



Risk of Facilitated Invasion Depends Upon Invader Identity, Not Environmental Severity, Along an Aridity Gradient

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Positive interactions can drive the assembly of desert plant communities, but we know little about the species-specificity of positive associations between native shrubs and invasive annual species along aridity gradients. These measures are essential for explaining, predicting, and managing community-level responses to plant invasions and environmental change. Here, we measured the intensity of spatial associations among native shrubs and the annual plant community—including multiple invasive species and their native neighbors—along an aridity gradient across the Mojave and San Joaquin Deserts, United States. Along the gradient, we sampled the abundance and species richness of invasive and native annual species using 180 pairs of shrub and open microsites. Across the gradient, the invasive annuals *Bromus madritensis* ssp. *rubens* (*B. rubens*), *B. tectorum*, *B. diandrus*, *Hordeum murinum*, and *Brassica tournefortii* were consistently more abundant under shrubs than away from shrubs, suggesting positive effects of shrubs on these species. In contrast, abundance of the invasive annual *Schismus* spp. was greater away from shrubs than under shrubs, suggesting negative effects of shrubs on this species. Similarly, native annual abundance (pooled) and native species richness were greater away from shrubs than under shrubs. Shrub-annual associations were not influenced by shrub size or aridity. Interestingly, we found correlative evidence that *B. rubens* reduced native abundance (pooled), native species richness, and exotic abundance (pooled) under, but not away from shrubs. We conclude that native shrubs have considerable potential to directly (by increasing invader abundance) and indirectly (by increasing negative impacts of invaders on neighbors) facilitate plant invasions along broad environmental gradients, but these effects may depend more upon invader identity than environmental severity.

Keywords: desert, facilitated invasion, facilitation, invasive species, positive interactions, shrubs, species-specificity, stress-gradient hypothesis

INTRODUCTION

Positive interactions among species (facilitation) enhance biodiversity and ecosystem functioning (Wright et al., 2017, 2021) while buffering communities against environmental change (Bulleri et al., 2018). Facilitation occurs when a foundation species alters the biotic or abiotic environment in a way that enhances the performance, survival, or fitness of beneficiary species (Bronstein, 2009; mechanisms reviewed by Filazzola and Lortie, 2014). Importantly, positive interactions can be species-specific because some foundation species are better facilitators than others, and not all beneficiary species are facilitated equally (Callaway, 1998). The intensity of facilitation also depends upon environmental severity. The stress-gradient hypothesis (SGH) predicts that the frequency (Bertness and Callaway, 1994) and intensity (le Roux and McGeoch, 2010) of positive interactions increase as environmental stress increases. Hundreds of studies have examined the SGH, and meta-analyses have found broad support for its basic predictions (e.g., Lortie and Callaway, 2006; He et al., 2013; Romero et al., 2015; Adams et al., 2022).

Positive interactions can also influence the trajectory of biological invasions by exotic plant species (Cavieres, 2021). Exotic species commonly facilitate each other (Braga et al., 2018), but native species also facilitate plant invasions (Northfield et al., 2018). Native facilitators can promote invasions directly by increasing the local abundance, performance, and fitness of invasive species; or indirectly by increasing the negative impacts of invasive species on neighbors. For instance, Lucero et al. (2021) showed that the invasive annual *Bromus tectorum* achieved much greater abundance, biomass, and fitness near native shrubs than away from shrubs; and Lortie et al. (2021) showed that invasive annual species had stronger competitive effects on native neighbors when they were facilitated than when they were not. Environmental context can mediate the strength of positive interactions experienced by invasive species (Cavieres et al., 2008; Saccone et al., 2010; Llambi et al., 2018; Filazzola et al., 2020), but we still know very little about the species-specificity of facilitated invasions.

