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RESEARCH ARTICLE

Biotic and abiotic treatments as a bet-hedging approach to restoring plant communities and soil functions

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Two related concepts in restoration ecology include the relative interchangeability of biotic and abiotic restoration treatments for initiating recovery and bet hedging using multiple restoration approaches to increase the likelihood of favorable restoration outcomes. We used these concepts as a framework to implement a factorial experiment including biotic (outplanting greenhouse-grown individuals of three perennial species) and abiotic treatments (constructing microtopography or vertical mulch consisting of upright, dead plant material). These treatments were designed to stimulate native plant recruitment and reverse soil degradation at four disturbed sites in the Sonoran Desert, U.S.A. The first growing season after the restoration treatments was the driest of the last 47 years, and 100% of outplants died. While the biotic treatment failed, the vertical mulch abiotic treatment increased native shrub seedling cover at the driest site and reversed soil loss across sites by increasing soil accumulation by 6× to 2 cm/year. Results revealed that (1) inexpensive, minimal-input abiotic treatments outperformed resource-intensive biotic treatments; (2) the restoration effort withstood the total failure of a major component (outplanting) to nevertheless achieve key restoration benefits within 2–3 growing seasons; and (3) incorporating multiple treatment types served as a bet-hedging approach to buffer against treatment failures. Integrating minimal-input abiotic treatments in restoration warrants consideration given their low cost and bet-hedging potential.

Key words: desert, drought, erosion, mounding, outplanting, partial restoration success, vertical mulch

Implications for Practice

- Outplanting has restored native perennials in a variety of drylands globally, but during droughts when potentially infeasible levels of plant care may be required, practitioners could consider using abiotic treatments as substitutes for live plants to restore ecological functions.
- Vertical mulch using dead plant material is promising for inexpensively initiating recovery in drylands including during droughts when seeding or outplanting is difficult.
- Implementing multiple treatment types, including inexpensive, minimal-input treatments, can be a bet-hedging strategy against treatment failures, enabling restoration projects to produce at least partially favorable outcomes despite failure of some treatments.

Introduction

Two concepts related to the success of ecological restoration include the relative interchangeability of biotic and abiotic restoration treatments for recovering ecological functions and bet hedging using multiple restoration approaches to increase chances of meeting restoration goals. Given challenges with directly reintroducing propagules or live plants and their uncertain survival, a key question is the degree to which abiotic structural restoration can stimulate native species recovery and at least partly provide the ecosystem functions of live organisms (Chiquoine et al. 2016; El-Keblawy et al. 2016; Li et al. 2017). For example, abiotic structures could substitute for live plants in slowing soil erosion, avoiding the uncertainty of needing timely establishment of live plants (Fick et al. 2016). This uncertainty in biotic and abiotic restoration input needs and variable effectiveness of restoration treatments in dynamic environments has further led to exploring bet-hedging approaches to restoration (e.g. Davies et al. 2018). Bet-hedging could take several forms, such as replicating treatments across years, using multiple species in planting mixtures, or applying both biotic and abiotic treatments (Doherty & Zedler 2015). As an example, Commander et al. (2013) found that reintroducing propagules of species at some semiarid Australian restoration sites failed entirely, but that a restoration goal of de-compacting soils to

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foster plant recruitment was nevertheless achieved through abiotic treatments.

Desert ecosystems, with their combination of climatic extremes, spatial concentration of biotic and abiotic resources into discrete patches within sites, and restoration difficulty, provide a model system for exploring concepts of biotic and abiotic treatments and bet-hedging approaches to restoration. Many undisturbed desert habitats contain widely spaced perennial plants separated by open interspaces between perennials, a spatial configuration concentrating resources in fertile islands below and immediately surrounding perennials (Brown & Porembski 1997). Compared to interspaces, surface soils in fertile islands are frequently nutrient-enriched, mounded and of finer texture via accumulating soil particles, and cooler and moister from shade cast by perennial plants and retention of soil organic matter (El-Bana et al. 2003). These fertile island microsites, often only 0.25–1 m^2 and comprising small total areas of sites, are biological hotspots of plant recruitment (Carrillo-Garcia et al. 1999). Because of the low availability of resources in deserts, the concentration of resources into fertile islands to reach levels required for biological activity is frequently considered fundamental to the healthy functioning of mature desert ecosystems (Hulvey et al. 2017). Severe anthropogenic disturbance typically homogenizes sites, disrupting fertile island structure, and necessitating its restoration as part of desert habitat recovery (Fuentes-Ramirez et al. 2015). As a result, biotic treatments to reestablish native perennials are commonly initial restoration steps. While seeding may succeed in certain circumstances, bypassing the uncertainty of germination and early seedling survival in extreme desert environments by outplanting greenhouse-grown seedlings has often more reliably restored desert perennials (Rathore et al. 2015; Rowe et al. 2020; Strohmeier et al. 2021). However, even outplanting with supplemental treatments (e.g. irrigation) has not always succeeded in deserts, particularly if performing intensive follow-up plant care is infeasible (Woods et al. 2012). This raises a question as to whether abiotic treatments could achieve commonly desired restoration benefits, such as slowing soil erosion and creating conditions for native plant recruitment.

