RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

THEMATIC SERIES Arid Lands

RESEARCH ARTICLE

Identifying restoration opportunities beneath native mesquite canopies

Elise S. Gornish[1,2], Hasbagan Ganjurjav[3], Maowei Liang[4], Juniper L. Simonis[5], Mitchel P. McClaran[1]

Effective restoration strategies are needed to address habitat degradation that accompanies worldwide environmental change. One method used to enhance restoration outcomes is the leveraging of beneficial relationships (facilitation) among plants. In the southwestern United States, native mesquite trees (*Prosopis* spp.) are commonly planted to stabilize soil, but the value of using mesquite canopies for enhancing restoration success is unknown. We explored this possibility in an attempt to understand how common species, that both are and are not typically used for restoration, might differentially respond to mesquite canopies. We used a Bayesian multivariate generalized mixed model structure to analyze a dataset describing natural vegetation density in the Santa Rita Experimental Range, Arizona, United States. We found that more dominant species were not more likely to be distributed under mesquite. We also found that, while all of the focal species were more likely to be under mesquite with increased mesquite cover, they varied in the strength of their responses and the degree of saturation. Finally, we found that the aggressive invasive grass *Eragrostis lehmanniana* was found at lower incidences with increasing mesquite canopy cover, compared to the total species average as well as several of the natives investigated in this study. This work highlights the importance of being conscious of canopy size and continuity when considering understory species for restoration. This work also suggests that mesquite canopies can be used to provide a "safe site" for restoration species because competitive pressure from invasives is slightly reduced.

Key words: facilitation, islands of fertility, Lehmann lovegrass, management, native *Prosopis*, restoration, revegetation

Implications for Practice

- Mesquite trees are very common in many dryland systems and their canopies could be a promising avenue for understory plant restoration.
- Practitioners who are considering seeding species under mesquite canopies for restoration do not need to be constrained to using dominant species.
- Because competitive pressure from invasives is slightly reduced under mesquite canopies, these sites can be used to seed competitively inferior but desired restoration species.

Introduction

As climate change, habitat loss due to human development, and invasion by non-native plants and animals continue to modify natural systems at an accelerating rate, management approaches, such as ecological restoration, become more critical for arresting and reversing habitat degradation. The immense challenges posed by widespread environmental change highlight the importance of identifying best management practices for designing and deploying effective restoration strategies that are logistically and monetarily feasible. This is particularly important in ecosystems characterized by high stress, such as drylands, where restoration success tends to be extremely low (Bourne et al. 2017; Svejcar & Kildisheva 2017).

One method that practitioners have started using to enhance restoration outcomes in high-stress systems is the leveraging of beneficial relationships among plants that commonly characterize these habitats (Padilla & Pugnaire 2006; Halpern et al. 2007). Facilitation—a type of positive species interaction—often operates in arid systems in the form of a nurse plant relationship where a "benefactor plant" or "nurse plant" that is particularly resilient to abiotic stress provides more favorable environmental conditions for neighboring plants (Bertness & Callaway 1994). For example, changed conditions under the canopy of nurse plants can include increased soil moisture and enhanced soil microbial communities (Monge & Gornish 2015). And although the explicit integration of

Author contributions: ESG came up with the idea; MPM provided the data; HG, JLS, ML analyzed the data; all authors contributed to writing the manuscript.

[1]School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, U.S.A.
[2]Address correspondence to E. S. Gornish, email egornish@email.arizona.edu
[3]Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, 100081, China
[4]Institute of Ecology, College of Urban and Environmental Science and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, 100871, China
[5]DAPPER Stats, Portland, OR 97212, U.S.A.

doi: 10.1111/rec.13334
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13334/suppinfo

facilitation in restoration strategies is still not widespread, it has proven to be an effective technique for enhancing germination, growth, and survival of seeded or planted species across degraded landscapes (e.g. Gedan & Silliman 2009; Avendaño-Yáñez et al. 2014), particularly arid ones (e.g. Zhao et al. 2007; Pueyo et al. 2009; Busso & Pérez 2018).

In grassland systems in the southwestern United States, individuals of *Prosopis* spp. (mesquite trees) have been increasing in density since 1900 (McClaran 2003), due in part to fire suppression activities (Humphrev 1958) and more recently, as a result of climate change (Campbell et al. 2000). These native species (mostly *P. glandulosa* and *P. velutina*, which can be invasive elsewhere, e.g. Wise et al. 2012) now dominate over 38 million hectares of southwestern drylands (Van Auken 2009) and have been documented as interacting strongly with understory plants (e.g. Tiedemann & Klemmedson 2004; Teague et al. 2008). The strength and direction of this relationship appear to be dependent on many factors. For example, the presence of grazing can affect facilitation because livestock behavior can modify resource availability through excretions and local topographic and moisture changes from hoofprints (e.g. Veblen 2008). Livestock can also change the condition of nurse plants or the density of understory species through browsing and grazing. Facilitation is density dependent and tends to be strongest at intermediate understory densities (Zhang & Tielbörger 2020). Therefore, livestock grazing can modify the positive relationships among plants by reducing understory plants below this intermediate density threshold.