Facilitation by desert shrubs is a useful framework for addressing these issues. Arid and semi-arid ecosystems cover over 40% of the earth's land surface, comprise 44% of the world's arable land, support more than 50% of the world's livestock, and contribute substantially to global biodiversity (Millennium Ecosystem Assessment, 2005; Davies et al., 2021). However, increasing aridity associated with anthropogenic climate change and accelerating biological invasions by exotic plant species are degrading the biodiversity and functioning of desert ecosystems at an alarming rate (DiTomaso et al., 2010; Huang et al., 2016; Phillips et al., 2022). Shrubs can facilitate desert plant communities by creating favorable microsites underneath their canopies that ameliorate environmental extremes (Callaway, 2007; Michalet and Pugnaire, 2016). For instance, shade from shrub canopies can buffer understory plants against solar radiation and heat (Valiente-Banuet and Ezcurra, 1991), and soil nutrients (Schlesinger et al., 1996) and water (Segoli et al., 2012) are often more concentrated under shrub canopies than

away from shrubs. Many exotic invaders capitalize on positive interactions in deserts (e.g., Butterfield et al., 2010; Badano et al., 2016; López et al., 2016; Filazzola et al., 2020; Slate et al., 2020), and sometimes to a greater extent than native competitors (Lucero et al., 2019). The SGH predicts that shrub-mediated interactions should be most positive in the most arid environments, but there remains considerable opportunity to test this relationship with multiple invasive species simultaneously (but see Holzapfel and Mahall, 1999; Brooks, 2003; Filazzola et al., 2020). Understanding of the species-specificity of facilitated invasions along aridity gradients—including indirect effects on native competitors—is necessary for explaining, predicting, and ultimately managing the ecological consequences of concomitant exotic plant invasion and environmental change in desert systems.

The objective of this study was to evaluate the potential for native shrubs to directly (by increasing the local abundance of invasive species) and indirectly (by increasing the negative impacts of invasive species on neighbors) facilitate annual plant invasions along an aridity gradient across the Mojave and San Joaquin Deserts, United States. We tested two interrelated hypotheses. First, we tested the hypothesis that the intensity of shrub-invasive annual associations depends upon invasive species identity and relative aridity. Specifically, we predicted that: (i) the intensity of shrub-invasive annual associations varies by species; and (ii) the intensity of shrub-invasive annual associations becomes more positive as relative aridity increases, as predicted by the SGH. Second, we hypothesized that association with native shrubs alters the outcome of biotic interactions (inferred *via* spatial relationships) between invasives and herbaceous neighbors, including native and exotic species. Specifically, we predicted that abundance relationships between invasive annuals and herbaceous neighbors are more negative (i.e., more competitive) near shrubs than away from shrubs (after Lortie et al., 2021).

MATERIALS AND METHODS

Study Area and Species

We surveyed annual plant communities at peak flowering in April 2020 at nine sites that spanned an aridity gradient (see **Supplementary Table 1** for site names, locations, and aridity values) across the Mojave ($n = 6$) and San Joaquin ($n = 3$) Deserts, United States. Sites in the Mojave Desert were located near Cal-Nev-Ari, NV; the Heart of the Mojave ORV Trail, CA; Mesquite, NV; Mojave, CA; Las Vegas, NV; and Yucca Grove, CA. Sites in the San Joaquin Desert were located near Carrizo Plain National Monument, CA; Cuyama, CA; and Panoche Hills, CA. We selected sites in climax native shrub communities that had not recently experienced a major disturbance (e.g., fire). One site (Carrizo) was grazed by cattle during the study year, but all others were not grazed. For each site, we calculated the de Martonne aridity index (A_{dM}) (de Martonne, 1920) during the study year as follows:

$$A_{dM} = \frac{P}{T + 10}$$

where P was the total precipitation (mm) from May 1, 2019, to April 30, 2020, and T was the mean daily temperature ($^{\circ}\text{C}$) during the same interval. Thus, low A_{dM} values indicated high aridity. We also calculated a 30-year A_{dM} value for each site by averaging yearly A_{dM} values from 1991 to 2020. Importantly, our statistical analyses used the A_{dM} of the study year (2019–2020), not the 30-year average, because current climatic trends are more relevant to the performance of annual plant species than long-term trends. We chose this aridity index because weather stations nearly always report its components, which allows for direct calculations of A_{dM} at spatiotemporal scales relevant to biotic interactions in local communities.

Sites in the Mojave Desert were dominated by the native shrub *Larrea tridentata*, and sites in the San Joaquin Desert were dominated by the native shrub *Ephedra californica*. Other shrub species were present at relatively low densities, but no one shrub species was present at all sites. We focused on the potential for native shrubs to act as facilitators because they are the dominant physiognomic class across our study area and are common targets for land management actions (Eldridge et al., 2011).

