Shrubs facilitate native forb re-establishment in an invaded arid shrubland

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ABSTRACT

Establishing native species within invaded ecosystems is important to increase biodiversity and ecosystem functioning. Seeding species with nurse plants can be effective at increasing establishment especially in high stress ecosystems. Invaded arid ecosystems are thus good candidates for testing this method of seeding. It is hypothesized that shrubs will facilitate native forbs in an invaded arid shrubland through reductions in consumer pressure, abiotic stress, and competition from non-native species. Five native forb species were seeded in a full-factorial design into shrub and open microsites, with and without exclosures, and with and without non-native removals. The response of forbs was monitored in two growing seasons (2016, 2017). Shrubs had a positive or neutral effect on biomass, but had a neutral or negative effect on abundance in both years. Interestingly, most natives co-existed with non-natives species. Exclosures provided positive effects for biomass and abundance of some species and were important for species to establish. Seeding native forbs with shrubs improved the establishment of native species but grazing or herbivory may need to be minimized. The observed lack of native plant species in this region may not be from non-native species competition, but due to seed limitation and intense consumer pressure.

1. Introduction

Invasion by non-native species has been described as a main contributing factor to the current biodiversity crisis (Dirzo and Raven, 2003; Sala et al., 2000). The effects of non-native species on introduced communities have been well documented and include reducing biodiversity, biomass, and ecosystem function (Flory and Clay, 2010; Kettenring and Adams, 2011). Restoring invaded ecosystems has been a focus for land managers (Suding, 2011); however, controlling non-natives has been challenging, and it has produced limited successes. Re-establishing native species within heavily invaded sites may be difficult as non-native species often exert negative effects such as soil legacies (Grman and Suding, 2010) and niche pre-emption (Dickson et al., 2012), which may allow continued dominance of non-natives. Non-native species dominance at invaded sites could lead to local extirpations and extinctions particularly on islands or in freshwater systems (Baider and Florens, 2011; Howald et al., 2007; Lodge et al., 1998). Therefore, identifying possible methods for increasing the establishment and persistence of native species within invaded landscapes is of critical importance for their successful restoration.

In high stress environments, such as deserts, some plants exert positive effects on other plant species and can increase their establishment

and persistence. These benefactors or "nurse-plant" species can increase the establishment of other plant species because their canopy has altered their environmental conditions. This is done through many mechanisms including reducing temperature extremes, increasing soil moisture and soil nutrients, and providing protection from herbivory, especially if the nurse-plant possess traits that deter consumers (Barbosa et al., 2009; Filazzola and Lortie, 2014; Hortal et al., 2013). The positive benefits of being associated with a nurse-plant has prompted suggestions for them to be used in restoration projects particularly in regions of high abiotic or biotic stress which might otherwise have low success (Brooker et al., 2008; Padilla and Pugnaire, 2006). Nurse-plants (mainly shrubs) have successfully been applied in reforestation efforts in Mediterranean and Atlantic forests and the success of this planting method has been attributed to reducing high abiotic (heat and drought stress) and biotic (high herbivory) stress (Gómez-Aparicio et al., 2008; Rey et al., 2009; Zwiener et al., 2014). However, the use of nurse-plants as a strategic planting method to increase the success of restoration projects has not (to our knowledge) been extended to forbs in arid or semi-arid ecosystems (for some example see: Bruno, 2000; Drezner, 2006; Groeneveld et al., 2007; He et al., 2013; Hupp et al., 2017). Thus, there is a need to test the ability of nurse plant facilitation to increase restoration success in desert

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ecosystems and on native forbs that are being outcompeted by non-native annual grasses (Salo, 2004; Salo et al., 2005).

Invaded ecosystems pose challenges for plant establishment (Callaway and Ridenour, 2004; Corbin and D'Antonio, 2010; Grman and Suding, 2010; Liancourt et al., 2005) that can be further complicated by nurse effects. The desert shrublands of Southwestern US are increasingly becoming invaded by non-native grasses, such as *Bromus tectorum* and *B. rubens* (Blank et al., 2013; Salo, 2005, 2004; Salo et al., 2005; Wilcox et al., 2012). The microclimate under shrub canopies provide greater resources, reduced herbivory, and lower environmental stress that can be favourable for these highly competitive species (Filazzola et al., 2017; Prevey et al., 2010; Rodriguez-Buritica and Miriti, 2009). Consequently, non-native species are more frequently associated with shrubs relative to open areas (Holzapfel and Mahall, 1999; Prevey et al., 2010; Rodriguez-Buritica and Miriti, 2009). Benefactors have also been shown to increase the phylogenetic and functional diversity of plant communities (Butterfield et al., 2013; Liancourt and Tielboerger, 2011; Valiente-Banuet and Verdu, 2007) that can support assemblages of species beyond non-native grasses. It remains unclear if shrubs would be able to increase the establishment of native plants for the purposes of restoration in an arid invaded landscape. There is a need to understand the extent that shrubs can increase the establishment of native plants within an invaded landscape if future restoration efforts are to be taken.

Here, we tested if shrubs facilitate native forb restoration by measuring the response of seeded native forbs within shrubs and open areas. To determine if herbivory/grazing and non-native competition limits native forb species from currently occupying this site, we also tested the effect of animal exclosures and non-native species removals at the shrub and open microsites. We hypothesized that shrubs facilitate the establishment of native forb species and we expect this positive effect to increase when non-natives are removed and herbivory is reduced. The following predictions were tested in the field: i) shrubs will facilitate native plant species establishment, ii) native species establishment will increase in both microsites with the removal of non-native plant species, and iii) reductions in consumer pressure through exclosures is more important in the open where there are no shrub effects. Collectively, this examines the potential contributions of shrubs to restore native forbs both directly through abiotic effects and indirectly through reducing the effects of non-native plant species and consumers.

