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Simultaneous, independent, and additive effects of shrub facilitation and understory competition on the survival of a native forb (*Penstemon palmeri*)

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Abstract There is increasing recognition that both competition and facilitation are important drivers of plant community dynamics in arid and semi-arid environments. Decades of research have provided a litany of examples of the potential for shrubs as nurse plants for establishment of desirable species, especially in water-limited environments. However, interactions with the existing understory community may alter the outcome of interactions between shrubs and understory plants. A manipulative experiment was conducted to disentangle interactions between a native forb species (*Penstemon palmeri* A. Gray), a native shrub (*Artemisia tridentata* Nutt.), and a diverse understory of exotic and native forbs and grasses in a semi-arid shrubland of Northern Utah, USA. Seedlings of *P. palmeri* were transplanted in a factorial design: (1) beneath shrub canopies or into their interspaces and (2) with understory interactions retained or removed. Transplant survival was tracked for roughly 1 year. Shrubs appeared to facilitate *P. palmeri* survival while interactions with the existing understory community were equivalently negative, leading to overall neutral interactions. Further, positive shrub interactions and negative understory interactions appeared to operate independently and simultaneously. While the debate over the importance of facilitation and competition in driving plant community dynamics continues, our observations strongly suggest that both have considerable effects on plant establishment in *A. tridentata* communities. Furthermore, our results inform the conservation and restoration of *P. palmeri* populations, and suggest the utility of nurse shrubs and/or understory thinning as strategies for increasing the diversity of desirable species in the arid and semi-arid western United States shrublands.

Keywords Facilitation · Nurse plants · Competition · Plant interactions · *Artemisia tridentata* · Great Basin

Introduction

Plant community dynamics are influenced by both positive and negative interactions within and between species, and the balance between these interactions fluctuates over space and time (Callaway and Walker 1997; Tielbörger and Kadmon 2000; Maestre et al. 2003). The balance of positive and negative species interactions may play especially important roles in plant communities characterized by environmental

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stress and limited resources, such as water-limited communities in arid and semi-arid regions (Phillips and MacMahon 1981; Fowler 1986; Griffith 2010). For example, shrubs frequently act as nurse plants in water-limited communities, facilitating a variety of plant life-forms (e.g., grasses, forbs, shrubs, and trees) (Brooker et al. 2008; Gómez-Aparicio 2009; Bonanomi et al. 2011). Facilitation by shrubs includes both direct (e.g., canopy shade and its buffering effects on local microclimate; Callaway 2007a) and indirect (e.g., associational defense, improved nutrient availability and water relations; Callaway 2007b) mechanisms.

While the importance of negative interactions in water-limited communities remains a subject of debate (Fowler 1986; Brooker et al. 2008; He et al. 2013; Soliveres et al. 2013), there is a growing recognition that competition can have pronounced effects on water-limited community dynamics (Fowler 1986; Reichenberger and Pyke 1990; Rayburn and Schupp 2013). It is becoming clear that quantifying the balance between positive and negative interactions may be critical to understanding the structure and function of these communities.