We identified exotic annuals to species at each site. *Bromus madritensis* ssp. *rubens* (*B. rubens* hereafter), *Schismus* spp. (*S. arabicus* and *S. barbatus* are difficult to reliably differentiate in the field and were thus combined as a taxa), and *Erodium cicutarium* were present at all sites. *Bromus tectorum* was present at Cuyama, Mesquite, Mojave, Las Vegas, and Yucca Grove. *Bromus diandrus* was present at Cuyama and Panoche Hills. *Hordeum murinum* was present at Carrizo and Cuyama. *Brassica tournefortii* was present at Cal-Nev-Ari and Mesquite. Each of these exotic species (1) was translocated at some point from a distant native range (Eurasia/Northern Africa) to North America, (2) has established self-sustaining populations in North America, (3) is expanding its range in North America, and (4) can negatively impact biodiversity and ecosystem functioning in North American plant communities. Thus, each of these species meets the criteria of Blackburn et al. (2011) for being “invasive,” and each is considered invasive by the California Invasive Plant Council (CAL-IPC, 2022).

During the study year, annual precipitation, mean annual temperature, and A_{dM} at the study sites ranged from 137 to 287 mm, 16.32–21.00 $^{\circ}\text{C}$, and 4.41–10.89 (A_{dM} is unitless), respectively. Thirty-year A_{dM} values ranged from 3.44 to 24.04, a much broader range than the study year. For six of our nine sites, the A_{dM} for the study year fell within the 95% CI of the 30-year A_{dM} , but Carrizo, Heart of the Mojave, and Panoche Hills were more arid than usual (Supplementary Table 1).

Sampling

We sampled the annual plant community using a paired shrub-open microsite contrast with a 0.5×0.5 m quadrat (Pescador et al., 2014). Shrub microsites were defined as the area immediately beneath the canopy of a focal shrub, and open microsites were defined as interstitial spaces at least 1 m from any shrub canopy but <5 m from the focal shrub. We did not sample areas more than 5 m away from shrubs. For shrub microsites, sampling quadrats were placed midway between the shrub center and dripline. A total of 180 pairs of shrub and open microsites

were sampled ($n = 20$ shrub-open pairs at each study site), and for each shrub-open pair, we noted the species, radius (r ; m), and height (h ; m) of the shrub. We used the formula for an oblate spheroid:

$$V = \frac{4\pi r^2 h}{3}$$

to estimate the volume (m^3) of each shrub. We used this formula to estimate shrub size because it is more nuanced than shrub height or width alone (Lortie et al., 2018; Lucero et al., 2021). Shrub-open pairs for sampling were chosen randomly by facing a random compass bearing and then blindly tossing a tennis ball backward in the opposite direction. The shrub-open pair nearest to the ball was sampled. In the Mojave, focal shrubs were *L. tridentata* ($n = 74$), *Ambrosia dumosa* ($n = 24$), *Coleogyne ramossissima* ($n = 12$), and *Lycium andersonii* ($n = 10$). In the San Joaquin, *E. californica* was the focal shrub for all shrub-open pairs ($n = 60$).

In sampling quadrats, we recorded the abundance (no. plants rooted inside the quadrat) of each exotic annual species, exotic annual species combined, native annual species combined, and the total annual plant community (all annual species combined); as well as the richness of native annual species, exotic annual species, and the total annual plant community (all annual species combined). Relationships among these particular measures are used to describe the invasiveness and impacts of exotic species in non-native communities (Pearson et al., 2016). We did not encounter species that reproduced asexually or vegetative mats suggestive of extensive tillering.

Statistical Analyses

Relative interaction indices (RIIs; Armas et al., 2004) were used as a simple effect size measure to estimate the intensity of shrub-annual associations. We calculated RII as follows:

$$RII = \frac{M_s - M_o}{M_s + M_o}$$

where M_s was a vegetation measure (e.g., *B. rubens* abundance, native species richness, etc.) in a shrub microsite and M_o was the same measure in the paired open microsite. RII values range from -1 to $+1$. Negative RII values indicate negative (competitive) shrub-annual associations, positive values indicate positive (facilitative) associations, and a value of 0 indicates no (neutral) association.