2. Methods

2.1. Study site

The experiment was conducted at Panoche Hills Recreation Area in California, USA (36° 41.776′ N, 120° 47.886′ W, 650 m. a. s. l.). This site is a shrubland located within the San Joaquin Desert (Germano et al., 2011) with sandy loam soils and a Mediterranean climate. This site is heavily invaded with non-native grasses including *Bromus madritensis ssp. rubens, Bromus diandrus, Bromus hordeaceus,* and *Schismus barbatus.* The dominant native shrub within the landscape and the focal shrub in this study is *Ephedra californica. E. californica* comprises greater than 80% of the shrub abundance at Panoche Hills and has been previously identified as a facilitator of annual plants (Filazzola et al., 2018). Other shrub species at Panoche Hills includes *Erinoginum fasiculatium* and *Marrubium vulgare,* but the facilitative ability of these shrubs is unknown. The overall landscape consists of steep hills and canyons, but the study site was located on a plateau. Native forb species comprise a very small proportion of the total plant biomass (1%) and are generally restricted to south facing slopes where Mojave Desert species may be found including *Chaenactis fremontii, Caulanthus inflatus, Malacothrix glabrata,* and *Salviacolumbariae.* Other native forb species include *Amsinckia tessellata, Calachortus clavatus, Castilleja brevistyla, Cryptantha sp., Eriogonum sp. Lasthenia sp., Lepidium nitidum, Monolopia lanceolata,* and *Phacelia tanacetifolia.* It is assumed that these native forbs used to

occupy a greater proportion of the plant biomass and that this site represented a desert scrub landscape (Germano et al., 2011). The non-native annual grasses that dominate the landscape were introduced to western North America in 1879 (Salo, 2005) and rapidly spread throughout much of the region.

The growing season is determined by seasonal rains that usually begin in October and last until March. The site on average receives 185 mm of rain annually and has a mean July maximum temperature of 38.2 °C (Panoche Road California weather station (CA2265A6), Western Regional Climate Center (WRCC, 2016), 36.72° N, 120.75° W, 619 m. a. s. l.). This site was surveyed over two growing seasons including 2015–2016 and 2016–2017. The 2015–2016 (hereafter referred to as the 2016 year of study) growing season began in October 2015 and ended in April 2016 (end of flowering and beginning of senescence). This was an El Niño year that resulted in above-average rainfall for both the study site and California with the study site receiving 201 mm of rain for the whole growing season. The 2016–2017 growing season (hereafter referred to as the 2017 year of study) began in November 2016 and ended in April 2017 with the site again receiving above-average rainfall (235 mm) during the growing season. Sheep grazing occurred during both years of the study from March until May. Other herbivores at this site include the black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), Heermann's kangaroo rat (*Dipodomys heermanni*), and the San Joaquin antelope squirrel (*Ammospermophilus nelsoni*).

2.2. Study species

The following five native forb species were selected for seeding: *Amsinckia tessellata (*A. Gray)*, Caulanthus lasiophyllus* (Hook & Arn) Payson*, Lepidium nitidum* (Torrey & A. Gray)*, Monolopia lanceolata* (Nutt.)*,* and *Phacelia tanacetifolia* (Benth.). *Caulanthus lasiophyllus* and *Lepidium nitidum* were collected locally in May 2015. The other three species were purchased from S&S Seeds Inc. located in Carpinteria, California in 2015 (approximately 400 km from the study site). The purchased seed was grown and harvested from a commercial nursery located in Acton, California. These species needed to be purchased because they are currently found at very low densities at or near the study location, although they are thought to have occurred here at higher densities previously (R. O'Dell, personal communication, May 2014). *Ephedra californica* is a perennial desert shrub found in arid regions of western North America. At the study site *E. californica* can grow quite large (average canopy area = 11.7 m³). It has a spindly appearance formed by the green twigs that make up most of its structure. It produces tiny leaves along the twigs.

2.3. Study design

Sixty pairs of shrub and open sites were used in this study. Each site consisted of a 50 × 50 cm quadrat that was marked using pin flags. Shrubs were randomly selected from a representative live shrub (at least 50% live canopy) size class for the plateau (shrubs within the 25–75% shrub size range excluded very large or very small shrubs). Shrub sites were placed within canopy drip line and on the north side of the shrub because this aspect has been shown to have the greatest facilitation effect in the Northern Hemisphere due to increased shade and lower temperature extremes (Castro et al., 2002). The paired open sites were located 2 m north of the shrub. A total of 30 of the paired shrub-open sites had animal exclosures erected in January 2014. Exclosures were circular in shape and constructed with a 70 cm diameter using 21 ga galvanized poultry netting buried 10 cm below ground and extending 1.2 m above the surface. Exclosures were constructed around the experimental plot within the dripline of the shrub canopy. Half of all pairs were then randomly selected to be used for the non-native plant removal treatment. Due to the heavily invaded nature of our study site, there were only non-natives removed from our experimental plots,

thus this treatment will be referred to as non-native removals. On October 24, 2015, seed from the five-forb species were added to 40 shrub-open pairs with half of each treatment (exclosure and removals) in a fully orthogonal design (10 replicates of each level). Seeds were not added to 20 shrub-open pairs to act as controls of each treatment effect on the ambient plant community. One gram of seed from each of the five-native species (mean number of seeds in 1 g: *Amsinckia tessellata* = 235.2 ± 7.612 SE; *Caulanthus lasiophyllus* = 3019 ± 8.916 SE; *Lepidium nitidum* = 752.4 ± 4.261 SE; *Monolopia lanceolata* = 737.8 ± 7.832 SE; *Phacelia tanacetifolia* = 772 ± 5.301 SE) was evenly added to hand-dug furrows within the center of each plot to avoid potential edge effects. Seeds of the five species were mixed in each plot. On January 15, 2016, all non-native emerging vegetation was hand-pulled from non-native plant removal treatment plots. We continued to remove non-native vegetation throughout the season as needed. Shrub area and volume were calculated as the area of a circle and volume of a hemisphere resectively. Canopy coverage was estimated on a scale of 1–10 with higher numbers indicating dense branching of the shrub.