Within semi-arid shrublands of the western United States, past studies have examined the importance of both positive (Huber-Sannwald and Pyke 2005; Griffith 2010) and negative (Campbell and Harris 1977; Phillips and MacMahon 1981; Fowler 1986; Callaway et al. 1996) plant interactions. In the region, the widespread native shrub *Artemisia tridentata* is thought to facilitate a wide range of plant species and growth forms, including both native and invasive grasses (Huber-Sannwald and Pyke 2005; Davies et al. 2007; Griffith 2010), forbs (Daubenmire 1970; Eckert et al. 1986; Wirth and Pyke 2003), shrubs (Eckert et al. 1986), and trees (Greenlee and Callaway 1996; Chambers 2001). Direct facilitation of understory species by *A. tridentata* can arise by microclimatic effects such as shading, which can reduce evapotranspiration and buffer soil temperature fluctuations (Eckert et al. 1986; Callaway et al. 1996; Davies et al. 2007). Facilitation of understory species has also been described via protection from herbivory and trampling (Eckert et al. 1986; Callaway et al. 1996), increased litter and soil nutrients under shrub canopies (Eckert et al. 1986; Bechtold and Inouye 2007), soil moisture enhancement through hydraulic lift (Richards and Caldwell 1987), and increased snow accumulation under shrub canopies (Allen 1988). However, competition from adult *A. tridentata* shrubs has also been shown to reduce seedling establishment of other Great Basin species (Reichenberger and Pyke 1990) and limit population growth rates of exotic forbs (Prevéy et al. 2010). Further, removal of *A. tridentata* has been linked to increased survival of seeded and transplanted native forbs (Wirth and Pyke 2003), and allelopathic effects of *A. tridentata* litter have been documented (e.g., Kelsey et al. 1978). Despite evidence for resource competition and allelopathy, the number of studies reporting understory plant facilitation by *A. tridentata* suggest that the net interaction between *A. tridentata* and understory species tends to be positive.

While studies of positive plant interactions in the western North American shrublands have focused almost exclusively on facilitation of understory species by woody vegetation; interactions among the understory plant community can also influence community dynamics. Competition within and between understory species for limited soil moisture and nutrients can influence species diversity and coexistence (Fansler and Mangold 2011; Soliveres et al. 2011; Rayburn and Schupp 2013), exotic species invasion (Cox and Anderson 2004), plant spatial patterns (Rayburn and Monaco 2011), and native species restoration (Wirth and Pyke 2003; Cox and Anderson 2004; Fansler and Mangold 2011). In semi-arid systems, presence of a herbaceous understory has been shown to reduce individual performance of transplanted seedlings (Maestre et al. 2004; Cuesta et al. 2010). The balance of positive and negative interactions is expected to influence natural community dynamics in arid and semi-arid shrublands throughout the western U.S., which are commonly dominated by *A. tridentata* shrubs associated with diverse understories of native and introduced grasses and forbs. Furthermore, the interplay between positive and negative interactions will also affect revegetation and restoration efforts in which native species are added into shrub communities through seeding or direct planting.

In this study, we conducted a manipulative experiment to assess survival of transplanted seedlings of Palmer's penstemon (*Pestemon palmeri*), a native Great Basin perennial forb, in the presence or absence of interactions with (1) *A. tridentata* shrubs and (2) a grass-forb understory community. *P. palmeri* is a drought and cold tolerant native perennial forb that is widespread throughout the western U.S. (Cronquist et al. 1984). It is a valuable restoration species for western ranges and wildlands, establishing readily on disturbed soils, assisting in beautification projects, and providing ecosystem services such as forage for ungulates and soil stabilization via deep roots and basal leaves (Stevens and Monsen 2004). Furthermore, *P. palmeri* nectar and pollen are used by a variety of insects and hummingbirds (Poulos 2013). Though generally preferring disturbed sites with well-drained soils (Cronquist et al. 1984), it also co-occurs with mixed shrub communities in its southern range, where it is often spatially associated with multiple species of shrubs at later life-stages (Poulos 2013). This association is likely due to net facilitation of *P. palmeri* seedling and juvenile survival under shrub canopies; experimental evidence suggests that the soil under *A. tridentata* canopies increases early *P. palmeri* survival relative to soils between shrubs, though it is not clear what mechanisms are responsible for this observation (Poulos 2013).

