species categorized by photosynthetic pathway. A positive ESV (+1; solid dots, colour coded by ES type) represents the presence of an ES outcome conferred by the plant species; a negative value (−1; barred grey circles) represents an ecosystem disservice. Empty cells represent a lack of evidence for positive or negative ES outcomes in the peer-reviewed literature and are assigned a value of 0. The total ESV of each photosynthetic pathway and mean ESV and 95% confidence interval (CI) per species for each photosynthetic pathway are reported. The total ESV of the plant community is the number of positive ES outcomes minus the number of divested ES outcomes. ^aSuperscript numbers represent unique Native American ethnic group ($n = 18$) use of plant species across cultural services: ¹Apache, ²Cahuilla, ³Chemehuevi (Nümü), ⁴Hia C-eđ O’odham, ⁵Hohokam, ⁶Hopi, ⁷Maricopa, ⁸Mayo, ⁹Navajo, ¹⁰Paiute, ¹¹Pima, ¹²Pueblo, ¹³Seri, ¹⁴Shoshone, ¹⁵Southern Paiute, ¹⁶Tohono O’odham, ¹⁷Ute and ¹⁸Zuni. The ethnic group value is the total number of individual Native American ethnic groups valuing each plant species for cultural services. The value of an individual plant species for cultural services among ethnic groups is depicted by a black box, representing use by one ethnic group; additional groups are represented by alternating concentric grey and black boxes. ^bdenotes seriously threatened cactus species in California and ^cdenotes invasive species. We recorded no ecosystem services and therefore included a value of 0 in calculations of value per species for the following C_3 plants: ^d*Amsonia tomentosa*, *Ericameria cooperi*, *Lycium cooperi* and *Thymopylla pentachaeta*. See the Methods and Supplementary Information for further details. Graphics use icons reproduced from the Noun Project (<https://thenounproject.com>).

regions: over 30% and 35% of the 322 native plant species recorded in the northwestern coastal desert of Egypt provided at least two economic services and one ecological service, respectively, to people across 16 villages from Burg El-Arab to El-Salloum²⁹. Following the philosophical argument for conserving ESs to promote positive socioecological outcomes in biodiversity hotspots, threats to desert ESVs are deserving of the same attention, especially ESs relevant to indigenous peoples in arid regions. Yet the scarcity of scientific information on desert plants and their ESVs has made it difficult to understand the socioecological effects of development decisions in

deserts, supplying little cautionary evidence about the consequences of anthropogenic disturbance²⁴.

Identifying and accurately weighing the effects of development decisions, a critical concept for sustainable solar energy development worldwide¹², is possible when ESs are quantified, particularly species-specific ESVs that allow for comparisons across functional and taxonomic groups. We show that solar energy development decisions regulate ESs, which, in turn, are critical factors that ultimately determine ecosystem resiliency in coupled human–natural energy systems³⁰. For example, we found