Here, we conducted a restoration experiment in a desert ecosystem using the concepts of potential functional interchangeability of biotic and abiotic restoration treatments for triggering restoration benefits and bet hedging using multiple species and treatment types. Based on this conceptual framework to include both biotic and abiotic treatments for bet hedging, we implemented a resource-intensive biotic treatment (outplanting) and two types of less-resource-intensive abiotic treatments (constructing microtopography or vertical mulching using upright dead plant material) at four disturbed sites spanning a gradient of surface soil conditions and compared treatment effectiveness. We assessed a range of functional restoration response metrics including 10 univariate plant community variables (e.g. shrub seedling cover), multivariate plant community composition, and four soil functional variables (e.g. soil accumulation). We evaluated a null hypothesis that restoration treatment approaches equally affected response variables.

Methods

Reference Conditions and Experimental Sites

We performed the experiment in the Lower Colorado River Valley subdivision, the largest and most arid subdivision of the Sonoran Desert and which is in California and Arizona, U.S.A., and northern Mexico (Turner & Brown 1982). Our study area occupies the northwestern part of the subdivision between the cities of Indio and Blythe, southeastern California. The study area encompassed four experimental sites along the Devers-Palo Verde No. 2 transmission line, a powerline corridor administered by the Southern California Edison Company and constructed between the mid-1980s and early 2010s. The sites, which are on public land overseen by the Bureau of Land Management, spanned a west–east extent of 62 km and averaged 23 km apart. Soils were generally derived from granite and gneiss alluvium parent material. Reflecting their arrangement along with a soil textural gradient, we named sites according to their surficial texture ranging from gravelly fine sand to loose, eolian sand (Table S1). As part of construction and maintenance activities for the powerline, the sites were disturbed before or during 2013 including removal of vegetation and alteration of surface soil (to a depth of 10–50 cm) by leveling the soil surface from heavy equipment and vehicular traffic. Site conditions in 2016, before restoration commenced, included minimal to no plant cover (<1%); visually altered, homogenous ground surfaces; and generally nutrient-poor 0–5 cm mineral soils compared to nearby, undisturbed, reference sites (Fig. S1; Tables S1 & S2). Reference sites contained mature desert shrubland dominated by the native shrubs creosote bush (*Larrea tridentata*) and bursage (*Ambrosia dumosa*), along with big galleta grass (*Pleuraphis rigida*). During years of favorable precipitation, sites also contained a mixed-species annual community with natives such as desert plantain (*Plantago ovata*) and Coulter's lupine (*Lupinus sparsiflorus*). Reference native perennial cover ranged from 2 to 5% and annual plant cover in wetter years also ranged from 2 to 5%. As exemplified by the reference sites, generalized target communities for restoration on the disturbed sites were desert shrubland (including perennial grasses where appropriate) and a mixed-species annual community dominated by native species.

Climate, measured in Blythe, California, at an elevation of 120 m on the eastern boundary of the study area, averages 88 mm/year of precipitation and daily temperatures of 4/20°C (low/high) in January and 26/43°C in July (1949 through 2019 records; National Centers for Environmental Information, Asheville, North Carolina). About half (48 mm) of the annual precipitation falls from November through March. This period represents the winter–spring growing season for winter annuals and spring growth of perennials. During our experiment, the first growing season (November 2017 through March 2018) was the driest in the last 47 years and the fifth driest in the 72-year record (Fig. S2). The 2019 growing season was 13% below average. The 2020 growing season was moist (231% of average precipitation).