Although environmental factors such as management regime can play a role in modifying facilitation, species-specific factors, such as functional type (e.g. grass vs. forb vs. shrub), are often identified as more important (e.g. Soliveres et al. 2012). For example, mesquite appears to interact particularly strongly with perennial grasses compared to forbs (Yavitt & Smith Jr. 1983; McClaran & Angell 2007). In many cases, perennial invasive grasses, such as *Eragrostis lehmanniana* (Lehmann lovegrass), have been documented as being negatively affected by mesquite canopies in southwestern U.S. dryland systems (e.g. Cable 1971; Tiedemann & Klemmedson 2004). Alternatively, native perennial grasses appear to often preferentially grow under mesquite canopies. This could be due to differences in soil factors between mesquite canopies and interspaces, such as increased soil nutrients (Tiedemann & Klemmedson 1973; McClaran et al. 2008) and moisture availability (Potts et al. 2010). Importantly, many native desert species are also shade tolerant, which is a distinct advantage under canopies in the presence of more shade intolerant invasives (Belsky 1994). These relationships coupled with mesquite presence and quantity in degraded arid land systems highlight their potential utility for restoration.

Mesquite has largely been used in restoration as a planted species for soil stabilization (e.g. Bashan et al. 2012) and weed control (e.g. Shafroth et al. 2005), but use of its canopy as an "island of fertility" to enhance restoration success (e.g. Hulvey et al. 2017) has almost never been recorded in the literature (but see Bacilio et al. 2006). In order to explore this possibility, we first need to understand how different types of common species that have differential utility for restoration might differentially respond to mesquite canopies and interspaces.

We used a dataset describing extant vegetation density and cover to highlight relationships between plant species and mesquite cover. To understand general trends, we first asked: do factors known to affect facilitation in arid systems, such as the presence of grazing, and plant functional type and native status modify plant response to mesquite canopy cover? To understand the value of mesquite canopy for restoration, we then focused on 10 species that differ in their relevance to restoration to explore differences in species specific responses to mesquite canopies. We expected grazing and native species status to be important for driving relationships between mesquite canopies and plant density. We also expected that species commonly used for ecological restoration in the region would be more likely to be found under mesquite canopies than species not typically used for restoration due to density. Positive plant–plant relationships are often strongest at intermediate neighbor densities—species used for ecological restoration in arid systems tend to be common, but these native plants do not typically demonstrate the type of high-density cover that is associated with invasive species.

Methods

Data

We used a dataset (https://cals.arizona.edu/srer/data.html) collected from long-term livestock exclosures on the Santa Rita Experimental Range (SRER; 31°50′ N, 110°53′ W) approximately 50 km south of Tucson, Arizona, United States. Across 13 pastures, 22 exclosures (1–4 per pasture) were established between 1916 and 1935, but the sampling transects were not created until 2011. At each of the 22 exclosures we sampled two transects inside the grazed area and two transects outside the grazed area (with two exceptions where three and three transects were sampled) for a total of 92 transects. The transects have been measured every 3 years starting in 2011, and so there are currently three sample points (2011, 2014, 2017) for each. The transects are permanently marked, so the repeat samples were of the same locations. The data also note the presence of fires across transects (there were fires in 1989, 1994, and 2017) and different soil types (sandy loam upland, sandy loam deep, and loamy upland).

At each transect on each sample date, density and cover data of all plant species were collected. For the present analysis, we focused on herbaceous plant density as a response variable, which was measured as a count of individuals for each of 44 species within a 9.29 m^2 (30.5 m × 0.3 m) belt transect. In addition to the total count of individuals, there are subcounts for individuals underneath mesquite canopy and for individuals outside of the mesquite canopy. The cover data were used to quantify the total amount of mesquite canopy in each transect (used as a predictor variable) and were measured visually at every 0.03 m point along the transect (for a total of 1,000 measurements per transect). We ignored age and size of individual mesquite trees in the dataset, which has been shown to not affect the relationships between woody and herbaceous species (McClaran & Angell 2007; but see Ludwig et al. 2004).

Although we collected data on all species present in our plots, for this article we focused on 10 taxa that are common to SRER and are either typically used in local restoration efforts or are not typically used in restoration efforts. We considered these focal species to explore general trends that might provide utility for considering mesquite canopies for restoration. Typically used species in local restoration efforts include native perennial bunchgrasses *Aristida* spp. (mostly *Aristida purpurea*, Parish's threeawn), *Bouteloua rothrockii* (Rothrock grama), *Heteropogon contortus* (Tanglehead), *Muhlenbergia porteri* (Bush muhly), and *Setaria macrostachya* (Large spike bristlegrass). Species that are not typically used in local restoration efforts include the native perennial forb *Haplopappus tenuisectus* (Burroweed), the invasive bunchgrass *Eragrostis lehmanniana* (Lehmann lovegrass), and native perennial cacti, including *Opuntia engelmannii* (Cactus apple), *Cylindropuntia fulgida* (Jumping cholla), and *C. spinosior* (Walkingstick cactus). We follow nomenclature from the well-established SEInet Arizona centric database (http://swbiodiversity.org/).