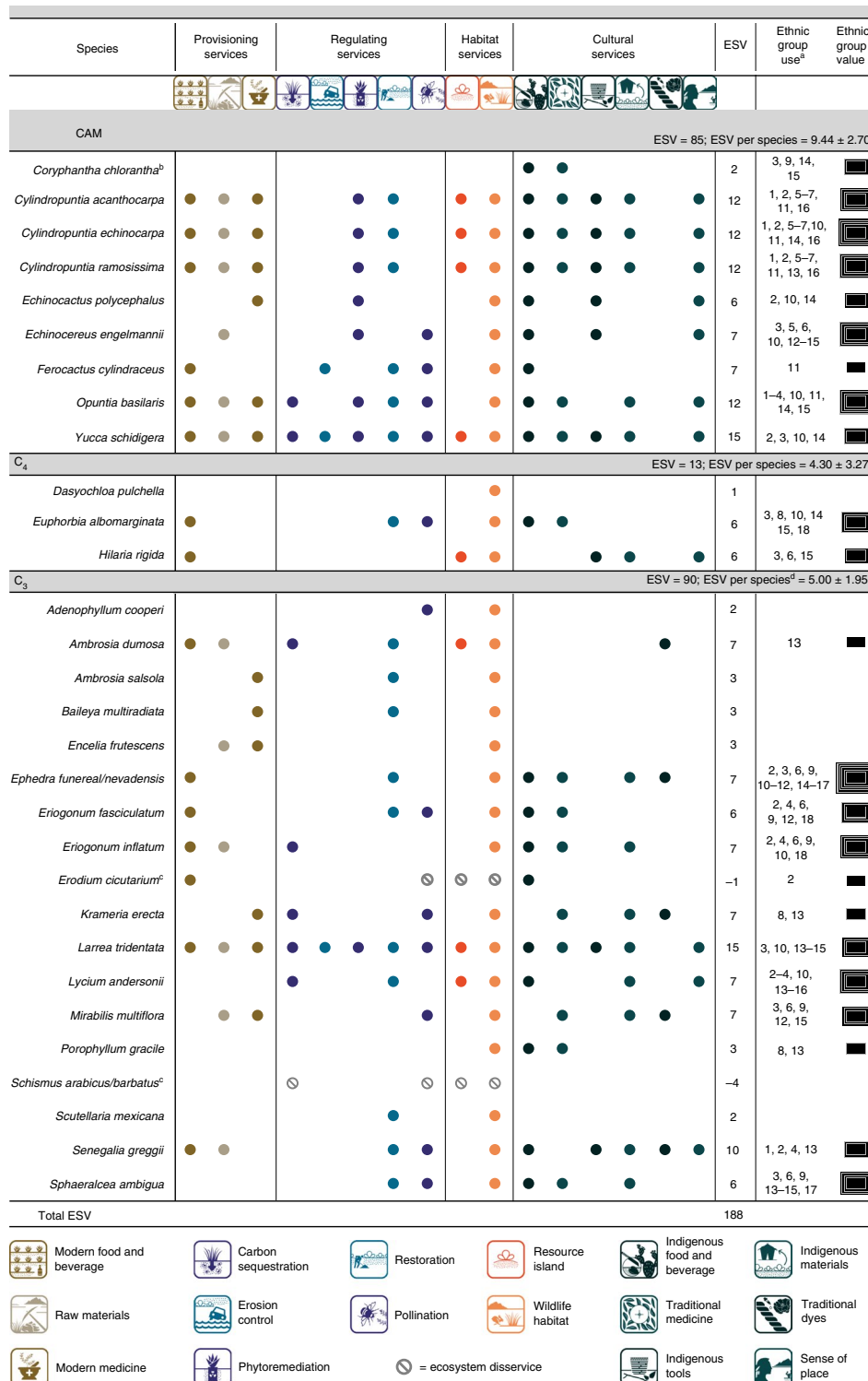




Fig. 2 | Spatial elements of the study site and design. Ivanpah Solar Electric Generating System (ISEGS; 392 MW), which consists of three concentrating solar power blocks (that is, tower and associated heliostats; replicated block) in Ivanpah Valley, Mojave Desert, California, United States. The symbols show the spatial orientation of 60 plant-sampling plots in treatments (see Methods) within ISEGS and in controls. We replicated control plots in undeveloped, natural desert scrub surrounding ISEGS. Inset, results of linear model showing a significant, negative relationship between heliostat density and increasing distance from power towers within blocks at ISEGS. The solar panel in the inset indicates that the heliostat density refers to the mirrors in ISEGS. Base map adapted from Google Earth, Maxar Technologies.

that decisions to prepare desert sites for solar energy development by bulldozing (blading) can lead to ubiquitous declines in ESs. Furthermore, bulldozing can facilitate the colonization of invasive

species that diminish ESs via trophic cascades, competition with high-ESV plants and increased risk of historically infrequent disturbances such as wildfires in desert ecosystems (Fig. 4c; refs. ^{31,32}).



Fig. 3 | Solar energy development decision treatments. Photographs of treatments in ISEGS and a control plot in relatively undisturbed desert scrub, Ivanpah Valley.