Micro-environmental conditions including air temperature, light, and relative humidity were measured in randomly selected shrub and open sites using HOBO pro-v2 loggers in 2016 and 2017 (six loggers per microsite, half were within removal plots, no loggers were placed in exclosures). The sensor for each logger was placed approximately 5 cm above the ground. Loggers within the shrub were placed on the north side. Photosynthetically active radiation (PAR) was also recorded using a Licor LI-250A light meter quantum sensor on February 4, 2015 (a clear, sunny day) between 10 a.m. and 12 p.m. Soil moisture levels (top 10 cm of soil) were measured using a Delta SM150 probe on January 16, 2016 and again on March 23, 2016. Soil moisture and PAR readings were taken at every experimental plot. Soil moisture readings were not repeated in 2017.

2.4. Data collection

Plant surveys of abundance (number of individuals per species), biomass (above and below-ground), and average number of flowers for each species were completed for all plots on March 12–13, 2016. In 2017, the only response variable that was measured was abundance (on March 30, 2017) because there were very few plants that emerged in this second year of study. Biomass was collected by harvesting a randomly selected individual plant from each species within a plot in 2016. Both above-ground biomass and below-ground biomass were harvested for analyses using hand-pulling. Above and below-ground biomass samples were then dried in Yamato DNK900 drying ovens at 85 °C for 7 days before weighing using a Mettler Toledo XS204 Excellence XS analytical balance. Flowers or fruits were counted from three random individuals of each species from each plot in the field. These counts were then averaged for each species within each plot and thus represent a continuous variable.

2.5. Statistical analyses

To test for evidence of shrubs altering microclimatic conditions within their canopy, environmental variables including soil moisture, temperature, and relative humidity were compared among microsites for each year of study. Soil moisture data (converted from a percentage to a proportion) from January and March were compared in separate models between the three factors (microsite, exclosure, removal) using Generalized Linear Models (GLMs, *glm* function) fit to a binomial distribution and the logit link function. Data for temperature (°C) and relative humidity (percent converted to a proportion) were subset to include only the growing season (November–April) and 2 h mid-day (12:00–14:00) because this time frame is the most variable period. Early (November–January), and late (February–April) growing season measures were contrasted to within-season variability. T-tests (*t.test*

function) were performed to examine differences between shrub and open microsites for temperature and variance throughout the growing season. Differences between shrub and open microsites in relative humidity and variance throughout the growing season were compared using GLMs fit to a binomial distribution with the logit link function.

For the 2016 data, each response variable (above-ground biomass, below-ground biomass, and mean number of flowers) was compared for the three factors (microsite, exclosure, removals) and their interaction terms. For the abundance that was measured in 2016 and 2017, we compared among the three factors (microsite, exclosure, removals) and their interaction terms with year as a covariate. Variable selection for covariates was performed using a correlation matrix *corrplot* function (*corrplot* package) to remove collinear variables, and best subsets regression using the *regsubsets* function (*leaps* package) to remove variables with low R^2 values. The covariates shrub volume and shrub area were highly collinear as well as shrub canopy density and PAR so only shrub area and PAR were included in the remaining models. Variable selection through best subsets regression showed that all covariates (shrub area, PAR, or soil moisture) explained a low proportion of the variation for the response variables, so they were not included in the final models. Initially, statistical models were performed with species, microsite, exclosure and removals as fixed factors (Table S1). However, the significant interactions with species as a factor were noticeably due to species-specific differences. Additionally, due to low sample sizes for *Monolopia lanceolata*, multiple comparisons would not be possible in subsequent *post hoc* analysis for this model. Therefore, models were applied separately for each species rather than including species as a fixed effect to take into consideration any species-specific influences. Each species can be considered independent (Cabin and Mitchell, 2000; Quinn and Keough, 2002), and as we are considering the influence of species identity to be an independent factor, and in the interest of saving statistical power, it was decided that separate models for each species would be performed as has been previously conducted in other studies (e.g. Bischoff et al., 2006; Maestre et al., 2001). To test for differences in abundance among the three factors (microsite, exclosure, and removal) and year, GLMs fit to a negative binomial distribution (to account for over-dispersion) using the *glm.nb* function (*MASS* package) were performed using the logit link function (*MASS* package). Above and below ground biomass, and mean number of flowers analyses were performed using an ANOVA using the function *aov* and normality and heterogeneity of variances were determined using Shapiro-Wilks (*shapiro.test* function) and Levene's test of homogeneity of variances (*leveneTest* function) respectively. To achieve normality and/or homogeneity in variances the following transformations were performed: *Caulanthus lasiophyullus, Monolopia lanceolata,* and *Phacelia tanacetifolia* above and below-ground biomass were log transformed, *Lepidium nitidum* above-ground biomass was log transformed, *Amsinkica tessellata* below-ground biomass was square-root transformed, *Monolopia laneceolata* mean number of flowers was log transformed, and *Phacelia tanacetifolia* mean number of flowers was square-root transformed. Interactions between factors could not be calculated for *Lepidium nitidum* mean number of flowers due to a low number of flowering individuals.

To further estimate the ecological effect of the three factors (microsite, exclosure, removals) on the response of native forbs we used boostrapped effect-size estimates were calculated using Cohen's *d* (*bootES* function, package *bootES*). Cohen's *d* values were weighted to range from +1 to −1 where positive values indicate facilitation, negative values indicate competition, and values that are not significantly different from zero indicate a neutral effect. Bootstrapped Cohen's *d* values approximate an unknown distribution of the effect sizes by resampling (999 iterations) the original data with replacement (Kirby and Gerlanc, 2013). Bias-corrected confidence intervals were calculated using the accelerated bootstrap method (Efron, 1987) for each factor and response variable among all species. All statistical analyses were performed in R (R Core Team, 2018).

Table 1
ANOVA results for above- and below-ground biomass for five native forb species between microsites, exclosures, and non-native removal treatments Bold values indicate significance at the α = 0.05 level and DF = 1.