We used t -tests and linear mixed-effects models to characterize relationships among shrubs and annual plant species. To evaluate the direction and intensity of shrub-annual associations at each site and across all sites, we performed one-sample t -tests with RII as the response variable. T -tests across all sites used RIIs averaged at the site level. We evaluated the influence of aridity and shrub size on the intensity of shrub-annual associations (i.e., RIIs) using linear mixed-effects models with RII as the response variable; A_{dM} , shrub volume, and their interaction as covariates; and shrub species nested within study site as a random effect. We inferred biotic interactions among neighboring annuals in shrub and open microsites using linear mixed-effects models with annual plant abundance or

species richness (log-transformed) as the response variable; exotic annual abundance (species-specific or combined) as a covariate (log-transformed); and shrub species nested within study site as a random effect. For these analyses, negative line slopes ($P < 0.05$) suggest negative interactions among neighbors, positive line slopes ($P < 0.05$) suggest positive interactions, and line slopes with $P > 0.05$ suggest neutral interactions. We performed species-specific analyses only for exotic annual taxa present at more than two study sites.

All analyses were performed in R, version 4.0.2 (R Development Core Team, 2020). We did t -tests using the t -test function (R Development Core Team, 2020). Linear mixed-effects models used the lmer function of the “lmerTest” package (Kuznetsova et al., 2017). R^2 -values were extracted using the r2 function (R Development Core Team, 2020).

RESULTS

Invasive annuals formed species-specific associations with native shrubs (Figure 1 and Supplementary Table 2). Across sites, mean RIIs for *B. rubens*, *B. tectorum*, *B. diandrus*, *H. murinum*, and *B. tournefortii* ranged from 0.829 (0.043 SE; $P < 0.001$) to 1.000, indicating that each of these invasive species formed remarkably intense positive associations with native shrubs across our study area. In contrast, mean RII across sites for invasive annual grass *Schismus* spp. was -0.435 (0.195 SE; $P = 0.032$), indicating a

negative association with shrubs across our study area. Mean RII across sites for *E. cicutarium* was -0.374 (0.147 SE; $P = 0.061$), indicating no strong associations with shrubs. Interestingly, at the site level, RIIs for *B. rubens*, *B. tectorum*, *B. diandrus*, *H. murinum*, and *B. tournefortii* were always positive and never fell below 0.545 (0.059 SE; $P < 0.001$), suggesting consistent positive associations with native shrubs at each site. At the site level, RIIs for *Schismus* spp. and *E. cicutarium* varied from -1.000 to 0.645 (1.06 SE), suggesting that their associations with shrubs were not only negative net neutral or, but also highly variable. Across sites, mean RIIs for native abundance and native species richness (all native species combined) were -0.358 (0.153 SE; $P = 0.024$) and -0.321 (0.132 SE; $P = 0.020$), respectively, suggesting that the native annual community was negatively associated with shrubs across our study area. Across sites, mean RIIs for exotic species richness (all exotic species combined) and total species richness (all species combined) were 0.014 (0.046 SE; $P = 0.740$) and -0.121 (0.074 SE; $P = 0.101$), respectively, suggesting no meaningful effect of shrubs on the species richness of the exotic or total annual community across our study area.

The intensity of shrub-annual associations was not influenced by aridity (i.e., A_{DM}) or shrub size (Table 1). As aridity and shrub size increased, RIIs for all vegetation measures remained constant. Thus, we found no support for the SGH. In addition, we found no evidence for aridity $\times$ shrub size interactions (Table 1).

Native shrubs altered abundance relationships between the invasive annual *B. rubens* and the native annual community