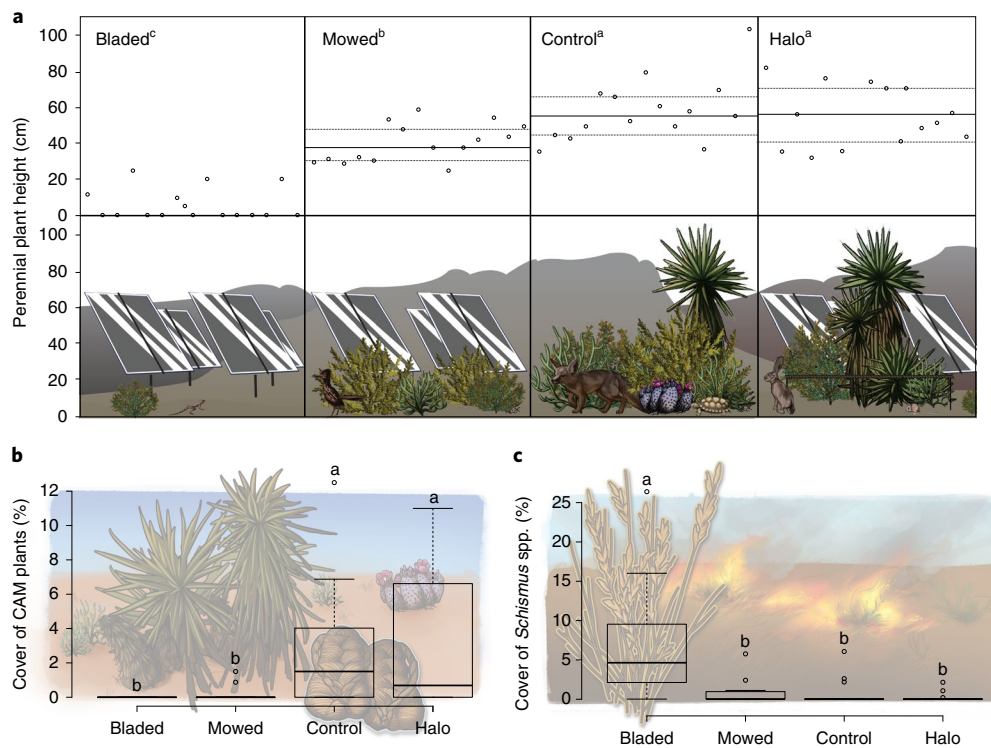


Fig. 4 | Effects of solar energy development decisions on perennial plant structure, cover of plants using the CAM photosynthetic pathway and cover of the invasive grasses *Schismus* spp. during peak spring growing season within ISEGS and in surrounding natural desert. **a**, Perennial plant height in treatments and controls (top), with illustrations of data-informed perennial plant structure and desert wildlife species to scale (bottom). Black horizontal lines show the median and 95% CIs; the median for bladed is zero. $H_{\text{Decision}} = 31.37$, $P < 0.001$. **b**, Cover of CAM species in treatments and controls, with an illustration portraying desert scrub CAM species and Chemehuevian woven sandals sourced from *Yucca schidigera*. $H_{\text{Decision}} = 21.92$, $P < 0.001$. **c**, Cover of *Schismus* spp. in treatments and controls, with an illustration of the morphology of *Schismus* spp. and wildfire spread by fine fuel beds of *Schismus* species in the Mojave Desert—an ecosystem with historically infrequent fires. Thick horizontal black lines show the median, the boxes the interquartile range, the whiskers the minimum and maximum, and the dots the outliers. $H_{\text{Decision}} = 27.19$, $P < 0.001$. Letters a–c indicate significant differences among treatments and controls. We set the statistical significance level (α) to 0.05.