Since the outcome of intra-trophic interactions depends on whether species are compared in isolation, or in the presence of the background community (reviewed in Callaway and Pennings 2000), we considered both direct effects of understory and shrub interactions as well as their combined effects on *P. palmeri* seedling survival. Based on past studies of positive and negative interactions in the western U.S. shrublands, we hypothesized that understory interactions would be net negative (i.e., competitive) and shrub interactions would be net positive (i.e., facilitative). We expected the highest levels of *P. palmeri* seedling survival in the absence of understory interactions and in the presence of shrub interactions; conversely, we expected the lowest seedling survival in absence of shrub interactions and in the presence of understory interactions. We made no predictions about the statistical interaction between understory and shrub interactions, but it was investigated since a significant interaction would indicate that the response of *P. palmeri* seedling survival to understory interactions depends on the presence or absence of shrub interactions, or vice versa. Our objectives were accomplished using experimental manipulations due to their potential to separate the effects of multiple simultaneous ecological processes (Callaway 2007a; McIntire and Fajardo 2009).

Methods

Study site

The study site was located in an *A. tridentata* dominated stand near Millville, UT, USA (lat 41°39′N, long 111°48′W, 1,370 m elevation) spanning roughly 11,000 m^2 (33 × 330 m). Soils were somewhat excessively drained nonsaline gravelly loams (Soil Survey Staff 2011), and the slope across the site was <5°. Based on 1969–2013 Utah Climate Center data from a nearby weather station (<10 km), mean annual precipitation was 463.8 mm (SD = 136.3 mm), mean temperature of the hottest month (July) was 21.3 °C, and mean temperature for the coldest month (January) was −5.9 °C (Utah Climate Center 2014). Overstory vegetation was composed almost exclusively of *A. tridentata*. Six 30 m line-point cover transects were used to determine that *A. tridentata* shrubs covered approximately 33 % of the study site. The understory plant community was surveyed in early May 2010 and was dominated by *Poa bulbosa* L., *Bromus tectorum* L., and *Erodium cicutarium* L., widespread introduced annual species found throughout the western U.S. A diverse mixture of both native and invasive grasses and forbs was also present (Table 2 in Appendix). Light grazing by cattle occurred prior to the study, but an electrified fence was constructed to exclude cattle and to eliminate potential indirect facilitation caused by shrubs protecting seedlings from trampling and grazing.

Seed collection and seedling preparation

Seeds from 38 *P. palmeri* individuals were collected along roughly 7 km of roadsides and in washes from the Harris Springs area (1,550–1,650 m elevation) in the Spring Mountains National Recreation Area, Nevada, in November 2008. Seeds were germinated and 383 seedlings reared in a sterilized mixture of three parts sand to one part Canadian peat moss in the Utah State University Research Greenhouses (Logan, UT, USA) from mid-December 2008 until mid-April 2010. Seedlings were watered once to twice daily and fertilized monthly.

Prior to selecting seedlings for transplant, we constructed an above-ground size-biomass curve by measuring the caudex diameter of 228 randomly selected seedlings and subsequently harvesting, drying, and weighing their above-ground biomass to the nearest 0.1 mg. Individuals with caudex diameters <2 mm or >6 mm were removed from the study since few seedlings were in these size classes. Using the remaining 220 seedlings, we regressed log-transformed dry mass on caudex diameter; this yielded strong evidence that caudex diameter was a linear predictor of above-ground biomass ($R^2 = 0.667$; $N = 220$; $P < 0.001$; Fig. 2 in Appendix).

We then measured the caudex diameters of 155 remaining unharvested seedlings, removing those with diameters <2 and >6 mm to avoid extrapolation beyond our size-biomass curve. A total of 123 seedlings remained for transplanting. These seedlings were transferred outdoors 24 days prior to transplanting and watered once daily to allow for acclimation to daily variations in temperature, solar radiation, and wind.