Model	Amsinckia tessellata		Caulanthus lasiophyllus		Lepidium nitidum		Monolopia lanceolata		Phacelia tanacetifolia	
	F	p	F	p	F	p	F	p	F	p
Above-ground biomass										
microsite	3.55	0.068	3.55	0.068	**5.17**	**0.030**	**7.32**	**0.013**	**21.2**	**< 0.001**
exclosure	0.198	0.659	0.198	0.659	2.55	0.120	0.012	0.914	**5.21**	**0.026**
removal	**6.95**	**0.013**	**6.95**	**0.013**	3.21	0.083	**18.3**	**< 0.001**	2.82	0.099
microsite * exclosure	0.002	0.962	0.002	0.962	0.673	0.418	1.98	0.173	1.29	0.262
microsite * removal	0.020	0.655	0.020	0.655	0.694	0.411	0.426	0.520	1.77	0.190
exclosure * removal	0.549	0.464	0.549	0.464	1.34	0.255	–	–	0.942	0.336
microsite * exclosure * removal	0.034	0.854	0.034	0.854	0.979	0.330	–	–	0.186	0.668
Below-ground biomass										
microsite	1.68	0.206	3.32	0.080	**14.3**	**< 0.001**	0.917	0.349	3.79	0.058
exclosure	0.040	0.840	**6.45**	**0.017**	0.752	0.392	0.001	0.990	0.445	0.508
removal	3.97	0.056	0.145	0.706	0.707	0.407	2.95	0.100	2.98	0.091
microsite * exclosure	0.189	0.667	0.105	0.748	0.192	0.665	1.49	0.235	1.13	0.294
microsite * removal	0.048	0.828	0.822	0.373	0.068	0.795	–	–	0.713	0.403
exclosure * removal	0.443	0.511	0.026	0.874	**5.35**	**0.027**	–	–	0.039	0.844
microsite * exclosure * removal	0.515	0.479	**7.89**	**0.009**	2.18	0.149	–	–	0.162	0.689

3. Results

3.1. Micro-environmental contrasts between shrub and open microsites

Shrub and open microsites differed in the mean and variance for temperature and humidity. Temperature was significantly different between the shrub and open for the entire growing season with shrubs being significantly cooler (Fig. S2). Temperature variability was also significantly different between shrub and open microsites with the shrub being consistently less variable (Fig. S2). Relative humidity was consistently lower within the shrub compared to the open (Fig. S2). In contrast, the variation in humidity was consistently higher in the shrub when compared to the open. Soil moisture was not different between microsites (Fig. S2).

3.2. Shrub effects on native forb recruitment

In 2016, shrubs increased the above-ground biomass *for Lepidium nitidum, Monolopia lanceolate*, and *Phacelia tanacetifolia* (Table 1; Fig. 1), but the below-ground biomass was increased by shrubs only for *Lepidium nitidum* (Table 1; Fig. 1). In both years, *Lepidium nitidum* and *Monolopia lanceolata* were more abundant in the open relative to the shrub (Table 2: Figs. 2 and 3). The shrub did not facilitate the abundance of any other species (Table 2). The abundance of all forb species was significantly lower (approximately 90% less individuals) in 2017 relative to 2016 (Table 2; Figs. 2 and 3). Shrubs facilitated the mean number of flowers for *Phacelia tanacetifolia* (Table 3, Fig. S3). Overall, the shrub effect on the five native forb species increased the above and below-ground biomass, but had no effect on abundance in either 2016 or 2017 (Fig. 4).

3.3. Effects of herbivory/grazing on native forbs

Exclosures had a positive effect on native forbs across all the response variables measured. The above-ground biomass increased for *Phacelia tanacetifolia* and *Caulanthus lasiophyllus* (Table 1, Fig. 1), but exclosures increased the below-ground biomass for only *Caulanthus lasiophyllus* (Table 1, Fig. 1). In both years, the forb abundances were increased for all species except *Caulanthus lasiophyllus* (Table 2, Figs. 2, 3). When seeded within exclosures with non-natives removed, *Amsinckia tessellata, Caulanthus lasiophyllus* and *Monolopia lanceolata* had increased abundance compared to when non-natives were present (Table 2, Figs. 2, 3). Only *Caulanthus lasiophyllus* had higher abundance without exclosures when non-natives were removed compared to when

they were present in 2016 (Fig. 2). When non-natives were removed within the exclosure all species had higher abundances except for *Lepidium nitidum* than when non-natives were present (Fig. 3). In 2017, *Amsinckia tessellata* and *Caulanthus lasiophyllus* had significantly greater abundances without exclosures and with non-natives present, but the mean abundance was very small (< 1). The mean number of flowers for *Caulanthus lasiophyllus* was increased within exclosures compared to open sites exclosures (Table 3). The overall effect of exclosures was positive for abundance in both years of study and was neutral for above and below-ground biomass (Fig. 4).

3.4. Non-native plant species effects on native forbs

The high density of non-native species (mainly *Bromus rubens* and *Erodium cicutarium*) was expected to have a large negative impact on native plant species. We tested the ability for these non-native species to limit native species establishment through a removal treatment. Removal treatments were randomly selected to ensure the removals were conducted in areas that were representative of the whole study site. Visual comparisons of removal sites also confirmed that the experimental locations were representative of the study site (both relatively high and low non-native density plots were selected for removals). The average abundance (± SD) of *Bromus rubens* and *Erodium cicutarium* within ten randomly selected control plots (i.e no native seed was added) is given. *Bromus rubens*: shrub = 75.1 ± 24.9, open = 30.8 ± 14.7, exclosure = 49.5 ± 28.8, no exclosure = 56.4 ± 33.3; *Erodium cicutarium*: shrub = 4.13 ± 7.68, open = 64.3 ± 19.1, exclosure = 37.0 ± 40.7, no exclosure = 31.4 ± 28.5. The control plots had the same abundance of non-native species as the treatment (i.e. seeded with native species) plots (T = 0.04, df = 65.6, p = 0.967). The non-native species within the study site had a consistent abundance throughout our experimental plots, therefore, we expect any negative effects from non-native species to be consistent across our study.