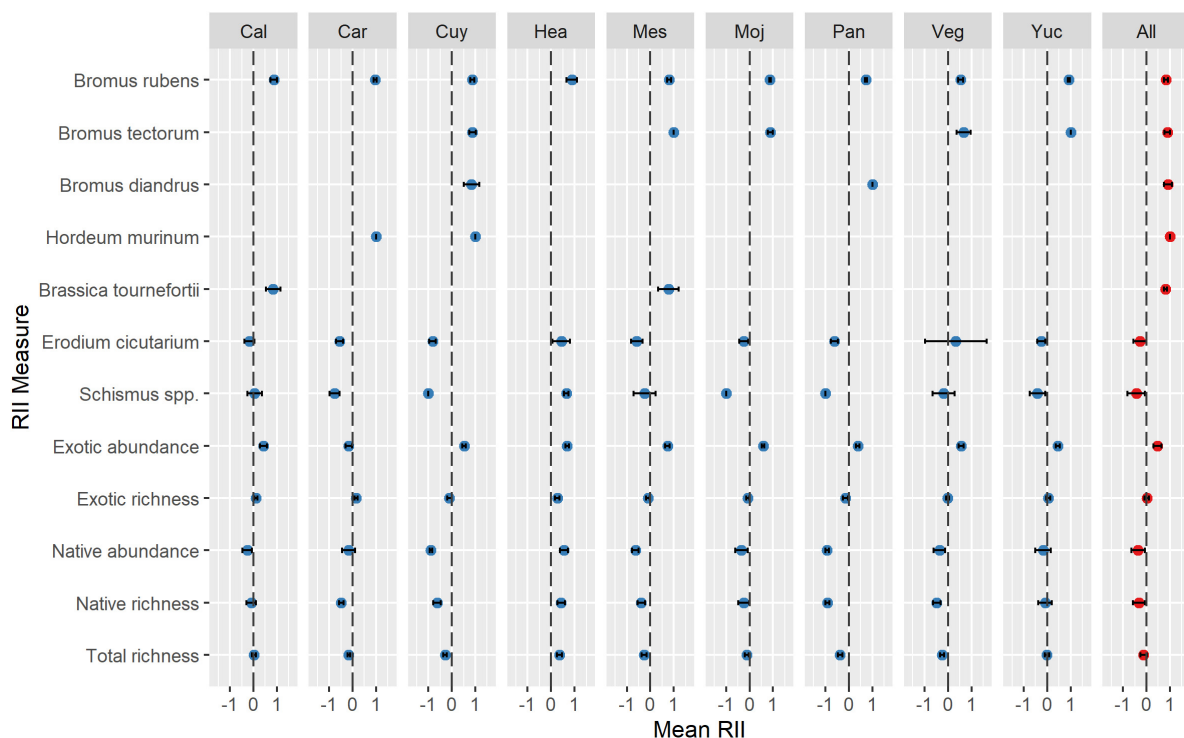


FIGURE 1 | Mean intensity (RII $\pm$ 95% CI) of shrub-herbaceous plant associations at each study site and averaged across all sites (“All”; shown in red). RIIs > 0 suggests positive (i.e., facilitative) shrub-annual associations; RIIs < 0 suggests negative (i.e., antagonistic) associations. Site names are abbreviated by their first three letters (see Supplementary Table 1 for full names).

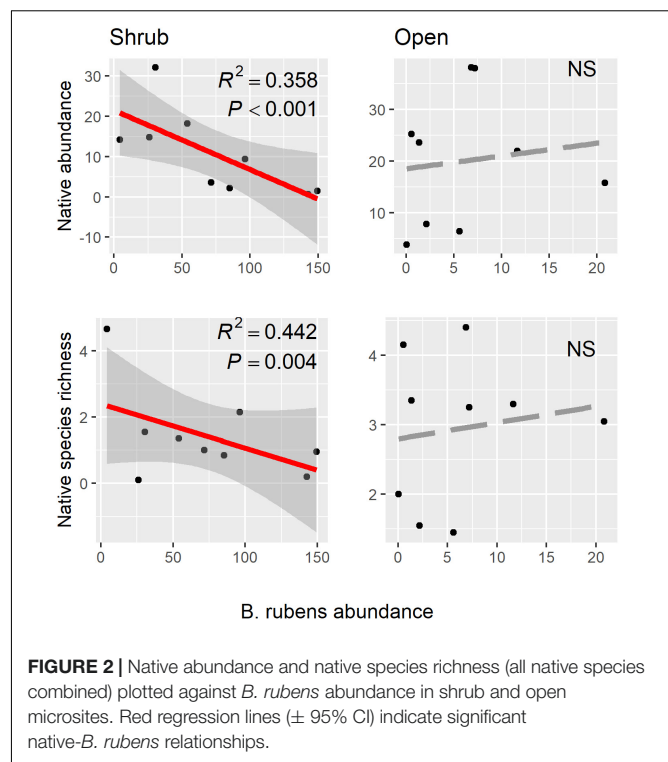
TABLE 1 | Results of linear mixed-effects models with RII as the response variable; de Martonne aridity score (Adm), shrub volume (Vol), and their interaction (AdM × Vol) as covariates; and shrub species nested within site as a random effect (not shown).