Experimental design

The experiment was initiated on 17 May 2010. A fully random selection of shrubs was not possible, due to logistical constraints that prevented the enumeration of all mature *A. tridentata* shrubs within the community. Instead, we selected 63 mature shrubs of similar size (1–2 m wide) in locations spanning the community to account for first-order effects due to environmental heterogeneity. Similarly, 60 shrub interspaces were also selected across the community; minimum gap size of interspaces was approximately 2 m. In 31 of the shrub and 30 interspace locations, we removed the existing understory community in 706 cm^2 circular plots (30 cm diameter) and transplanted a single *P. palmeri* seedling into the center of the cleared area. Circular plots were placed so as to fit completely under the canopy on the shaded north side of shrubs ("shrub interactions + no understory interactions" treatment; "+SI, −UI"; $N = 31$) or in the approximate center of interspace locations ("no shrub interactions + no understory interactions" treatment; "−SI, −UI"; $N = 30$). Understory vegetation was not removed at the remaining shrub ("shrub interactions + understory interactions" treatment; "+SI, +UI"; $N = 32$) and interspace ("no shrub interactions + understory interactions" treatment; "−SI, +UI"; $N = 30$) locations, and seedlings were planted into the existing understory community as described for cleared treatments. All seedlings were randomly assigned to treatments and supplemental water (~100 ml) was applied immediately before seedling transplantation, but not after; conditions were rainy for several weeks following transplantation, providing favorable establishment conditions.

Data collection and analysis

Survival was monitored monthly throughout summer and fall (until 28 October 2010) and then once again the following spring (2 May 2011). Survival was modeled using Cox proportional hazards (PH) models in SAS 9.2 (Proc PHREG; SAS Institute Inc. 2008). Cox PH models are similar to standard regression models, but differ in that they treat the response as a "hazard," i.e., risk of death. This allows for easy comparison of hazard between treatments by interpreting "hazard ratios" (HRs). For categorical variables, the HR represents the risk of death in one treatment relative to another, while for continuous variables, the HR represents the risk of death associated with an arbitrary unit of increase in that variable. Another key difference is that Cox PH models allow for the "censoring" of individuals that survive past the final census; despite lack of knowledge of their true time of death, they can remain in the analysis. Lastly, imprecise knowledge of the exact time of mortality between censuses can be accounted for through the use of "exact ties" (see Allison 2010 for details).

In this study, two Cox PH models were constructed that asked similar questions in different ways. Both models included a continuous "size" variable based on the caudex diameter of individuals when they were transplanted and both included significant statistical interactions. The first model investigated differences in hazard between treatments, e.g., "−UI, −SI" versus "+UI, +SI," by including a four level "treatment" categorical variable and its interaction with plant size; this permitted explicit pair-wise comparisons of the HRs between each of the four treatments. The second model investigated the effects of the two factors, e.g., shrub interactions versus understory interactions, by including two covariates, both with two levels (present or absent), and a statistical interaction term, if significant. Thus, it was possible to assess the degree to which the existing understory community and *A. tridentata* interacted with each other to influence *P. palmeri* survival.

Table 1 Two alternative Cox regression models examining either (a) pair-wise treatment comparisons of the hazard ratio (HR) of transplanted *P. palmeri* seedlings in one treatment (numerator) relative to the another (denominator), or (b) effects of the two factors, "understory interactions" (UI) between *P. palmeri* and the herbaceous plant community and "shrub interactions" (SI) between *P. palmeri* and *A. tridentata*. Directionality of the effects can be negative (−) or positive (+). Comparisons were produced from PROC PHREG in SAS 9.2 (SAS Institute Inc. 2008) using EXACT ties (Allison 2010) and controlled for the initial size (caudex diameter) of transplanted seedlings

	HR[c]	95 % CI	χ^2_1	*P* value
(a) Treatment effects model[a]				
Contrast				
(1) +SI, +UI ÷ −SI, −UI	0.707	0.380–1.183	1.49	0.168
(2) −SI, −UI ÷ −SI, +UI	0.173	0.094–0.320	31.28	<0.001
(3) +SI, −UI ÷ +SI, +UI	0.136	0.055–0.334	18.82	<0.001
(4) +SI, −UI ÷ −SI, −UI	0.091	0.036–0.228	26.14	<0.001
(5) +SI, +UI ÷ −SI, +UI	0.116	0.061–0.220	43.41	<0.001
(6) +SI, −UI ÷ −SI, +UI,	0.016	0.006–0.042	68.36	<0.001
(b) Factor effects[b]				
Understory interactions				
(7) −UI versus +UI	0.160	0.096–0.266	49.67	<0.001
Shrub interactions				
(8) +SI versus −SI	0.107	0.063–0.184	65.66	<0.001