Experimental Design and Treatments

We used a randomized block, two-factor, factorial design consisting of sites ($n = 4$) as blocks, two levels of biotic treatment

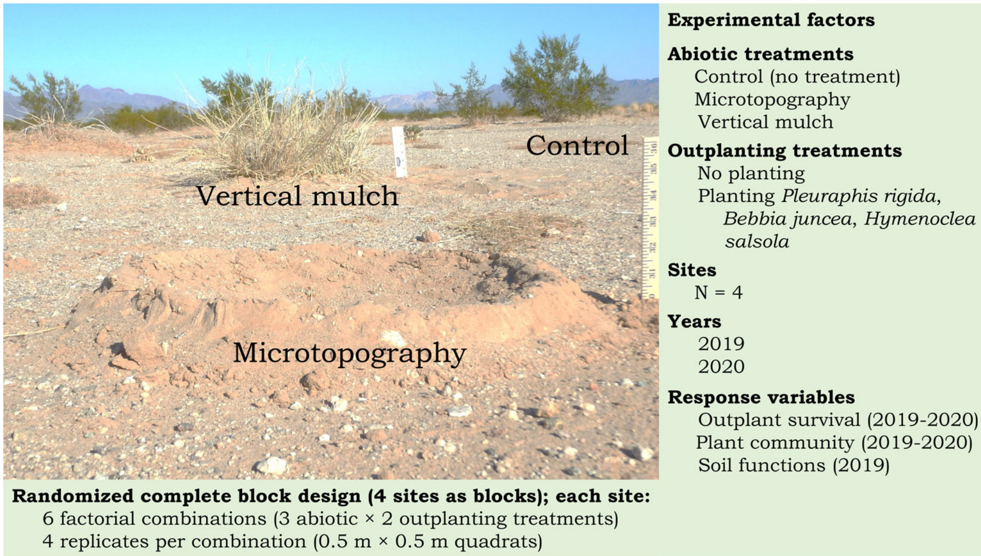

Figure 1. Design of an ecological restoration experiment on sites disturbed by construction activities along an energy transmission corridor in the Sonoran Desert, California, U.S.A. Half the quadrats of each abiotic treatment received outplanting, consisting of one seedling of each of three species spaced in a triangular pattern within the abiotic treatment (outplants not shown in the photo). Vertical mulch consisted of dead stalks of the native perennial grass *Pleuraphis rigida* placed upright into the ground to form a doughnut pattern. The photo was taken in December 2017 when treatments were implemented and before three additional soil erosion pins were inserted around abiotic treatments to measure soil accumulation.

(none, outplanting), and three levels of abiotic treatment (non-manipulated control, microtopography, vertical mulch; Fig. 1). At each of the four disturbed sites, we established a 20 m × 14 m (280 m^2) plot. In each plot, 24 quadrats (each 0.5 m × 0.5 m, 0.25 m^2) were randomly located at least 2 m from each other. We then assigned one of the six treatment combinations to each quadrat (with four quadrats per treatment combination) as a randomized complete block.

We installed treatments in December 2017. The microtopography treatment consisted of contouring the soil surface into a cylindrical ring with an outer diameter of 0.5 m, an outer height 10 cm higher than the surrounding surface soil, an elevated ring width of 10 cm, and a basin in the center (Fig. 1). Building each vertical mulch structure entailed digging a circular trench (10 cm wide and 10 cm deep) with an outer diameter of 0.5 m, gathering 0.013 m^3 of senesced shoots of big galleta grass from nearby washes, placing the shoots vertically to fill the trench, and pressing adjacent soil into and against the trench to hold the shoots upright. The result was a ring-pattern arrangement of vertical mulch, with the ring 30 cm tall and 10 cm wide, encircling an open interior (Fig. 1). Vertical mulch structures remained intact and no maintenance was required for the duration of the experiment.

To prepare the outplanting treatment, we collected seeds of three native perennials (big galleta grass and the shrubs bursage and sweetbush [*Bebbia juncea*]) from nearby undisturbed areas in spring 2017. Seeds were germinated and seedlings were grown for 9 months in 30-mL (12.7 cm tall × 3 cm top diameter) plastic cones filled with an 80:20 sand:organic mixture in an indoor nursery (Center for Urban Water Conservation, University of Nevada, Las Vegas). Soil in cones was watered twice daily to field capacity during the first 8 months of the propagation period, then tapered to once daily in the ninth month, when seedlings were moved outdoors under a shade cloth (50% shade). The nine-month propagation period produced seedlings 10–20 cm tall for outplanting. In December 2017 after abiotic treatments were implemented at the restoration sites, we planted one seedling of each of the three species within abiotic treatment quadrats by placing seedlings 10 cm apart in a triangular pattern in the interiors of abiotic structures. Planting holes (dug by hand, 15 cm deep) were filled with water and allowed to drain before seedlings were inserted. Seedlings were then provided with 1 L of water applied to the soil surface followed by another 1 L 2 months later in February 2018.