Response	Covariate(s)	Coefficient	df	t	P
<i>B. rubens</i>	AdM	0.026	9,046	1.232	0.296
	Vol	0.019	169,248	1.230	0.269
	AdM × Vol	−0.002	169,635	0.833	0.363
<i>B. tectorum</i>	AdM	0.031	3,410	0.826	0.423
	Vol	0.014	38,182	0.231	0.633
	AdM × Vol	−0.002	39,471	0.307	0.583
<i>Schismus</i> spp.	AdM	−0.125	9,062	1.474	0.256
	Vol	0.011	135,814	0.057	0.811
	AdM × Vol	−0.003	134,624	0.152	0.698
<i>E. cicutarium</i>	AdM	−0.096	8,862	1.640	0.233
	Vol	−0.010	70,339	0.068	0.795
	AdM × Vol	<0.001	108,185	0.004	0.953
Native ab.	AdM	−0.073	7,954	0.792	0.400
	Vol	−0.020	98,070	0.290	0.592
	AdM × Vol	−0.003	129,867	0.308	0.580
Native rich.	AdM	−0.044	7,968	0.368	0.561
	Vol	−0.020	137,756	0.422	0.517
	AdM × Vol	0.002	156,068	0.291	0.591
Exotic rich.	AdM	−0.031	8,351	1.526	0.250
	Vol	−0.006	175,450	0.190	0.663
	AdM × Vol	0.001	175,258	0.076	0.783
Total rich.	AdM	−0.024	7,662	0.334	0.580
	Vol	−0.004	122,375	0.065	0.799
	AdM × Vol	<0.001	148,493	0.072	0.788

We performed species-specific analyses only for species present at more than three sites. Note that there are no significant ($P < 0.05$) effects.

(Figure 2 and Table 2). In shrub microsites, increasing *B. rubens* abundance corresponded to decreasing native abundance and native species richness, suggesting competitive interactions between *B. rubens* and native annuals under shrubs. In contrast, in open microsites, we found no significant relationships between *B. rubens* abundance and native abundance or native species richness, suggesting relatively weak interactions in the open. Increasing exotic abundance (all exotic species combined) corresponded to decreasing native abundance and native species richness in shrub microsites, but again, not in open microsites (Figure 3). These negative relationships under shrubs were apparently driven primarily by *B. rubens*, because removing *B. rubens* from the exotic abundance data eliminated all significant exotic-native relationships (Figure 4).

Shrubs also altered abundance relationships between *B. rubens* and the broader exotic annual community (all exotic species combined except for *B. rubens*) (Supplementary Figure 2 and Supplementary Table 3). In shrub microsites, increasing *B. rubens* abundance was negatively related to exotic abundance but had no relationship to exotic species richness. In open microsites, increasing *B. rubens* abundance had no relationship to exotic abundance but was positively related to exotic species richness.



DISCUSSION

Our study enriches our understanding of the species-specificity of facilitated invasions. We have long known that not all species are facilitated equally (Callaway, 1998). However, few studies have evaluated the potential for positive interactions to affect multiple invasive species simultaneously along aridity gradients. We found that spatial association with native shrubs consistently increased the abundance of some invasive annual species (*B. rubens*, *B. tectorum*, *B. diandrus*, *H. murinum*, and *B. tournefortii*), decreased the abundance of other invasive annuals (*Schismus* spp.), and had no consistent effects on another invasive annual (*E. cicutarium*). These findings support our hypothesis that the intensity of shrub-invasive annual associations depends strongly upon invasive species identity. Interestingly, the direction and intensity of these associations were unaffected by shrub size or relative aridity across our observed gradient. Thus, we found no support for the hypothesis that the intensity of shrub-invasive annual associations depends upon relative aridity. Additionally, we found correlative evidence (*via* abundance relationships) that native shrubs exacerbated the negative impacts of *B. rubens* on neighboring annuals. This supports the hypothesis that spatial association with native shrubs can alter the outcome of biotic interactions between invasive annuals and herbaceous neighbors. Taken together, our main findings suggest that native shrubs have considerable potential to facilitate exotic plant invasions across a broad spatial scale, but this potential may depend more upon invader identity than environmental severity. This accords with studies showing that species-specific factors can be more important than environmental conditions as drivers