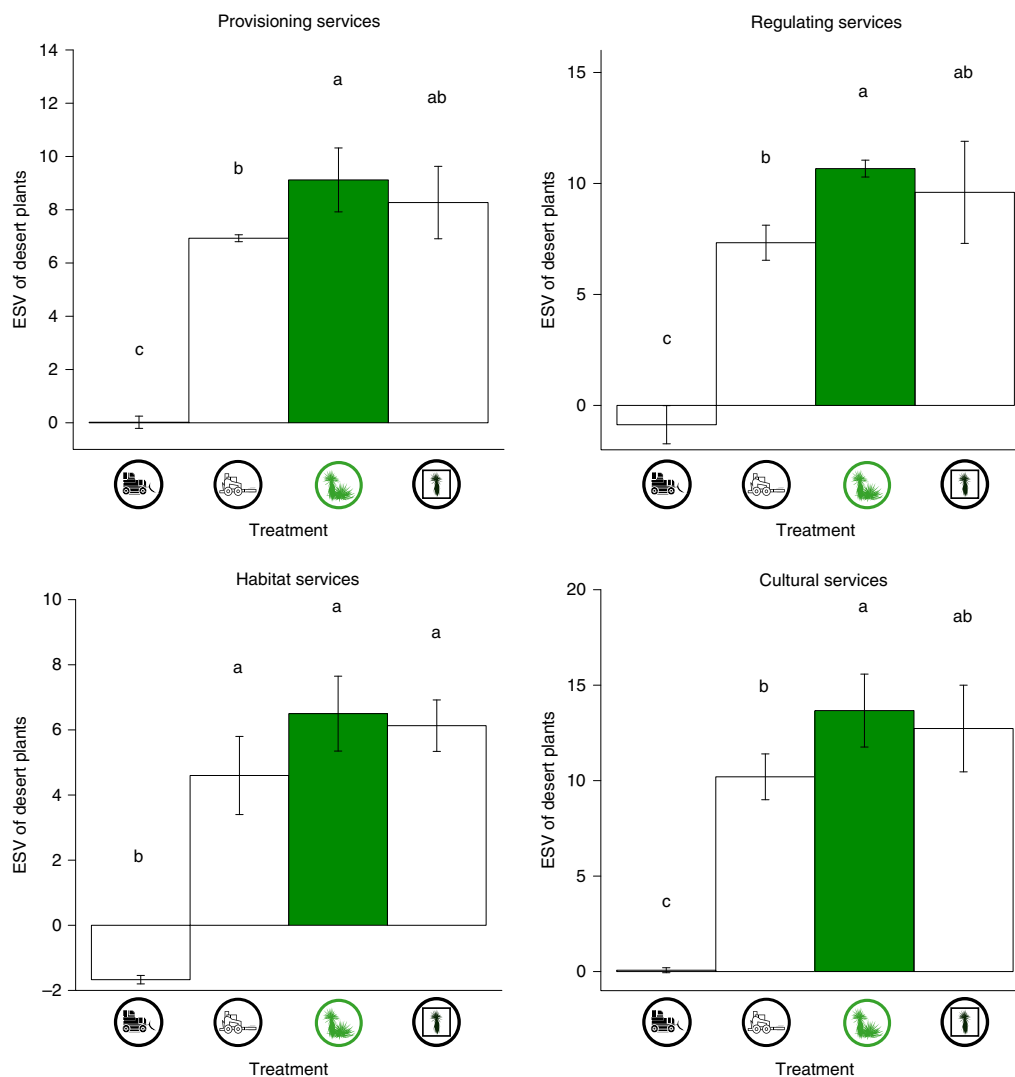


Fig. 5 | Effects of solar energy development decisions on the ESV of plants among first-tier ES categories. Bars show the mean and error bars represent the 95% CIs for provisioning services ($F_{\text{Decision}} = 74.75$, $P < 0.001$), regulating services ($F_{\text{Decision}} = 61.74$, $P < 0.001$), habitat services ($F_{\text{Decision}} = 64.99$, $P < 0.001$), and cultural services ($F_{\text{Decision}} = 58.40$, $P < 0.001$). Letters a–c indicate significant differences among treatments and controls. We set the statistical significance level (α) to 0.05.

Globally imperilled CAM species maintain the highest ESVs, supply the most cultural services (for example, providing sources of fibre for Native Americans; Fig. 4b) and exhibit the greatest resilience to increasing temperatures and atmospheric CO_2 from climate change among desert scrub plants^{33,34}.

Our study demonstrates that changes to desert plant communities and the ESs they supply under development decisions are considerable when field-based plant surveys are paired with assessment of species-specific ESVs. In contrast, remote sensing and modelling studies on the effects of renewable energy development on desert vegetation at coarse spatial scales (for example, refs. 26,27) may underestimate biodiversity loss, invasive species colonization and species-specific ESVs. Studies that pair field-based observations and ESs assessments to indicate species-specific changes and alteration of plant functional traits from energy development decisions, complemented by remote sensing and modelling activities mapping variations in climatic and vegetation properties (for example, the NDVI), can provide a more holistic approach to inform socioecologically sustainable energy development at local to ecosystem levels^{35,36}.