Analysis

We analyzed the density of understory plants with a Bayesian multivariate generalized mixed model structured fit via Markov chain Monte Carlo (MCMC; Hadfield 2010; Hadfield & Nakagawa 2010). This approach was employed as it can accommodate for multiple levels of dependency. Our response variable consisted of the total count and a pair of counts for under and not under mesquite for a given taxon. Total count data were modeled as Poisson with a log link, and the distribution pairs of data were modeled as binomial with a logit link. We modeled the responses as covarying within observational units, such that we could estimate the degree to which transects with more mesquite tend to have more (or less) of a plant distributed under the mesquite. To understand general trends, we used a fixed effects model, where we included mesquite cover (changed from percentage to a continuous proportion between 0 and 1, as a linear and quadratic term to allow for curvilinear relationships), grazing history/presence (binary), burn history (binary), soil type (categorical with three types), and year (as a continuous variable although there were only three possible values). The quadratic term for mesquite indicates a greater than linear increase/decrease in response species as mesquite cover increases. No interactions among fixed effects were included. To avoid data dredging, we did not conduct stepwise model selection, but rather constructed only the most inclusive model of interest and evaluated its multivariate posterior distribution.

We included random effects to account for both spatial sampling arrangement as well as taxonomic-level patterns and responses to covariates. We modeled the sampling hierarchy using a three-level nested random effect of transect within exclosure within pasture, each with independent variance for the two responses (total density and the fraction under mesquite) within them. We accounted for species-level general trends with a random effect that allowed for covariance between the two responses to estimate the degree to which species that are more common tend to be more (or less) likely to be found under mesquite. To understand species-level responses to mesquite canopy, based on whether a plant was likely to be used in restoration, we model species-specific responses to mesquite cover and included random effects on the slopes for both the first- and second-order mesquite cover covariates with possible covariance across the responses (such that an increase in mesquite cover could increase a species' density and cause it to be more associated with mesquite). We included random effects for each of the other covariates except year (i.e. soil type, burn history, grazing) to allow for species-specific responses to each and modeled the impacts as independent across the response types. Species were also grouped according to the three classifications: native versus not native, functional group (grass, forb, or shrub, which included cacti), and lifecycle (annual or perennial) via random effects. All analysis were executed in R v.3.5.3 (R Core Team 2019) using the MCMCglmm function in the *MCMCglmm* package v.2.26 (Hadfield 2010). All analyses are available on github (https://github.com/dapperstats/mesquite_understory) and are archived in zenodo (https://doi.org/10.5281/zenodo.3934930).

Results

General Trends

The dataset describes a variety of species, including four forb species, 21 grass species, and 19 shrub species (see McClaran 2003 for full details about plant species). Forbs are predominately not present when mesquite is present (co-occurrence of forbs and mesquite together was 3.5%), but at least some representative of both grasses and shrubs tended to co-occur with mesquite (95.1 and 83.7%, respectively). Although grasses and shrubs had similar average proportions of plants under mesquite (0.35 and 0.33, respectively), the proportion distribution was unimodal and more evenly distributed for grasses compared to bimodal and dense at the extremes of 0 (never found under mesquite) and 1 (always found under mesquite) for shrubs (Fig. 1). The 41 native plants exhibited a relatively uniform distribution of density under mesquite, whereas the three non-native plants were distributed more towards the low-end extreme of 0 with respect to proportion of density under mesquite (Fig. 1). Both the density of plants and the fraction of plants distributed under mesquite showed substantial over-dispersion. There was substantial overlap in the covariance of the two responses with 0 (95% HPD: −0.518–0.134; Table S1). This indicates that along transects with higher focal plant density, there is not a related shift in distributions with respect to mesquite.

Overall, there was no discernable covariance between the response variables for species (i.e. species that were more likely to have higher densities were not more likely to be distributed under mesquite; median: 0.09, 95% HPD: −2.46–2.77; Table S2). Across species, there was a significant negative but curved relationship between mesquite cover and the total density of plants (linear effect: median = 0.57, 95% HDP: −3.46–