[a] Overall model was significant ($P < 0.001$; $\chi^2_4 = 80.08$) and controlled for a statistically significant effect of initial transplant size (caudex diameter) ($P = 0.035$; $\chi^2_1 = 4.45$; HR = 1.241) and overall the treatment effect was statistically significant ($P = < 0.001$; $\chi^2_3 = 79.60$). The interaction between plant size and treatment was not significant ($P = 0.728$; $\chi^2_3 = 1.31$) and was removed from the model

[b] Overall model was significant ($P < 0.001$; $\chi^2_3 = 83.41$) and controlled for a statistically significant effect of initial transplant size (caudex diameter) ($P = 0.038$; $\chi^2_1 = 4.32$; HR = 1.237). Non-significant interactions ($P > 0.26$) between factors were removed

[c] Represents the risk of death for seedlings in the numerator treatment relative to the denominator treatment. Subtracting HR from 1 gives probability of survival of the numerator relative to the denominator (ex: if HR = 0.2, survival probability of seedlings in the numerator treatment is improved by 1 − 0.2 = 0.8)

Results

We observed no mortality during the first month; however, by mid-July (day 60) seedlings began to die. Within the "treatment" based Cox PH model, which examined pair-wise differences in hazard between treatments, hazard depended on initial transplant size (caudex diameter) and treatment, but not their interaction, which was removed from the model (Table 1a). Based on the estimated effects of size, a 1 mm increase in initial plant caudex diameter was predicted to produce a 24.1 % ([HR − 1] × 100) increase in risk of mortality (Table 1). The probability of survival was highest for *P. palmeri* seedlings transplanted under shrubs without understory interactions (Fig. 1; "+SI, −UI"). The next highest probability of survival was for seedlings either transplanted under shrubs with understory interactions (Fig. 1; "+SI, +UI") or into interspaces without understory interactions (Fig. 1; "−SI, −UI"), with the latter faring slightly, but not significantly, worse. Lastly, seedlings in interspaces with understory interactions had the lowest probability of survival by far (Fig. 1; "−SI, +UI"). Pair-wise comparisons between treatments were highly significant for all treatment combinations ($P < 0.001$) except for the comparison between "+SI, +UI" and "−SI, −UI" (Table 1a; Contrast 1). For *P. palmeri* transplanted to interspaces ("−SI"), limiting understory interactions (i.e., removing the understory community) reduced the risk of seedling mortality by about 83 % (Table 1a; Contrast 2). Similarly, for seedlings under shrubs ("+SI"), limiting understory interactions reduced the risk of mortality by about 86 % (Table 1a; Contrast 3). For *P. palmeri* transplanted into cleared plots ("−UI"), the presence of shrub interactions reduced the risk of

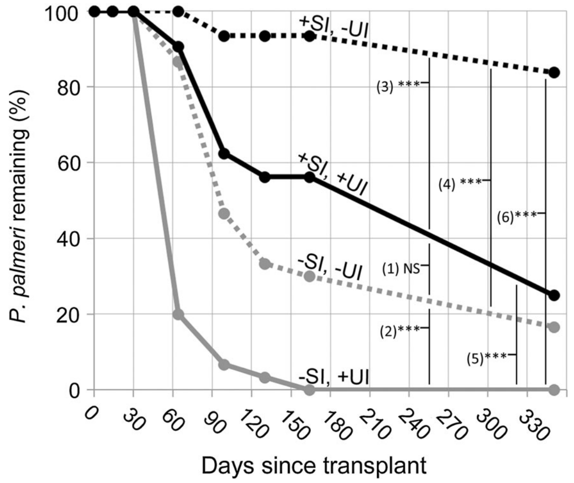

Fig. 1 Data showing the percentage of remaining transplanted *P. palmeri* seedlings over time. Seedlings were transplanted into four treatments varying the presence or absence of shrub interactions (+SI vs. −SI) and understory interactions (+UI vs. −UI). *Brackets connecting lines* refer to the contrasts in Table 1. Comparisons were either not significant ("NS"; $P \geq 0.05$) or highly significant ("***"; $P < 0.001$)