Records confirm that indigenous desert peoples have been subjected to environmental injustices and disenfranchisement, often

by the Westernization of their native lands and the exploitation of natural resources that follows^{37,38}. For example, development activities in deserts, including mining in the Atacama of Chile, nuclear bomb testing and waste storage in the Mojave of the United States and military bases in the Arabian Desert of the Middle East, remain controversial topics today, owing to the resultant socioenvironmental injustices inflicted on the local human inhabitants^{37,39,40}. We identified a total of 18 Native American tribes with members accounting for approximately half a million people in the Desert Southwest (United States) who use and value native desert plants affected by solar energy development for plant-based ESs. Although renewable energy development in desert ecosystems may mitigate climate change for society at large, it can simultaneously reduce socioecological resources for resident indigenous peoples, most of whom already are environmentally vulnerable^{20,41}, and diminish local ecosystem resilience¹⁵. For example, the construction of solar energy facilities in the Mojave Desert has led to the destruction of Native American geoglyphs and cremation sites, which tribal elders considered a disruption of the peace of their ancestors and Native Americans' relationship with their land⁴². On the other hand, solar energy development on tribal lands in the United States may

increase revenue streams, energy security and energy independence for Native American communities^{43,44}.

Solar energy development may alter biodiversity in deserts. Under the International Union for Conservation of Nature Red List Categories and Criteria, cacti are among the most globally threatened taxonomic groups³³. Cacti support a diversity of wildlife species in desert ecosystems⁴⁵. For example, cacti bear extrafloral nectaries that are pivotal to the survival of desert ant communities⁴⁶ and provide nesting structures for desert birds (such as the cactus wren (*Campylorhynchus brunneicapillus*))⁴⁷. Cactophilic invertebrates (for example, the cactus fly (*Odontoloxozus longicornis*)) feed and breed in the necrotic tissue of cacti⁴⁸. The obligate pollination mutualisms between yucca moths (Lepidoptera, Prodoxidae) and yuccas (*Yucca* spp.) displayed in North American deserts are considered among the most apparent cases of coevolution between plants and insects in ecology; the moths exclusively pollinate the yucca flowers and, in turn, the moth larvae feed on some developing seeds of the yucca plant⁴⁹. Biodiversity loss from reduced cover of cacti and yucca may be further exacerbated by the promotion of invasive grasses such as *Schismus* spp., which provide low-quality forage for threatened herbivores like the desert tortoise (*Gopherus agassizii*) and contribute fuel to wildfires that damage or kill native desert plants⁵⁰.

Loss of desert plant-based socioecological resources can be limited by sustainable decision-making for solar energy development. Site preparation for ground-mounted concentrating and photovoltaic solar power both modify desert land surfaces. Based on the succession of vegetation seven years after site preparation, virtually no perennial vegetation cover was present following blading but cover of some common desert shrubs (such as creosote, white bursage) recovered to levels recorded in controls in the mowed treatments. However, cacti and Mojave yucca did not recover from any form of disturbance in the same time span, and these species have taken hundreds of years to restore following other desert disturbances²⁴. Mowing, rather than blading, desert sites for solar energy development may therefore limit some loss of ESs conferred by desert shrubs but the more valuable and iconic CAM plants may not recover from any method of site preparation within the lifespan of a solar facility (~30 years). On the basis of our results, we encourage future studies to assess the long-term response of desert plants to solar energy development decisions, especially mowing and the establishment of undisturbed islands within solar fields, to inform about the restoration and resilience of desert scrub plant species affected by solar energy development.

Siting renewable energy facilities on marginalized lands (for example, abandoned farmland, contaminated sites) and in the built environment (that is, distributed solar on residential/commercial rooftops and over parking lots) rather than in undisturbed desert environments will sustain the ESVs of desert plants while potentially offering techno-ecological synergies. Techno-ecological synergies optimize both technological and ecological systems, thereby minimizing unintended consequences of energy development^{13,25,51}. In this study, we find that the socioecological effects of solar energy development decisions are identifiable and comparable when the ESs of natural resources, in this case desert plants, are quantified. Ultimately, this information bolsters not only our ability to identify diverse ESs (for example, ref. ¹⁶) but also to increase usable knowledge (for example, ref. ⁵²) and realize the effects of renewable energy development with respect to people during an unprecedented and rapid global energy transition.