The above-ground biomass was increased when non-natives were removed for *Amsinckia tessellata* and *Monolopia lanceolata* (Table 1, Fig. 1). There was no difference in below-ground biomass with non-natives removed or present (Table 1, Fig. 1). In both years, the abundance of *Caulanthus lasiophyllus* was increased with non-native removals (Table 2, Figs. 2, 3). The abundance of *Monolopia lanceolata* was also increased with non-native removals but in exclosures only (Table 2; Figs. 2 and 3). In 2017, *Amsinckia tessellata, Caulanthus lasiophyllus,* and *Monolopia lanceoloata* had greater abundances when non-natives were removed compared to when they were present, but the average
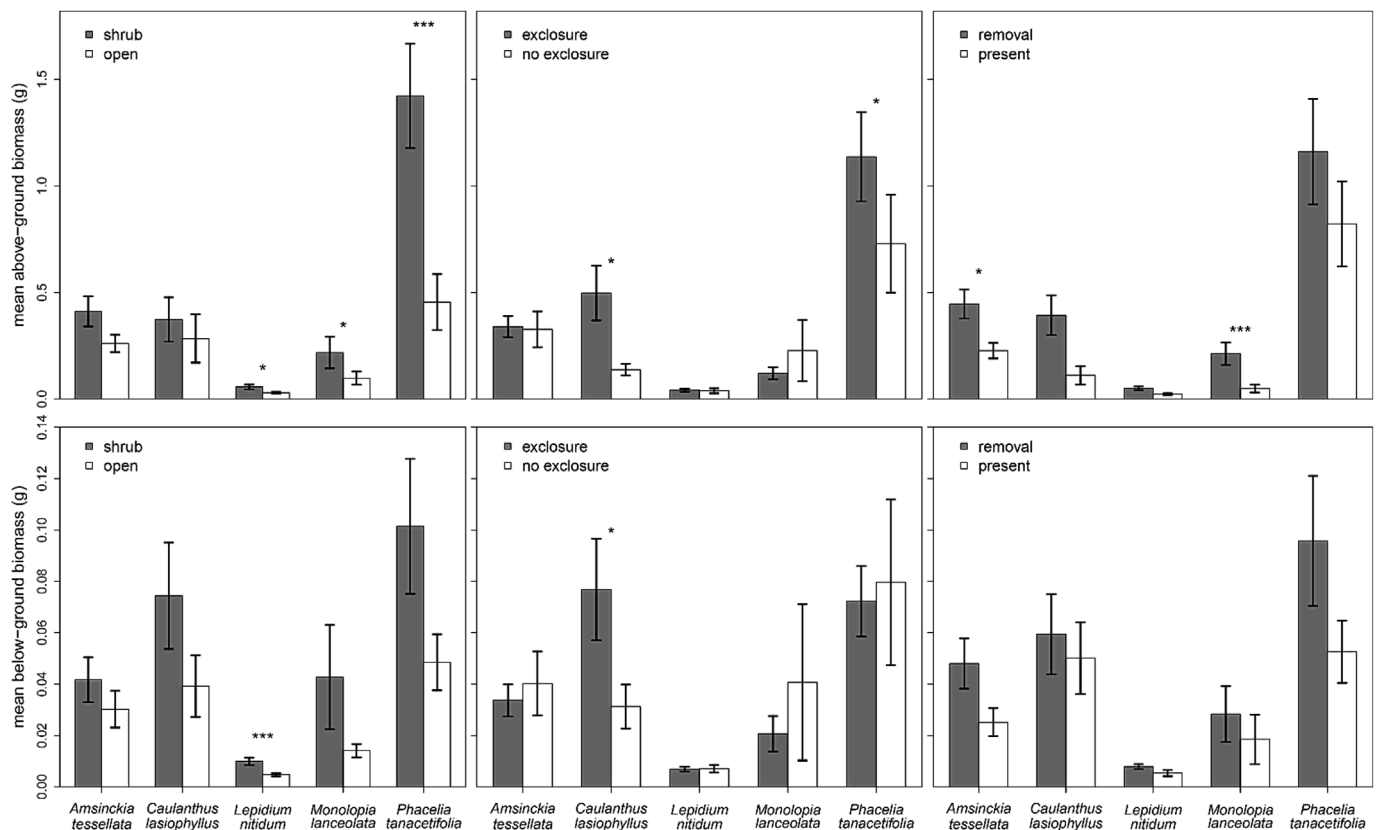
Fig. 1. Mean above and below-ground biomass for five native forbs seeded within shrub and open microsites, with and without exclosures and non-native species. Error bars presented are standard error. Significance at α < 0.05 denoted by *** = ≤ 0.001, ** = ≤0.01, * = ≤ 0.05.

abundance was low, i.e. < 1 per plot (Fig. 3). Removing non-native species had no effect on the mean number of flowers for any of the native forbs (Table 3, Fig. S3). The overall effect of non-native removals was positive for both above and below-ground biomass and neutral for abundance in 2016 and 2017 (Fig. 4).

4. Discussion

Shrub facilitation increases the establishment of beneficiary species in environments with high abiotic and/or biotic stress. In this study, we tested whether shrubs could be effectively used to promote the restoration of native forbs within a heavily invaded arid ecosystem and to test the influence that non-native competition and grazing/herbivory could have on this planting method. We found support for the prediction that shrubs can improve the establishment of native forbs within this invaded arid ecosystem, particularly when grazing/herbivory was limited. The second prediction was not supported because non-native

competition does not appear to exclude most of the native species examined in this study despite the known competitive effects of the non-natives in this system (Salo, 2004; Schutzenhofer and Valone, 2006). Additionally, we did not find support for the third prediction because the shrub did not appear to reduce herbivory/grazing. No significant microsite by exclosure effect was observed, and due to the nearly consistent positive effect on all native forbs when seeded in exclosures for abundance in both 2016 and 2017, it is likely that herbivory/grazing limits native species establishment at this site. Planting native forbs within shrub microsites in invaded arid ecosystems is a promising strategy for increasing native species, however, grazing/herbivory may need to be limited to ensure the success of restoration projects.