Data Collection

We assessed outplant survival 1, 3, 6, and 28 months after planting. We measured plant communities in each quadrat (0.25 m^2) in each plot by recording the aerial cover using cover classes (Peet et al. 1998) by species (Natural Resources Conservation Service 2021) for vascular plants rooted in quadrats. To allow for an initial growing season of germination and plant establishment following disturbance from implementing treatments, we performed plant community measurements 16 (March 2019) and 28 months (March 2020) after treatment installation. Sixteen months after treatments, we assessed four soil functional variables along perimeters of each quadrat. The soil responses were measured or sampled in the four cardinal directions and averaged on a quadrat basis. Soil compaction (0–5 cm depth) was measured with a penetrometer (AMS G 281 E-280; American Falls, Idaho, U.S.A.). Soil aggregate stability was measured following Herrick et al. (2006). To assess soil moisture, samples 5-cm deep and 10 cm in diameter were sealed in glass jars and analyzed gravimetrically via oven drying at 105°C for 24 hours. Soil accumulation or loss, quantified as the change in soil depth, was measured by anchoring four 25-cm long soil erosion pins (Hancock & Lowry 2015) 10 cm deep into the soil around each quadrat.

Data Analysis

We analyzed univariate plant community response variables using a generalized linear mixed model including sites as blocks, biotic treatment (two levels: none or outplanting), abiotic treatment (three levels: non-manipulated control, microtopography, or vertical mulch), and year as a repeated measure (spring 2019 and 2020). We analyzed 10 univariate plant community variables, ranging from total native plant cover to non-native annual grass species richness (per 0.25 m^2; Table S3). Soil functional variables were analyzed using the same model but without year. Models were implemented in SAS 9.4 using PROC GLIMMIX, with appropriate data distributions assigned (lognormal for cover and continuous soil variables; Poisson or negative binomial for species richness and soil stability). For models with effects significant at $p < 0.05$, means were separated using Tukey tests. In the paper, we focus on interactions or main effects involving treatments and report variation involving only site, year, or significant overall interactions but without significant Tukey separations in Tables S3 and S4.

To analyze species composition among abiotic treatments, we applied permutational multivariate analysis of variance (Anderson 2001) to a matrix of relative cover (cover of species$_i$/$\sum$ cover of all species, where cover for each species was averaged across years) as a randomized block design including sites as blocks and abiotic treatment. We used Sørensen distance and default settings for the analysis in PC-ORD 7.07 (McCune & Mefford 1999). To examine the fidelity of individual species to abiotic treatments, we used blocked indicator species analysis, with sites as blocks, applied to a matrix of relative