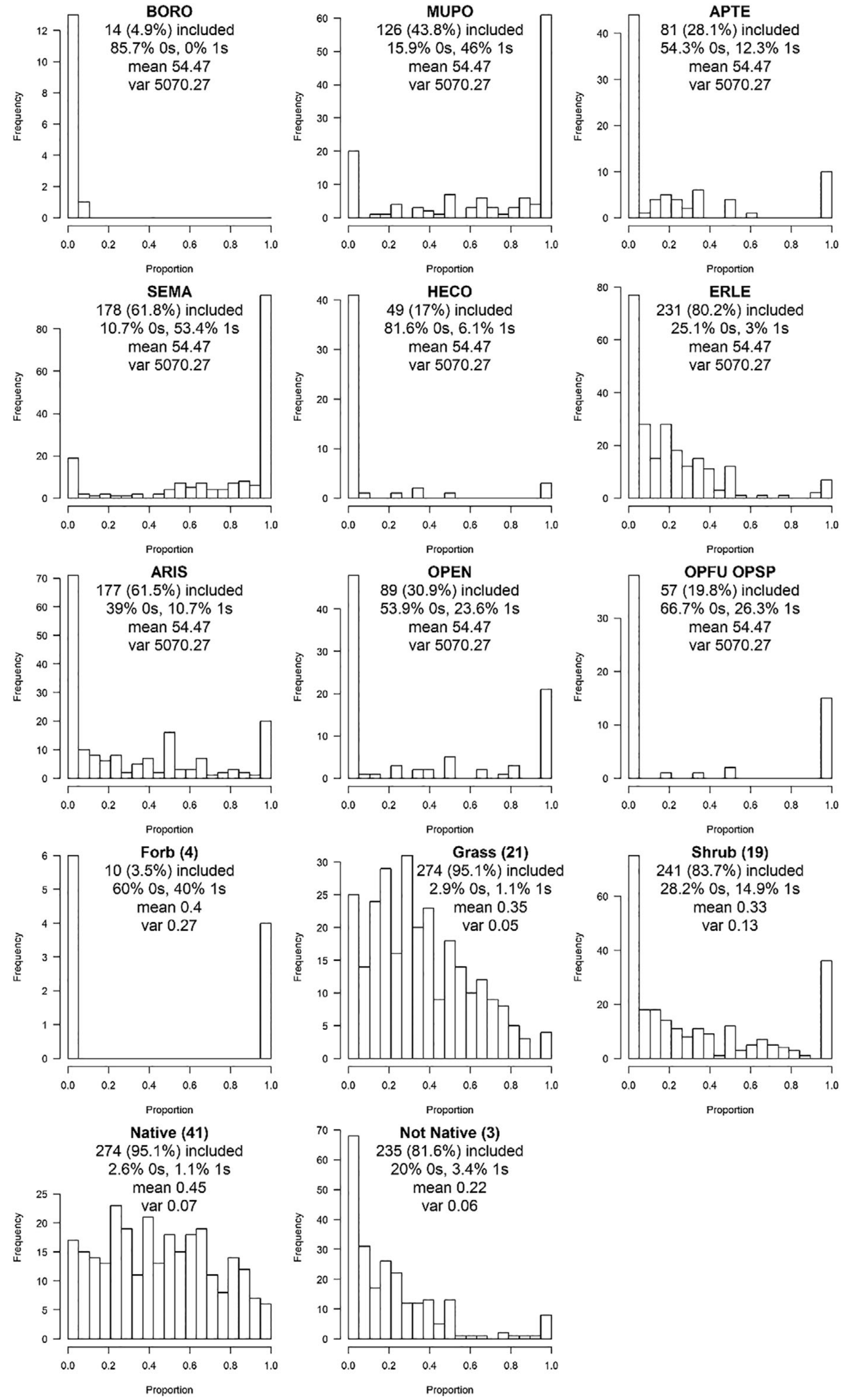

Figure 1. Frequency distributions for the percentage of plants under mesquite cover based on densities of each species/genus/pair of species, functional group, or native status grouping. Note that the y-axes change among panels. Species code names follow those used in Table 1.

4.51, $p = 0.7733$; quadratic effect: median: −10.62, 95% HDP: −20.05to −2.71, $p = 0.0066$; Table S3) as well as a significant, positive but saturating relationship between mesquite cover and the proportion of plants under mesquite (linear effect: median: 11.58 95% HDP: 7.63–15.49, $p < 0.0001$; quadratic effect: median: −9.38, 95% HDP: −17.33 to −1.70,

Table 1. Taxon level summaries of distributions, densities, and presences.

Taxon	*Presence*	*Density (mean)*	*Density (SD)*	*Proportion Under Mesquite (mean)*	*Proportion Under Mesquite (SD)*
ARIS	0.653	6.358	16.015	0.308	0.349
BORO	0.049	1.031	8.610	0.007	0.019
HECO	0.191	3.806	22.922	0.092	0.255
MUPO	0.444	3.028	6.031	0.698	0.380
SEMA	0.622	5.698	7.907	0.765	0.340
APTE	0.285	1.590	4.964	0.218	0.333
ERLE	0.851	51.788	70.267	0.196	0.225
OPEN	0.316	0.944	2.313	0.341	0.426
OPFU	0.024	0.028	0.185	0.214	0.393
OPSP	0.201	0.351	1.690	0.286	0.446

Taxon codes are as follows: APTE, *Haplopappus tenuisectus*; ARIS, *Aristida* spp.; BORO, *Bouteloua rothrockii*; ERLE, *Eragrostis lehmanniana*; HECO, *Heteropogon contortus*; MUPO, *Muhlenbergia porteri*; OPEN, *Opuntia engelmannii*; OPFU, *Cylindropuntia fulgida*; OPSP, *C. spinosior*; SEMA, *Setaria macrostachya*. Bold abbreviations of species name indicate the species is commonly employed in local restoration.

$p = 0.0162$; Table S3). The presence of grazing had no effect on density of plants under mesquite (median: 0.413, 95% HDP: −0.282–1.141, $p = 0.2331$).