Protection from herbivores by nurse plants has been previously reported as a mechanism of facilitation for other plant species. However, this study found that shrubs did not deter consumer pressure at this site. Previous studies have found reducing consumer pressure to be the most important facilitation mechanism in dryland savannas (Louthan et al.,

Table 2
Results of Generalized Linear Models (GLMs) comparing the abundance in 2016 and 2017 of five native forb species between microsites, exclosures, and non-native removals. Bold values indicate significance at the α = 0.05 level and DF = 1.

| Model	Amsinckia tessellata		Caulanthus lasiophyllus		Lepidium nitidum		Monolopia lanceolata		Phacelia tanacetifolia	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
microsite	0.89	0.34	0.92	0.34	**6.40**	**0.011**	**16.2**	**< 0.001**	0.01	0.93
exclosure	**9.43**	**0.002**	2.31	0.13	**34.6**	**< 0.001**	**79.3**	**< 0.001**	**55.1**	**< 0.001**
removal	1.37	0.24	**41.1**	**< 0.001**	0.08	0.78	**5.74**	**0.017**	0.35	0.56
year	**43.4**	**< 0.001**	**39.1**	**< 0.001**	**33.8**	**< 0.001**	**35.4**	**< 0.001**	**95.7**	**< 0.001**
microsite * exclosure	0.67	0.41	0.96	0.33	0.02	0.90	3.22	0.073	2.09	0.15
microsite * removal	1.06	0.30	0.99	0.32	0.91	0.34	3.12	0.077	0.17	0.68
exclosure * removal	**10.9**	**0.001**	0.71	0.39	0.90	0.34	**15.4**	**< 0.001**	1.34	0.25
microsite * exclosure * removal	0.99	0.32	0.11	0.74	1.02	0.32	0.01	0.99	0.01	0.96
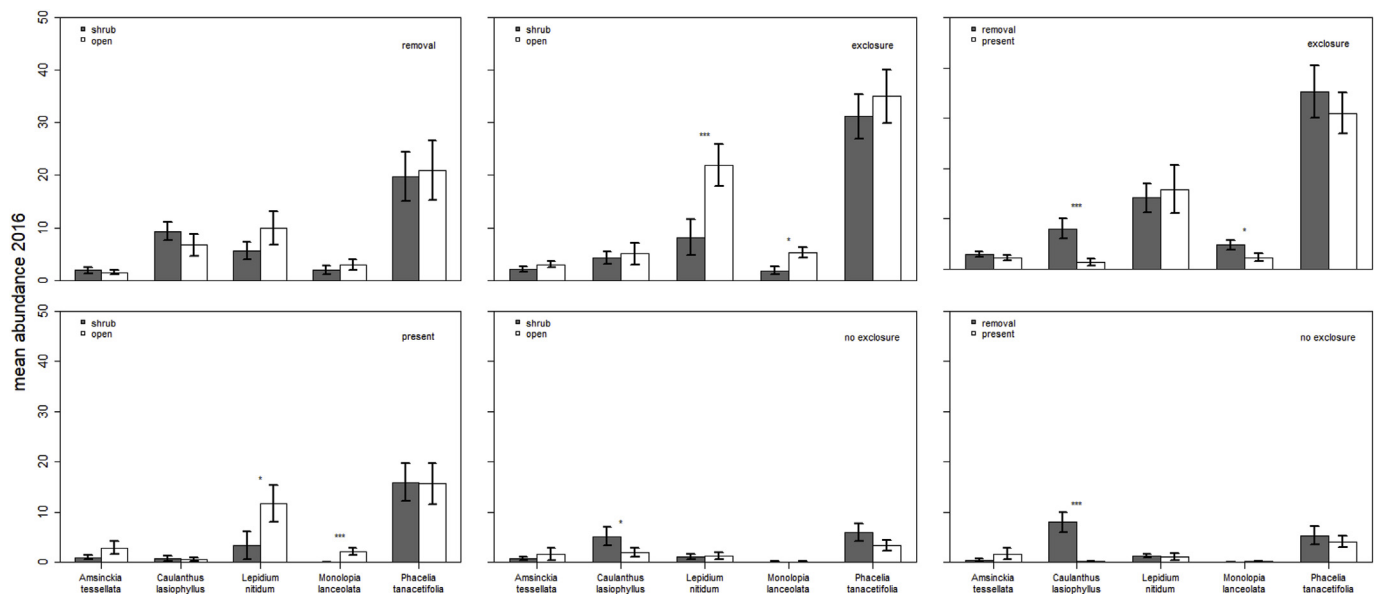
Fig. 2. Mean abundance (± SE) in 2016 for five native forb species among the three treatments. The left panels show the effect of shrub and open microsites with non-natives removed (top-left) and non-natives present (bottom-left). The middle panels show the effect of shrub and open microsites with exlosures (top) and without exclosures (bottom). The right panels are the effect of non-native removals with exclosures (top-right) and without exclosures (bottom-right). Significance at α < 0.05 denoted by *** = ≤ 0.001, ** = ≤0.01, * = ≤ 0.05.

2014; Torres and Renison, 2015). Although there is no evidence in this study that shrubs could reduce consumer pressure, an alternative explanation could be that the grazing intensity by sheep at the site may have been too high and there was a collapse of facilitation (Smit et al., 2007). It is possible that in the absence of grazing, or at much lower levels of grazing, shrubs may have been able to reduce consumer

pressure. It may be necessary to test other nurse plant species with more obvious defense mechanisms (i.e. thorns) to determine if shrubs with these traits are more effective facilitators. However, it appears, at least at this site, that grazing or herbivory is having a significant negative impact on native species establishment and should be limited.