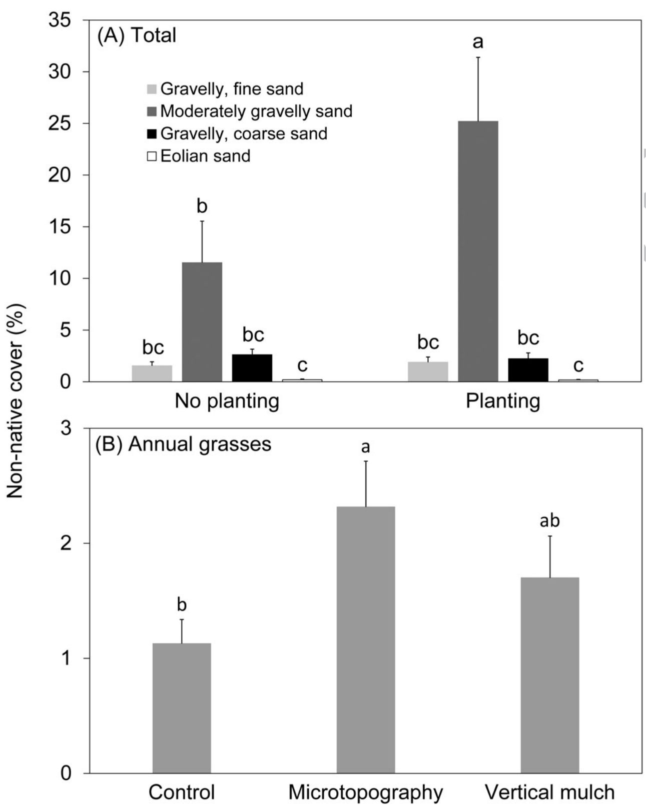

Figure 2. Cover of non-native plants in outplanting and abiotic treatments in an ecological restoration experiment in the Sonoran Desert, California, U.S.A. For (A) total non-native plant cover, outplanting interacted with sites, named according to their surface soil properties. For (B) non-native annual grass cover, no interactions occurred with abiotic treatment (non-manipulated control or addition of microtopography or vertical mulch), so it is shown as a main effect. Bars are means and error bars are ±1 SE. Means without shared letters differ at $p < 0.05$ (Tukey tests). All non-natives were annuals (Table S5).

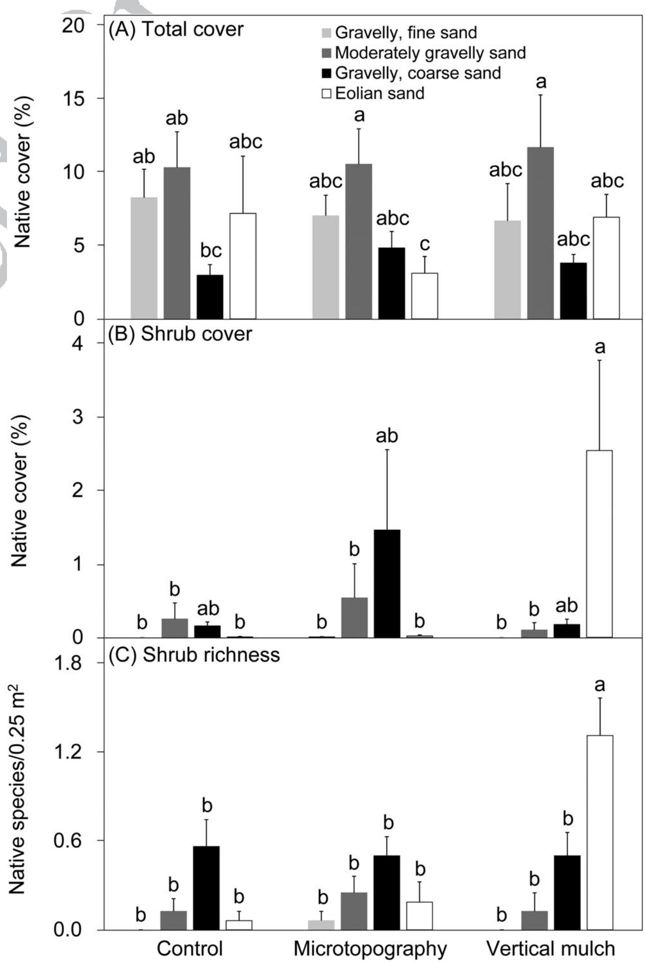

Figure 3. Variation in native plant species variables that displayed interactions between abiotic treatment (non-manipulated control or addition of microtopography or vertical mulch) and site (named according to their surface soil properties) in an ecological restoration experiment in the Sonoran Desert, California, U.S.A. Bars are means and error bars are ±1 SE. Means without shared letters differ at $p < 0.05$ (Tukey tests).

cover (Dufrêne & Legendre 1997). We dropped the biotic treatment to simplify multivariate analyses as all outplants died.

Results

None of the 144 outplants (48 each of big galleta grass, bursage, and sweetbush) had live aboveground foliage by 3 months after planting at the four sites, and the 100% mortality was confirmed through 28 months after planting. The activity of outplanting in our experiment did not significantly affect soil functions or univariate plant community variables, with one exception (Table S3). The exception was non-native annual plant cover via a site × outplanting interaction, where the cover was higher in quadrats receiving outplanting compared with no outplanting at the moderately gravelly site (Fig. 2A).

The abiotic treatment affected several univariate plant community variables for at least 28 months after treatment (Table S3). For example, at the eolian sand site, constructing vertical mulch increased shrub seedling cover and species richness above levels in quadrats receiving microtopography or no treatment (Fig. 3A & 3B). Constructing microtopography resulted in non-native annual grass cover (all *Schismus* spp.) significantly higher than in the control (Fig. 2B).