Focal Species

Each of the 10 focal taxa showed a wide range of mean density across transects (from <1 to >50 plants per transect; Table 1, Fig. 2). The set of distributions of species with respect to mesquite canopy (when the species and mesquite are both present on a transect) is overall U-shaped, with most observations being 0% or 100% under mesquite (Fig. 2). Species showed differences in how they responded to an increase in mesquite density. For example, some native herbaceous species, such as *Setaria macrostachya* and *Haplopappus tenuisectus*, appeared to increase in percentage under mesquite as mesquite cover increased until a saturation point of approximately 35% (Fig. 3). Cacti, such as *Cylindropuntia spinosior* and *Opuntia engelmannii*, demonstrated a generally stable increase in percent under mesquite canopy with increasing cover (at least up until our maximum mesquite canopy cover of 56%). Finally, with increasing mesquite canopy cover, invasive *Eragrostis lehmanniana* was found at a lower incidence than the total species average as well as several of the natives investigated in this study (Fig. 3).

There were substantial differences among species with respect to intercepts and responses to mesquite cover for both the density and distributional responses (Fig. 3, Table S1). In particular, while all of the focal taxa were more likely to be

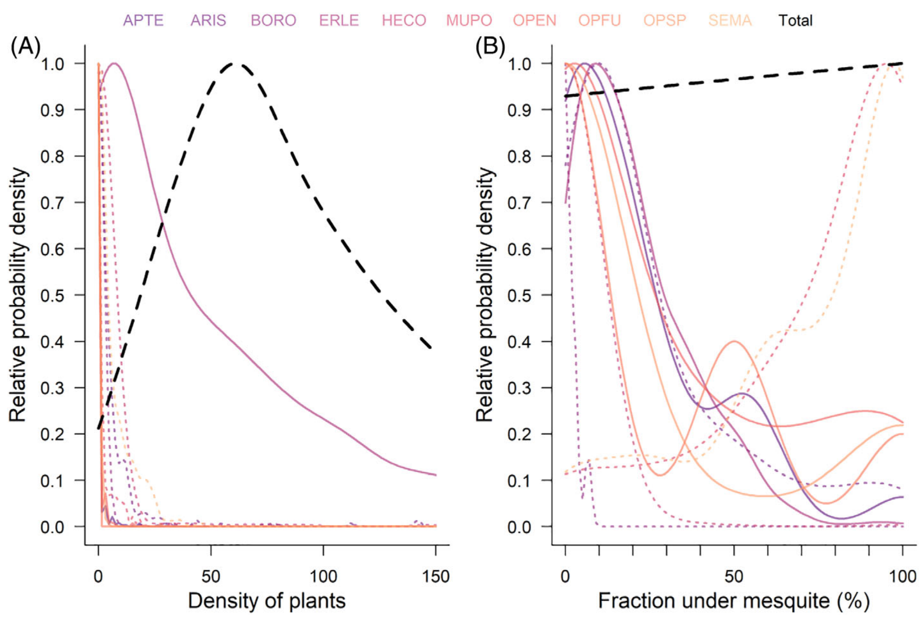

Figure 2. Empirical kernel density functions for the density (A; counts of individuals per 9.29 m^2) and fraction of plants under mesquite (B) for each of the 10 focal taxa identified by hue (see Table 1 footnote) and the total across all taxa (black lines). Target species for local restoration are noted with dashed lines. Kernels were evaluated at 100 values across each variable and made relative (maximum density value set to 1.0) to facilitate comparisons among taxa. Line hues identify taxa as in Table 1.