The response of plants to a facilitator has been shown to depend on
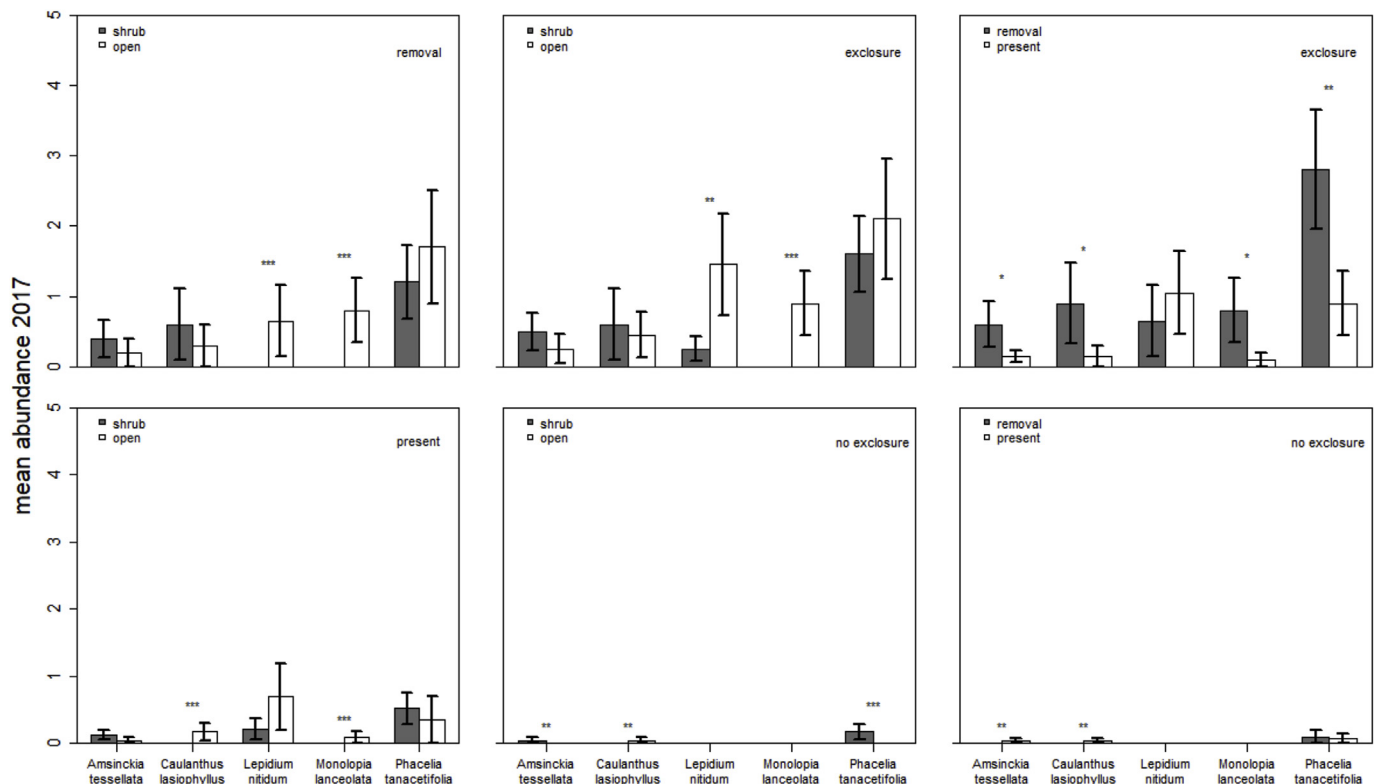
Fig. 3. Mean abundance (± SE) in 2017 for five native forb species among the three treatments. The left panels show the effect of shrub and open microsites with non-natives removed (top-left) and non-natives present (bottom-left). The middle panels show the effect of shrub and open microsites with exclosures (top) and without exclosures (bottom). The right panels are the effect of non-native removals with exclosures (top-right) and without exclosures (bottom-right). Significance at α < 0.05 denoted by *** = ≤ 0.001, ** = ≤0.01, * = ≤ 0.05.

Table 3
ANOVA results for the mean number of flowers for five native forb species between microsites, exclosures, and non-native removal treatments. Bold values indicate significance at the α = 0.05 level and DF = 1.

Model	Amsinckia tessellata		Caulanthus lasiophyllus		Lepidium nitidum		Monolopia lanceolata		Phacelia tanacetifolia	
	F	p	F	p	F	p	F	p	F	p
microsite	1.35	0.254	0.041	0.841	7.40	0.113	3.68	0.068	**9.96**	**0.003**
exclosure	2.20	0.147	**6.21**	**0.020**	8.46	0.101	0.113	0.740	**18.5**	**< 0.001**
removal	0.580	0.452	1.22	0.281	0.96	0.431	1.59	0.221	1.52	0.225
microsite * exclosure	0.002	0.962	0.183	0.673	–	–	1.84	0.189	0.364	0.549
microsite * removal	1.92	0.175	0.047	0.831	–	–	0.308	0.585	0.178	0.675
exclosure * removal	0.257	0.615	1.88	0.184	–	–	–	–	1.59	0.213
microsite * exclosure * removal	0.286	0.596	–	–	–	–	–	–	0.056	0.814

the beneficiary plant species traits as well as the traits of the nurse-plant species (He et al., 2012; Noumi et al., 2015). In this study, we found species-specific responses to each of our treatments, including to shrub facilitation, with some species showing a positive response while others had a neutral effect. This species-specificity can have important implications when selecting target species to be seeded in a restoration project within shrub microsites and when selecting potential nurse-plant species, as some species will not tolerate the low light conditions and potentially more competitive environment within the shrub (Forseth et al., 2001; Holmgren et al., 1997; Tian and Wang, 2015). Some shrubs may also have allelopathic characteristics or may have canopy structures incapable of reducing abiotic or biotic stress (Tian and Wang, 2015; Zhang and Zhao, 2015). The species-specific responses observed in our study thus could reflect environmental preferences among species. Future studies considering facilitation as a planting method for restoration should take plant traits and environmental preferences into consideration when choosing target species and potential nurse plants to increase the likelihood of success.