In contrast to their influence on univariate plant community variables, abiotic treatments did not affect species composition based on permutational multivariate analysis of variance (Table S4). Blocked indicator species analysis reinforced this finding, as none of the 29 taxa (3 non-native, 26 native) recorded among the sites were associated with a particular abiotic treatment (Table S5). Non-natives with the most cover included Sahara mustard (*Brassica tournefortii*) and *Schismus* spp. Cheesebush (*Hymenoclea salsola*) and bursage had the most cover among four native perennial species. Native annuals were the most diverse with 22 taxa, dominated by desert plantain, cryptantha (*Cryptantha* spp.), coastal bird's-foot trefoil (*Lotus salsuginosus*), and chuckwalla combseed (*Pectocarya heterocarpa*).

Among soil functional variables, three of them (moisture, stability, and compaction) varied only with site, while the fourth (soil accumulation) varied with abiotic treatment (Table S6).

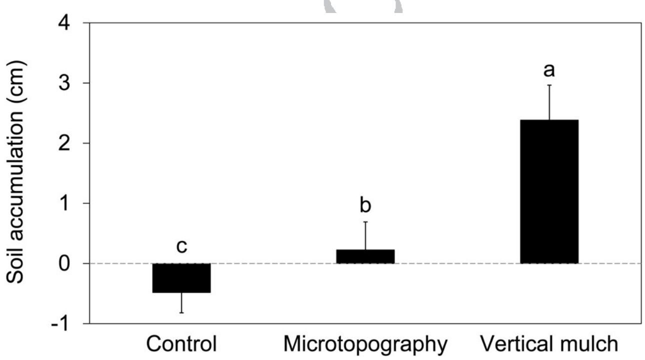

Figure 4. Cumulative change in soil depth (16 months) among abiotic treatments during ecological restoration in the Sonoran Desert, California, U.S.A. Bars are means and error bars are one standard error of means. Means without shared letters differ at $p < 0.05$ (Tukey tests).

The control incurred a net loss of soil over 16 months (Fig. 4). Meanwhile, quadrats receiving vertical mulch accumulated over 2 cm of soil, significantly more than in quadrats receiving microtopography or in the control.

Discussion

Results revealed three main findings: (1) an abiotic treatment (vertical mulch) outperformed the biotic treatment (outplanting); (2) a major component (outplanting) of the set of restoration treatments failed entirely, but key functional outcomes (initiating soil accumulation and conditions for shrub recruitment) were nevertheless achieved by treatments that were effective; and (3) a bet-hedging approach including multiple species in propagule reintroduction mixtures was unsuccessful, but a broader bet-hedging approach of employing both biotic and abiotic treatments did produce restoration benefits. In turn, three conclusions from these findings can be drawn for practical application in ecological restoration: (1) minimal-input treatments can outperform intensive treatments in some cases, such as using minimal-input vertical mulch in our experiment to initiate structural and process restoration as resource-intensive use of greenhouse-grown outplants was ineffective; (2) applying a diverse suite of treatments as a bet-hedging strategy in dynamic restoration environments can help buffer restoration projects from uncertainty and potential failure; and (3) incorporating some minimal-input treatments in restoration warrants consideration given their low cost and potential for bet hedging against the possibility that more expensive treatments fail.

Functional Benefits

While not all restoration response variables changed favorably, three key variables (soil accumulation and native shrub cover and richness) did achieve desired increases at all or some sites. Soil erosion and the resulting fugitive dust is problematic in disturbed desert habitats (Munson et al. 2011). In the Mojave Desert, for example, fugitive dust has triggered safety hazards for vehicle or airplane travel and exposed humans and wildlife to particulate matter (Grantz et al. 1998). Mobile soils can also disrupt plant regeneration processes, creating a positive feedback whereby lack of vegetative cover perpetuates soil degradation (Fick et al. 2016). Vertical mulch was the most effective treatment for promoting soil accumulation. While landscape-scale evaluations of atmospheric dust were beyond the scope of our experiment, previous research suggests that even sparsely distributed structures (akin to distributed vertical mulch) can increase surface roughness, slow winds, and reduce soil erosion cumulatively across landscapes (Grantz et al. 1998; Munson et al. 2011; Fick et al. 2016). This is noteworthy for our study area as wind speeds average 12 km/hour annually, and for the last 20 years, at least 1 day of every month has experienced peak winds exceeding 48 km/hour (Blythe station, National Centers for Environmental Information, Asheville, North Carolina).