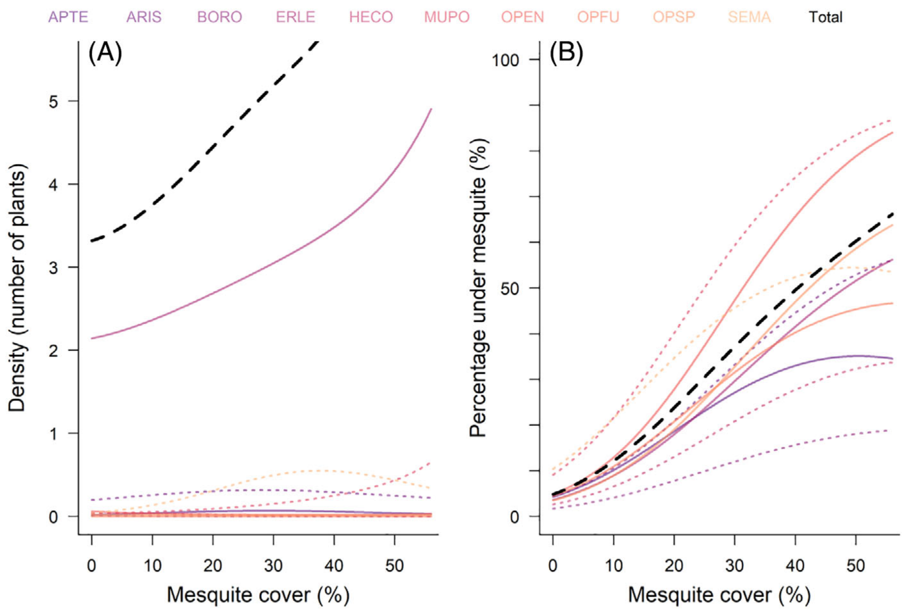

Figure 3. Mean taxon-specific (for the 10 focal taxa) and total (for all taxa, shown as black line) plant responses of densities (A) and distributions (B) to mesquite cover over the range observed (0–56% mesquite cover). Line hues identify taxa as in Table 1 (see footnote). Target species for local restoration are noted with dashed lines. Total density is cutoff from the figure after ~40% and reaches a maximum of 156 at the extreme of the range (56% mesquite cover).

under mesquite with increased mesquite cover suggesting a random relationship with mesquite cover (proportion of total density under mesquite increases at the same rate as mesquite cover increases along the transect), they varied in the strength of their responses and the degree of saturation (Fig. 3, Table S4). More striking was the variation in the overall density curves, where the focal taxa differed in their intercepts and responded in both directions to mesquite cover (Fig. 3, Table S4).

Discussion

Leveraging natural ecosystem dynamics and local heterogeneity can significantly enhance restoration outcomes. Since the density of mesquite is important for plant communities (Whittaker et al. 1979), mesquite canopies could be considered "islands of fertility" in ecological restoration projects in arid systems where positive relationships tend to predominate (Scholes & Archer 1997). A site associated with mesquite canopies could generate more mild environmental conditions in arid systems. Leveraging these areas for seeding might enhance restoration outcomes through increased germination and establishment success of seeded species, as well as the maintenance and enhancement of nutrient cycling in degraded areas (Lopez-Lozano et al. 2016). However, whether mesquite canopies could actually serve as a conducive nursery site for native seeds used in restoration projects is still unknown. Restoration candidates are largely chosen to replace conspecifics that were displaced by habitat degradation. However, usually, the number of species employed in a restoration project is smaller than the total number of species lost after a disturbance. The condensed species list is often a cumulative result of (among several factors) dominance in the system. This is because dominant species tend to be drivers of plant community response to disturbance (e.g. Smith & Knapp 2003; Oñatibia et al. 2018). We found that more dominant species (based on density) were not more likely to be distributed under mesquite. This suggests that practitioners who are considering using mesquite canopies as "islands of fertility" do not need to be constrained to using dominant species. Indeed, the call to use less dominant and even rare species in restoration, based on their disproportionate contribution to species richness across sites, has been noted elsewhere (e.g. Baur 2014).

Species showed differences in how they responded to an increase in mesquite density as some species increase under mesquite until a saturation point while other species continually increased with increasing canopy cover. This highlights the importance of being conscious of canopy size and continuity when considering understory species (Tewksbury & Lloyd 2001; Incerti et al. 2013) as canopy coverage values that facilitate the growth of one restoration candidate might actually inhibit the growth of others. For example, in many cases, nurse plants provide protection from excessive solar radiation in arid systems to vulnerable seedlings (e.g. Valiente-Banuet et al. 1991). Low canopy cover of mesquite might provide protection to certain robust cactus species, but might only be able to provide adequate protection to other vulnerable species, such as native agave seedlings—which are notoriously sensitive to direct sunlight in early age classes—at higher canopy coverages. Of course, very high canopy coverage can negatively impact understory species by providing an overabundance of shade (Reisman-Berman 2007) or plant growth inhibitory alkaloids (Nakano et al. 2004). Since canopy characteristics play such an important role in driving facultative relationships, outcomes from one species (or one type of species) might not necessarily translate well into effective management strategies for other species.

As mesquite canopy cover increases in a plot, the expectation is that a higher proportion of species will be found under mesquite in the plot (e.g. more of the plot is covered). However, we found a significant negative relationship between mesquite canopy and density of herbaceous plants. Mesquite canopies might inhibit understory plant density by limiting their root growth (Slate et al. 2020). Mesquite trees can produce massive quantities of fine woody roots in the upper soil profile, outcompeting understory plants with extensive root systems. This suggests that more shallow rooted species, such as annuals, might do better as restoration candidates when using an island of fertility approach.

One of the focal invasives in the study, *Eragrostis lehmanniana*, was found to decrease with increasing mesquite cover. This is not surprising based on the well documented relationship between mesquite and *E. lehmanniana* (e.g. Kincaid et al. 1959; Martin & Morton 1993; Tiedemann & Klemmedson 2004). However, this highlights another utility for restoration under mesquite canopies in arid systems. Since *E. lehmanniana* is one of the most dominant invasives in these systems (Anable et al. 1992), mesquite canopies can be used to provide a 'safe site' for restoration species where competitive pressure from invasives is slightly reduced.