seedling mortality by approximately 91 % (Table 1a; Contrast 4). Similarly, in plots with understory interactions ("+UI"), shrub interactions reduced the risk of mortality by approximately 88 % (Table 1a; Contrast 5). Finally, risk of mortality for seedlings growing under shrubs without understory interactions was 98 % lower than for seedlings growing in interspaces with understory interactions (Table 1a; Contrast 6).

The second, "factor" based Cox PH model, which examined differences in hazard based on the two types of interactions revealed highly significant effects of understory interactions, shrub interactions, and caudex diameter (Table 1b). All two- and three-way statistical interactions were insignificant ($P > 0.26$), and thus removed. In this model, limiting understory interactions reduced the risk of *P. palmeri* seedling mortality by 84 % (Table 1b; Contrast 7), while the presence of shrub interactions reduced the risk of mortality by 89 % (Table 1b; Contrast 8).

Discussion

Positive and negative plant interactions can critically influence seedling survival and establishment, especially in more stressful habitats (Maestre et al. 2003; de la Cruz et al. 2008). Examining the effects of both shrub and understory interactions on transplanted *P. palmeri* seedlings provided evidence to support our hypothesis that shrubs positively influenced seedling survival while the effects of understory vegetation on seedlings were negative. Furthermore, we found that eliminating understory interactions and/or adding shrub interactions similarly increased *P. palmeri* seedling survival. Our study demonstrates the importance of considering interactions between plants in the context of a background of understory interactions (Callaway and Pennings 2000) and highlights the importance of using manipulative experiments to disentangle the effects of potentially interacting ecological processes (Callaway 2007a; de la Cruz et al. 2008; McIntire and Fajardo 2009).

Competition from understory species at the study site was apparently intense. The understory community was dominated by exotic species known to be highly competitive, including *P. bulbosa* (Hull 1974), *B. tectorum* (Humphrey and Schupp 2004), and *E. cicutarium* (Schutzenhofer and Valone 2006). Shrub interactions were also important drivers of community dynamics, as *P. palmeri* seedlings had greater mortality in interspaces relative to those growing under shrubs, even in the absence of understory interactions. However, it is interesting to note that the positive effects of adding shrubs were additively balanced by the negative effects of adding understory interactions (see Table 1, contrast 1; +SI, +UI vs. −SI, −UI). Our study provides supplemental evidence of the potential for *A. tridentata* to facilitate species that grow under shrub canopies, adding to an evolving body of the literature on the subject (e.g., Davies et al. 2007; Reisner 2010; Alpert and Loik 2013; Ziffer-Berger et al. 2014). While other studies show evidence that *P. palmeri* can be facilitated by *A. tridentata* in its southern, more arid range (Poulos 2013), we found that *P. palmeri* was also facilitated by *A. tridentata* in the relatively temperate, northern range of its distribution.