The trend for increased abundance of native shrub seedlings in the vertical mulch and microtopography treatments at some sites suggests that at least conditions enabling recruitment opportunities were reinstated. In natural, undisturbed desert ecosystems, pulses of native perennial seedlings can appear relatively frequently among years, but survival of the seedlings across multiple years rarely occurs (Abella et al. 2019). Bowers et al. (2004), for example, found that on average, only 0.1% of native perennial seedlings lived as long as 4 years in the Sonoran Desert. These observations suggest that while multi-decade, long-term data would likely be required to determine whether restoration treatments facilitated long-term shrub establishment, a first step of fostering the process of seedling appearance was achieved. Given the long life spans of native desert shrubs, even a single successful recruitment event from restoration actions could initiate revegetation benefits lasting decades. The two native shrub species most abundant in the vertical mulch treatment, bursage and cheesebush, are considered to have moderately long-lived individuals (30–50+ years) capable of being initial colonizers of severe disturbance, then persisting in maturing shrublands (e.g. Bowers et al. 2004).

Failure of the Biotic Treatment

The total failure of outplanting was unusual, as some outplant survival occurred in dozens of previous restoration experiments in North American (e.g. Edwards et al. 2000; Glenn et al. 2001; Devitt et al. 2020) and global drylands (e.g. Commander et al. 2013; Rathore et al. 2015; Strohmeier et al. 2021). A likely factor was that the growing season (November 2017–March 2018) in which outplanting occurred in our experiment was the driest of the last 47 years. Thus, this was apparently proportionally the driest period in which any published outplanting experiment occurred in the Sonoran or Mojave Desert dating back to the earliest outplanting research in the 1970s (Abella & Berry 2016). Although we provided outplants with initial watering and a third were enclosed in protective vertical mulch, the possibility that intensive treatments (e.g. regular irrigation) could have kept outplants alive even under the extreme drought conditions cannot be ruled out. However, attempting to implement that level of treatment intensity for just the possibility of outplant survival does raise operational feasibility questions. Establishing relatively permanent irrigation infrastructure (sensu Bean et al. 2004) was not feasible in the site context of our experiment along the energy transmission corridor. In lieu of intensive treatments, these observations suggest that outplantings phased across multiple years may be another bet-hedging strategy (Davies et al. 2018). While adding to complexity of restoration, performing the same treatments across multiple years may be particularly suited for restoration in deserts given not only their low average rainfall, but also their extreme variability in rainfall among years (Commander et al. 2013). Moreover, abiotic treatments for bet hedging may become increasingly useful if conditions suitable for directly restoring biota become less frequent, as climate warming and drying trends suggest in southwestern deserts (Ehleringer & Sandquist 2018).

Effects of Treatments on Non-Native Plants

Restoration inadvertently facilitating non-native species through creating favorable conditions needed by native plants, through reinstating natural disturbances (e.g. reintroducing fire) or through activities of implementing treatments (e.g. reconfiguring soil surfaces) is an issue in restoration generally (Larkin et al. 2006). In deserts specifically, the fundamental need to restore fertile islands critical to functioning of natural desert ecosystems can inadvertently enhance habitat for non-native plants as well (Abella et al. 2012; Abella & Chiquoine 2019). In our experiment, although all outplants died, the activities of outplanting increased total non-native annual cover at one site but not at the other three sites. The increase, which occurred at the moderately gravelly sand site which had the highest cover of non-native annuals, resulted from Sahara mustard. This forb produces copious seed and can dominate soil seed banks particularly on disturbed, sandy sites (Abella et al. 2013). Apparently where Sahara mustard was already abundant on or near the site, the activity of outplanting native species or perhaps the few irrigations of outplants somehow promoted this invasive, while implementing the abiotic treatments did not. With lower cover than Sahara mustard but with more consistent presence among sites, non-native annual grass cover (all *Schismus* spp.) increased in quadrats receiving microtopography and tended to increase with vertical mulch addition. It is possible that the microtopographic structures trapped seeds or triggered germination of soil seed banks (Chambers 2000; Biederman & Whisenant 2011), disproportionately benefitting the non-native grasses which can dominate seed banks (Schneider & Allen 2012).