Our work suggests that the use of mesquite canopy for strategic plant restoration is a fruitful avenue to investigate for management purposes. Knowing which native species might benefit most from canopies requires either intimate manager knowledge or existing datasets that describe relationships between mesquite and understory species. The use of large, existing datasets to direct restoration efforts is ideal for identifying restoration candidates (e.g. Gornish & Miller 2013) but such datasets are obviously unavailable for most locations. In many cases, only short-term datasets are available, which can be useful; however, care must be taken when using short-term datasets to inform fertile island development as annual climate variations can modify the strength of facultative interactions (Gómez-Aparicio et al. 2004). All data are freely available for download from the Santa Rita Experimental Range website: https://cals.arizona.edu/SRER/

LITERATURE CITED

Anable ME, McClaran MP, Ruyle GB (1992) Spread of introduced Lehmann lovegrass Eragrostis lehmanniana Nees. in southern Arizona, USA. Biological Conservation 61:181–188

Avendaño-Yáñez M, Sánchez-Velásquez LR, Meave JA, Pineda-López MR (2014) Is facilitation a promising strategy for cloud forest restoration? Forest Ecology and Management 329:328–333

Bacilio M, Hernandez JP, Bashan Y (2006) Restoration of giant cardon cacti in barren desert soil amended with common compost and inoculated with *Azospirillum brasilense*. Biology and Ferility of Soils 43:112–119

Bashan Y, Salazar BG, Moreno M, Lopez BR, Linderman RG (2012) Restoration of eroded soil in the Sonoran Desert with native leguminous trees using plant growth-promoting microorganisms and limited amounts of compost and water. Journal of Environmental Management 102:26–36

Baur B (2014) Dispersal-limited species – a challenge for ecological restoration. Basic and Applied Ecology 15:559–564

Belsky AJ (1994) Influence of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology 75:922–932

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends in Ecology and Evolution 9:191–193

Bourne A, Muller H, de Villiers A, Alam M, Hole D (2017) Assessing the efficacy and effectiveness of rangeland restoration in Namaqualand, South Africa. Plant Ecology 218:7–22

Busso CA, Pérez DR (2018) Opportunities, limitations and gaps in the ecological restoration of drylands in Argentina. Annals of Arid Zones 57:191–200

Cable DR (1971) Lehmann lovegrass on the Santa Rita experimental range, 1937-1968. Journal of Range Management 24:17–21

Campbell BD, Stafford Smith DM, Pastures GCTE, Rangelands Network Members (2000) A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. Agriculture, Ecosystems and Environment 82:39–55

Core Team R (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Gedan KB, Silliman BR (2009) Using facilitation theory to enhance mangrove restoration. Ambio 38:109

Gómez-Aparicio L, Zamora R, Gómez J, Hódar JA, Castro J, Baraza E (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128–1138

Gornish ES, Miller TE (2013) Using long-term census data to inform restoration methods of coastal dune vegetation. Estuaries and Coasts 36:1014–1023

Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:2

Hadfield JD, Nakagawa S (2010) General quantitative genetic methods for comparative biology: phylogenies, taxonomies, and multi-trait models for continuous and categorical characters. Journal of Evolutionary Biology 23: 494–508

Halpern BS, Silliman BR, Olden JD, Bruno JP, Bertness MD (2007) Incorporating positive interactions in aquatic restoration and conservation. Frontiers in Ecology and the Environment 5:153–160

Hulvey KB, Leger EA, Porensky LM, Roche LM, Veblen KE, Fund A, Shaw J, Gornish ES (2017) Restoration islands: a tool for efficiently restoring dryland ecosystems? Restoration Ecology 25:S110–S113

Humphrev RR (1958) The desert grassland. Botanical Review 24:193–253

Incerti G, Giordano D, Stinca A, Senatore M, Termolino P, Mazzoleni S, Bonanomi G (2013) Fire occurrence and tussock size modulate facilitation by *Ampelodesmos mauritanicus*. Acta Oecologia 49:116–124

Kincaid DR, Holt GA, Dalton PD, Tixier JS (1959) The spread of Lehmann lovegrass as affected by mesquite and native perennial grasses. Ecology 4: 738–742

Lopez-Lozano NE, Carcaño-Montiel MG, Bashan Y (2016) Using native trees and cacti to improve soil potential nitrogen fixation during long-term restoration of arid lands. Plant and Soil 403:317–329

Ludwig F, de Kroon H, Berendse F, Prins HHT (2004) The influence of savanna trees on nutrient, water, and light availability and the understory vegetation. Plant Ecology 170:93–105

Martin SC, Morton HL (1993) Mesquite control increases grass density and reduces soil loss in southern Arizona. Journal of Range Management 46: 170–175

McClaran MP (2003) A century of vegetation change on the Santa Rita Experimental Range. Pages 16–33. In: McClaran MP, Folliott PF, Edminster CB (tech. coords.) *Santa Rita Experimental Range: 100 years (1903 to 2003) of accomplishments and contributions*. Proceedings RMRS-P-30. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado

McClaran MP, Angell DL (2007) Mesquite and grass relationships at two spatial resolutions. Plant Ecology 191:119–126

McClaran MP, Moore-Kucera J, Martens DA, van Haren J, Marsh SE (2008) Soil carbon and nitrogen in relation to shrub size and death in a semi-arid grassland. Geoderma 145:60–68