Multi-year restoration experiments are important as inter-annual differences in environmental conditions have been shown to influence treatment effects and study outcomes (Vaughn and Young, 2010). Although our study is short-term, there were some differences in trends between the two years of study. The largest difference and biggest limitation in this study is the extremely limited number of native forbs that emerged in the second year. Although there were also some different trends observed between years among treatments and response variables, this is difficult to interpret meaningfully when in 2017 the average number of species is a few of individuals, or in some cases, even less than one individual. The extremely low emergence within the second year could be due to differences in climatic conditions between 2016 and 2017 or potentially due to intense herbivory or granivory occurring at this site. Conditions in 2017 for plant emergence were less favourable than in 2016. In 2017 the rain was less consistent then 2016, as most of it came early in the season, and 2017 was a much cooler year with many days below freezing around the rainy period (Panoche Road California weather station (CA2265A6), Western Regional Climate
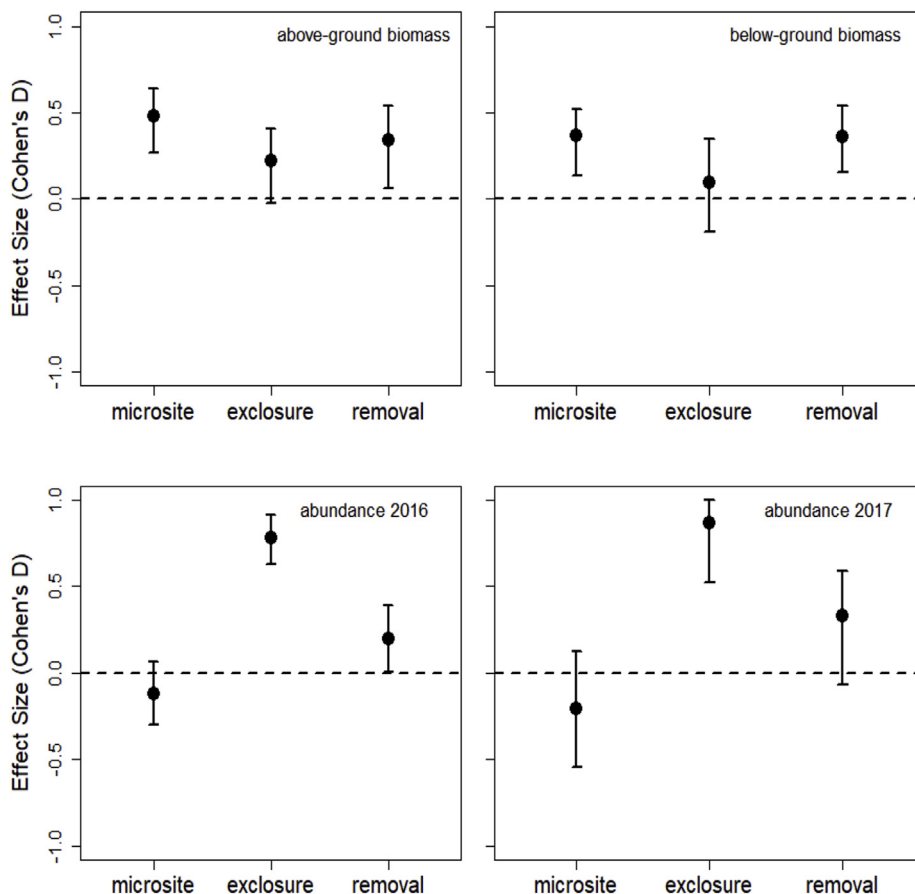
Fig. 4. Cohen's D mean effect size estimates (± bootstrapped 95% confidence intervals) among the three experimental factors microsite, exclosure, and removal for the five native annual species. Each panel is represented by a different response variable. Estimates above zero indicate a positive effect of the experimental factor, while values below zero indicate a negative effect and values that cross zero indicate a neutral effect.

Center (WRCC, 2016), 36.72° N, 120.75° W, 619 m. a. s. l.). Temperatures did not begin to warm in 2017 until mid-March (compared to early February for 2016) which was well after the significant rains had ceased and thus the native forbs may not have received both the moisture and temperatures to break dormancy in 2017 (Adondakis and Venable, 2004; Finch-Savage and Leubner-Metzger, 2006; Levine et al., 2008). Excessive herbivory or granivory also could have influenced second year emergence of the native forbs. The site is grazed by sheep and other herbivores and granivores including rabbits, birds, ants and kangaroo rats that could have influenced the reproduction of the native forbs (Kelt et al., 2004; Schooley et al., 2000). Although sheep and kangaroo rats should have been kept out of exclosures, birds and ants could still have taken seeds from experimental plots with exclosures and thus there may not have been enough seed remaining to germinate.

Given the extremely invaded status of our study site we were surprised that there was not a clear benefit to native species when non-natives were removed in 2016, although in 2017 we begin to see the trend that we expected, (again, with so few individuals emerging it is difficult to draw conclusions). We suspected that the reason the site lacked native species due to competitive exclusion by non-native species, but it appears that this may not be the case, at least not in the first year of seeding. It is suggested that native and non-native species do not differ in competitive ability, and natives are generally able to out-compete non-natives in low resource condition (Daehler, 2003; Funk, 2013; Vasquez et al., 2008). In our study, native species are at least able to co-exist with non-natives in one high resource year (i.e. El Niño wet year) so it may be other factors such as grazing which non-natives may be more adapted to (Kimball and Schiffman, 2003)or seed/recruitment limitation (Frances et al., 2010; Gioria and Osborne, 2014; Long et al., 2014) which have resulted in so few native plant species. A significant positive effect of non-native removals was observed in the second year of study for the few individuals that did emerge, and this could potentially be due to excessive propagule pressure from non-natives in non-removal sites compared to the removal sites that reduced the ability for native species to emerge and establish (Schantz et al., 2015).

This study demonstrates a first test of the ability for shrubs to successfully increase the establishment of native forbs within an invaded arid ecosystem, at least within the first year of study. However, excluding or reducing herbivory/grazing may be an even more important consideration for increasing the success of restoration plantings, at least at this site. Continued monitoring of the persistence of the seeded natives should be conducted to determine if the lack of natives in the second year of study were due to unfavourable environmental conditions or extreme consumer pressure. Future studies would benefit by not only addressing this important concern, but by also examining the potential for shrubs to promote nucleation, or planting native species within clusters around shrubs (i.e. Holl et al., 2011). There is also a need to determine the ability of these natives to disperse into surrounding areas from shrubs, which can increase the overall success of restoration projects while decreasing the cost of seeding large areas. With climate change predicting the negative impacts of non-native species to increase (Smith et al., 2000), it is necessary to develop novel techniques to mitigate these effects on biodiversity and ecosystem function. Increasing native forb establishment within this landscape dominated by invasive Mediterranean grasses will be an important focus for increasing biodiversity and ecosystem function with the area. Facilitation by nurse plants could be an example of an effective method for re-introducing native biodiversity to these ecosystems. Given the global loss of diversity that has been attributed to invasions by non-native species, identifying methods of preserving and increasing natives within these landscapes is essential.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2019.103998.

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