Methods

We developed an ESV system for a model desert plant community (here designated 'desert scrub') occurring in the Ivanpah Valley of the Mojave Desert, California (United States) (Fig. 1). We define ESVs as ESs (and disservices) of desert plants contributing to a value system with the capacity to guide human judgments and actions pertaining to solar energy development in deserts. Globally, desert scrub is a dominant vegetation type in hot deserts, which, in turn, comprise a large portion of Earth's land surface and presently support expansive solar energy development²².

For example, creosote desert scrub dominates the Californian Mojave Desert, covering 6,542,395 ha—an area 400,000 ha larger than the state of West Virginia (United States). Furthermore, desert scrub is inhabited by cacti (Cactaceae), one of the most threatened plant families in the world³³. We based the ESV system on The Economics of Ecosystems and Biodiversity (TEEB) Initiative's ESs framework (www.teebweb.org), which designates the following four first-tier ESs categories: (1) provisioning services; (2) regulating services; (3) habitat or supporting services; and (4) cultural services. We co-developed second-tier ESs subcategories from TEEB, incorporating ESs relevant to the Mojave Desert and its historical and current human inhabitants. We assigned a positive value (+1) to represent the presence of an ES outcome conferred by plant species or a negative value (−1) to represent an ES outcome divested by plant species for each species–service pairing for 33 perennial plant species and 2 invasive plant species in the Ivanpah Valley based on a systematic assessment of peer-reviewed journal articles in the ecology, environmental management and sociology literature. We assigned a value of 0 to species–service pairings unsupported in the literature, under the assumption that the lack of support may indicate the absence of studies rather than the absence of ESs. We examined anthropological documentation to identify potential human–plant interactions for Native American ethnic groups inhabiting regions of the Desert Southwest (United States) and desert scrub species; we then determined the ethnobotanical associations (that is, cultural ESs) of these ethnic groups with each plant species in the ESV system on the basis of a systematic assessment of peer-reviewed anthropology, human ecology and ethnobotanical literature.

We quantified the effects of concentrating solar power development, including site preparation and heliostat density, on desert scrub plant functional groups, species, community properties and total ESVs using ISEGS as a model system. ISEGS has a gross power production of 392 MW, serving approximately 140,000 Californian homes annually. ISEGS also consumes natural gas to start the boilers in the power towers; from January 2014 to April 2019, ISEGS consumed 5,790,918 million British thermal units (MMBtu) of natural gas, resulting in 307,266,109 kg of CO₂ emissions. Within ISEGS, we designated each of the three power blocks (that is, tower and associated heliostats; Fig. 2a) as replicated blocks. We defined treatments in each block representing three unique site preparation decisions as follows: (1) bladed, intensive site preparation via blading (that is, 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 field, which were roped off and left undisturbed (that is, no site preparation, no heliostats) (Fig. 3). We designated replicated control plots in natural desert scrub immediately surrounding ISEGS. During the spring 2018 growing season, we sampled plants in 15 spatially independent plots in each of the three treatment units in blocks (five plots per treatment per block) and in control sites (total plots = 60) (Fig. 2). We also recorded the presence of biological soil crusts and measured heliostat density at each plot to determine the effects of spatially heterogeneous shading throughout each block. See the Supplementary Information for detailed methods.

We compared the observed species-level effects of solar energy development with the ESVs of each photosynthetic pathway category and individual species within the ESV system. For this assessment, we defined ESV as the total number of ESs outcomes conferred by each species, the cumulative ESs outcomes supplied by each species in each photosynthetic pathway category, and the cumulative ESs outcomes for each solar energy development decision treatment (that is, bladed, mowed, halo) versus controls, respectively. Our primary objectives were to determine effects of solar energy development decisions on the native desert scrub plant community with respect to the ESVs of plant functional groups and species and to test the efficacy of an ESV system as a sustainability assessment tool to measure the socioecological effects of renewable energy development.

Data availability

An Excel workbook with all raw plant data is included as Source data.

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Author contributions

S.M.G. and R.R.H. conceptualized the study, designed the experiment and collected field data. S.M.G. conducted literature syntheses and analysed the data. S.M.G. and R.R.H. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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