Lack of Treatment Effects on Species Composition

While abiotic treatments affected some univariate vegetation variables, multivariate plant community composition showed minimal variation with respect to treatments. There could be several reasons for the lack of variation. While native annuals comprised most of the species present, a disproportionately large amount of the total annual plant cover was concentrated in two of the three non-native taxa. This may have served to both homogenize overall species composition and to competitively limit differentiation of native annual composition among treatments. Non-native annuals can competitively exclude native annuals at microsite scales, and this effect may be most pronounced in the most favorable microsites, such as fertile islands (Brooks 2000). It is possible that the competitive, homogenous mixture of non-natives limited colonization of treatments by native annuals. However, it is also possible that dynamic niche partitioning in native annual communities limited the development of consistent compositional variation among treatments, at least within the first three growing seasons. As an example of this possible effect, spatial distributions of native annual species with respect to fertile islands or interspaces can vary among years, limiting consistent distributions among microsites (Berg & Steinberger 2012). Another possibility at our study sites is that given the homogenizing effect of severe disturbance creating nearly uniformly de-vegetated sites, the present species composition among treatment quadrats remained relatively uniform or random (both of which would limit compositional difference among treatments) because seeds of many native annuals disperse only short distances. In the Sonoran Desert, Venable et al. (2008), for example, found that most seeds of the native annual curvenut combseed (*P. recurvata*) dispersed less than 2 m.

Interchangeability of Biotic and Abiotic Treatments

A longstanding question in restoration ecology generally and in desert restoration specifically is how well abiotic structures serve as functional substitutes for foundational live organisms, such as trees in forests or fertile island-forming perennials in deserts (Larkin et al. 2006). Research is beginning to address this question in deserts, and results thus far are mixed. For example, in the Chihuahuan Desert over 10 years, soil developing beneath artificial, plastic shrubs exhibited similar texture (likely by trapping fine particles) but did not accumulate carbon or nitrogen like natural shrubs did (Li et al. 2017). In the Arabian Desert, more plant species grew below the canopies of dead perennials than below the canopies of live perennials (El-Keblawy et al. 2016). Similarly, in the Sonoran Desert, Peters et al. (2008) found that nurse rocks were more important than live nurse plants for cactus recruitment. Contrasting with these findings of greater plant recruitment associated with abiotic objects, live 9-year-old outplants in the Mojave Desert supported more native annual species than did interspaces, whereas vertical mulch did not (Abella & Chiquoine 2019). The relative functional benefits of biotic versus abiotic structures are likely to hinge on differences stemming from numerous processes, such as trapping of windblown soil, precipitation throughfall and shading, litter deposition, faunal activity, and belowground processes (Li et al. 2017). Further assessment of these processes and the functional benefits of biotic and abiotic structures may help advance fundamental questions concerning community assembly, fertile island ecology, and the degree to which substitution of abiotic for biotic restoration treatments or bet hedging using both can improve restoration outcomes in variable environments.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Characteristics of four disturbed sites in an experiment evaluating biotic and abiotic restoration treatments in the Sonoran Desert, California, U.S.A.

Table S2. Characteristics of four undisturbed reference sites, each paired with a disturbed site of the same name in Table S1, in the Sonoran Desert, California, U.S.A.

Table S3. Statistical results for univariate plant community variables in an ecological restoration experiment in the Sonoran Desert, California, U.S.A.

Table S4. Statistics for permutational multivariate analysis of variance of plant species composition in an ecological restoration experiment in the Sonoran Desert, California, U.S.A.

Table S5. Indicator values, average cover, and frequency of 29 plant taxa in three abiotic treatments (non-manipulated control, microtopography, or vertical mulch) at four restoration sites in the Sonoran Desert, California, U.S.A.

Table S6. Statistical results for soil functional variables in an ecological restoration experiment in the Sonoran Desert, California, U.S.A.

Figure S1. Views of disturbed sites (top row) and their paired undisturbed reference sites (bottom row) along an energy transmission corridor, Sonoran Desert, California, U.S.A.

Figure S2. Winter growing season (November through March) precipitation by year as a percent of the long-term, 1949 through 2020 average of 48 mm at the Blythe, California, U.S.A. weather station.

Figure S3. Measures of native plant species richness displaying abiotic treatment × year interactions in an ecological restoration experiment in the Sonoran Desert, California, U.S.A.

Figure S4. Soil functional variables that did not differ across restoration treatments but did differ across sites in an ecological restoration experiment in the Sonoran Desert, California, U.S.A.

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