Monge J, Gornish ES (2015) Positive species interactions as drivers of vegetation change on a barrier Island. Journal of Coastal Research 31:17–24

Nakano H, Nakajima E, Hiradate S, Fujii Y, Yamada K, Shigemori H, Hasegawa K (2004) Growth inhibitory alkaloids from mesquite (*Prosopsis juliflora* (Sw.) DC.) leaves. Phytochemistry 65:587–591

Oñatibia GR, Boyeo L, Aguiar MR (2018) Regional productivity mediates the effects of grazing disturbance on plant cover and patch-size distribution in arid and semi arid communities. Oikos 127:1205–1215

Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4: 196–202

Potts DL, Scott RL, Bayram S, Carbonara J (2010) Woody plants modulate the temporal dynamics of soil moisture in a semi-arid mesquite savanna. Ecohydrology 3:20–27

Pueyo Y, Alados CL, Garcí-Ávila B, Kéfi S, Maestro M, Rietkerk M (2009) Comparing direct abiotic amelioration and facilitation as tools for restoration of semiarid grasslands. Restoration Ecology 17:908–916

Reisman-Berman O (2007) Age-related change in canopy traits shifts conspecific facilitation to interference in a semi-arid shrubland. Ecography 30:459–470

Scholes RJ, Archer S (1997) Tree-grass interactions in savannas. Annual Reviews in Ecology and Systematics 28:517–544

Shafroth PB, Cleverly JR, Dudley TL, Taylor JP, Van Riper IIIC, Weeks EP, Stuart JN (2005) Control of *Tamarix* in the Western United States: implications for water salvage, wildlife use, and riparian restoration. Environmental Management 35:231–245

Slate ML, Tsombou FM, Callaway RM, Inderjit El-Keblawy AA (2020) Exotic *Prosopsis juliflora* suppresses understory diversity and promotes agricultural weeds more than a native congener. Plant Ecology 221:659–669

Smith MD, Knapp AK (2003) Dominant species maintain ecosystem function with non random species loss. Ecology Letters 6:509–517

Soliveres S, Eldridge DJ, Hemmings F, Maestre FT (2012) Nurse plant effects on plant species richness in drylands; the role of grazing, rainfall and species specificity. Perspectives in Plant Ecology, Evolution and Systematics 14: 402–410

Svejcar LN, Kildisheva OA (2017) The age of restoration: challenges presented by dryland systems. Plant Ecology 218:1–6

Teague WR, Ansley RJ, Pinchak WE, Dowhower SL, Gerrard SA, Waggoner JA (2008) Interannual herbaceous biomass response to increasing honey mesquite cover on two soils. Rangeland Ecology and Management 61:496–508

Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse plants: spatial scale, stress gradients and benefactor size. Oecologia 127:425–434

Tiedemann AR, Klemmedson JO (1973) Nutrient availability in desert grassland soils under mesquite Prosopis juliflora trees and adjacent open areas. Arizona Agricultural and Experimental Station 1906:163–164

Tiedemann AR, Klemmedson JO (2004) Responses of desert grassland vegetation to mesquite removal and regrowth. Journal of Range Management 57:455–465

Valiente-Banuet A, Bolongaro-Crevenna A, Briones O, Ezcurra E, Rosas Nuñez H, Barnard G, Vazquez E (1991) Spatial relationships between cacti and nurse shrubs in a semi-arid environment in Central Mexico. Journal of Vegetation Science 2:15–20

Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931–2942

Veblen KE (2008) Season- and herbivore-dependent competition and facilitation in a semiarid savanna. Ecology 89:1532–1540

Whittaker RH, Gilber LE, Connell JH (1979) Analysis of two-phase pattern in a mesquite grassland, Texas. Journal of Ecology 67:935–952

Wise RM, van Wilgen BW, Le Maitre DC (2012) Costs, benefits and management options for an invasive alien tree species: the case of mesquite in the Northern Cape, South Africa. Journal of Arid Environments 84:80–90

Yavitt JB, Smith EL Jr (1983) Spatial patterns of mesquite and associated herbaceous species in an Arizona desert grassland. The American Midland Naturalist 109:89–93

Zhang R, Tielbörger K (2020) Density-dependence tips the change of plant-plant interactions under environmental stress. Nature Communications 11:2532

Zhao H, Zhou R, Su Y, Zhang H, Zhao L, Drake S (2007) Shrub facilitation of desert land restoration in the Horqin sand land of Inner Mongolia. Ecological Engineering 31:1–8

Supporting Information

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

Table S1. Among-response residual variance and covariance estimates of the model.
Table S2. Random effects variance and covariances estimates.
Table S3. Fixed effects estimates for the density and distribution components of the model.
Table S4. Focal taxon-specific and total plant maximal slopes, maximal percentage, and mesquite cover values when maximum percentage is reached for the relationships between mesquite cover and percentage of plants under mesquite cover.

Coordinating Editor: Zhanhuan Shang

Received: 12 October, 2020; First decision: 19 November, 2020; Revised: 20 November, 2020; Accepted: 30 November, 2020