The lack of a statistical interaction between treatment factors indicates that the presence or absence of shrub interactions did not alter the effect of understory interactions, and vice versa. This finding supports other studies showing that positive and negative interactions can act simultaneously (Callaway 2007c), but also provides unique evidence that simultaneous positive and negative interactions may be largely independent. This apparent independence between interactions contrasts with the findings of Callaway and Pennings (2000), who explicitly examined both facilitation and diffuse competition (i.e., “understory interactions” in our study). In their study, there was evidence of an interaction between facilitation and competition; facilitation appeared to buffer the effects of diffuse competition among salt marsh plants; i.e., the effect of competition depended on the presence or absence of the facilitating plant. A similar result was found in a manipulation experiment in a semi-arid shrubland in which nurse shrubs appeared to facilitate seedling survival by reducing understory competition during average rainfall years, but during humid spring and dry summer seasons, understory herbs reduced seedling mortality equally under nurse shrubs and between them (Cuesta et al. 2010). The complexity and inconsistency of outcomes in these studies demonstrate the importance of considering the direct interactions between species of interest and their potential nurse plants and understory communities while also considering the potential indirect effects of nurse plants on the interactions among understory species. Furthermore, these complex interactions should ideally be examined over a variety of climatic conditions.

Although the results of this study strongly support our hypotheses, this study has some limitations. First, using a seed source from a different climatic regime may have altered the outcome of interactions. Specifically, seedlings from a more local *P. palmeri* population could have been less resilient to resource stress but could potentially have a greater competitive ability than individuals from populations in drier, less vegetated regions of the upper Mojave Desert. Second, using only a single life-stage to conclude facilitation has occurred is not recommended since interactions can shift with ontogeny (Miriti 2006; Schiffers and Tielbörger 2006; Poulos 2013). However, the seedling stage is a common focus of facilitation studies (e.g., Gómez-Aparicio 2009) and it is clear that *A. tridentata* shrubs facilitated at least the early survival of *P. palmeri* in this experiment. Third, a single site was used in this research, yet the balance of competition and facilitation is known to be highly dependent on where interactions occur along a gradient of stress and productivity (Bertness and Callaway 1994). A more comprehensive study would include replicate experiments along these gradients. Fourth, it must be recognized that the outcome of this type of experiment is expected to be contingent on the species pair(s) examined since species identity is known to be an important factor relating to the outcome of interactions (Callaway 2007d). Finally, the precise mechanisms responsible for the observed survival patterns cannot be ascertained, since environmental conditions were not measured; a more comprehensive study may benefit by measurements of microclimatic conditions, including soil characteristics (e.g., Gómez-Aparicio et al. 2005). Nonetheless, our results are robust for the context studied.

Ecosystem restoration efforts traditionally focused on the elimination of competition as a means to promote native or desirable plant establishment (see review by Gómez-Aparicio 2009); however, there is increasing recognition that positive plant interactions (e.g., nurse plants) can be utilized for the successful establishment of desirable plant populations (Gómez-Aparicio et al. 2004; King and Stanton 2008; Gómez-Aparicio 2009; Jensen et al. 2012). As noted, *P. palmeri* is a forb species used in restoration efforts in the western U.S., providing a range of valuable ecosystem services related to forage, soil stabilization, pollinator resources, and landscape esthetics (Stevens and Monsen 2004; Poulos 2013). Our results, which can be used to inform the conservation and restoration of populations of *P. palmeri,* and perhaps other similar forbs, suggest that an ideal strategy would be to remove understory competitors from beneath existing canopies of *A. tridentata* and other potential nurse species and plant seeds or seedlings into these areas. However, since the understory community may contain desirable native species, selectively eliminating invasive competitors is recommended, but likely infeasible and/or costly; as such, relying only on using *A. tridentata* as a nurse plant may be preferable. Further, seedling size may be a critical factor to consider during planting, as we found evidence that survival was greater for smaller *P. palmeri* seedlings compared to larger seedlings. If the use of nurse plants becomes impractical, then our results suggest that removal of competitors could be a viable option to improve the establishment of transplanted forb seedlings. However, a similar result could be achieved without removing competition but instead using shrubs as nurse plants, suggesting that managers should consider using nurse plants to improve establishment of target species when minimal disturbance is desired or if the cost of removing understory competition is prohibitive. Land managers could benefit greatly by using these relatively simple experimental manipulations to ascertain the potential for using nurse plants and/or removing competition in specific regions.

Conclusion

We found support for our hypotheses that, relative to transplanted seedlings of the native forb *P. palmeri*, shrub interactions would be net positive and understory interactions would be net negative; when combined, their additive effects led to overall neutral interactions. Furthermore, support was also found for our predictions that *P. palmeri* seedling survival would be highest in the absence of understory interactions and in the presence of shrub interactions, and lowest in the absence of shrub interactions and in the presence of understory interactions. This study provided valuable insight about the balance of positive and negative plant interactions in semi-arid shrublands and the potential use of alternative management strategies (removal of competitors and/or use of nurse plants) for promoting desirable plant establishment. This straightforward experiment should be easily replicable in other regions where establishment of native and/or desirable plants is of key importance. The debate over the importance of positive and negative plant interactions in arid and semi-arid communities is likely to continue; however, our results add to the growing body of evidence demonstrating that both processes are simultaneously important drivers of plant community dynamics.

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Appendix

See Table 2 and Fig. 2.

Table 2 Species at the site in order of the percentage of cleared plots in which they were present. Plant names follow the USDA NRCS Plants Database (NRCS 2013. Certain species could not be identified past the life-form or genus level since they lacked flowers or fruits required for identification

Species	Common name	Life-form	Plots (%)
Poa bulbosa	Bulbous bluegrass	Grass(P)	100
Bromus tectorum	Cheatgrass	Grass(A)	97
Erodium cicutarium	Redstem stork's bill	Herb(A)	78
Draba reptans	Carolina draba	Herb(A)	42
Zigadenus sp.	Deathcamus	Herb(P)	40
Unknown perennial grasses	NA	Grass(P)	30
Tragopogon dubius	Yellow salsify	Herb(A/B)	20
Convolvulus arvensis	Field bindweed	Herb(P)	13
Medicago sp.	Alfalfa	Herb(A/P)	10
Viola beckwithii[a]	Beckwith's violet	Herb(P)	10
Oenothera caespitosa	Tufted evening primrose	Herb(P)	5
Sphaeralcea grossulariifolia	Gooseberryleaf globemallow	Herb(P)	5
Artemisia ludoviciana	White sagebrush	Herb(P)	3
Lomatium sp.	Desertparsley	Herb(P)	2
Cryptantha sp.	Cryptantha	Herb(B/P)	2
Achillea millefolium	Common yarrow[b]	Herb(P)	0
Astragalus spp. (2)	Milkvetch[b]	Herb(P)	0
Isatis tinctoria	Dyer's woad[b]	Herb(B/P)	0
Penstemon cyananthus	Wasatch beardtoungue[b]	Herb(P)	0

A annual, *P* perennial, *B* biennial

[a] Transplanted adjacent to thinned plots due to its rarity

[b] Not found within any thinned plots, but were present within the community

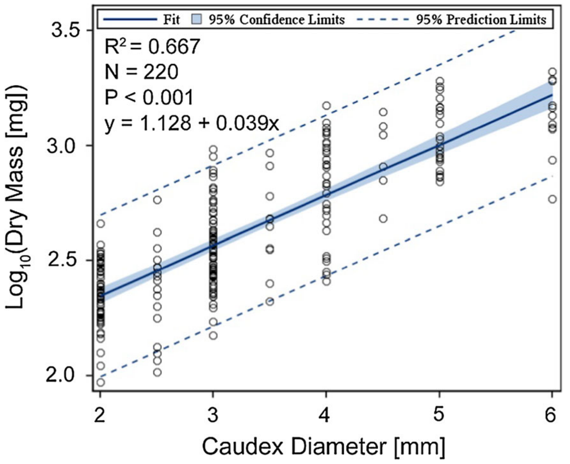

Fig. 2 Size (caudex diameter; mm) regressed on the logarithm of biomass (dry above-ground mass; mg) produced from 220 destructively sampled *P. palmeri* seedlings

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