TABLE 2 | Results of linear mixed-effects models replicated for shrub and open microsites with native abundance or native species richness (all native species combined) as the response variable; abundance of *B. rubens*, *B. tectorum*, *E. cicutarium*, *Schismus* spp., all exotic species combined (Total exotic ab.), or exotic species except for *B. rubens* (Exotic ab. -*Brru*) as the covariate; and shrub species nested within study site as a random effect (not shown).

Response	Covariate	Shrub						Open					
		Coeff.	SE	df	t	P	Outcome	Coeff.	SE	df	t	P	Outcome
Native ab.	<i>B. rubens</i> ab.	-0.328	0.069	99.150	-4.781	<0.001	Competition	0.097	0.097	170.857	1.003	0.317	Neutral
	<i>B. tectorum</i> ab.	0.022	0.160	40.151	0.141	0.889	Neutral	0.382	0.321	40.755	1.190	0.241	Neutral
	<i>E. cicutarium</i> ab.	0.094	0.077	155.900	1.210	0.228	Neutral	-0.099	0.113	119.392	-0.877	0.382	Neutral
	<i>Schismus</i> spp. ab.	-0.032	0.061	145.840	-0.532	0.595	Neutral	0.155	0.082	145.082	1.891	0.061	Neutral
	Total exotic ab.	-0.793	0.106	173.027	-7.451	<0.001	Competition	0.072	0.109	175.141	0.663	0.508	Neutral
	Exotic ab. - <i>Brru</i>	0.010	0.057	173.835	0.170	0.865	Neutral	0.059	0.089	174.987	0.659	0.511	Neutral
Native rich.	<i>B. rubens</i> ab.	-0.080	0.027	159.243	-2.957	0.004	Competition	0.022	0.041	141.657	0.531	0.596	Neutral
	<i>B. tectorum</i> ab.	0.032	0.054	41.535	0.588	0.559	Neutral	0.092	0.133	41.357	0.693	0.492	Neutral
	<i>E. cicutarium</i> ab.	0.016	0.010	152.515	1.566	0.119	Neutral	-0.077	0.046	86.943	-1.685	0.096	Neutral
	<i>Schismus</i> spp. ab.	0.006	0.022	145.723	0.289	0.773	Neutral	0.073	0.037	144.889	1.970	0.051	Neutral
	Total exotic ab.	-0.185	0.042	177.131	-4.405	<0.001	Competition	0.019	0.047	154.602	0.399	0.690	Neutral
	Exotic ab. - <i>Brru</i>	0.010	0.021	172.700	0.474	0.636	Neutral	0.004	0.006	163.065	0.660	0.510	Neutral

We interpreted negative coefficients ($P < 0.05$) as evidence for competition, positive coefficients ($P < 0.05$) as evidence for facilitation, and coefficients with $P > 0.05$ as neutral. Analyses were performed on log-transformed data.

of nurse plant effects in drylands (Soliveres et al., 2012; Filazzola et al., 2020).

Our main findings corroborate that desert shrubs can facilitate heterospecific neighbors, including invasive annuals. Positive effects of desert shrubs on annual species include increased abundance, performance, and population growth (Callaway, 2007; Griffith, 2010). Desert shrubs and their interactions can bolster the biodiversity (Bashirzadeh et al., 2022) and

functioning (Khosravi Mashizi and Sharafatmandrad, 2019) of desert ecosystems (but see Báez and Collins, 2008), but desert shrubs do not facilitate all taxa equally (Filazzola et al., 2020). In this context, our findings coincide nicely with the literature review of Abella and Smith (2013), who found that across the Mojave Desert, exotic annuals were generally more abundant near native perennials than in interspaces, suggesting overall facilitation of exotic annuals by native perennials. In particular,

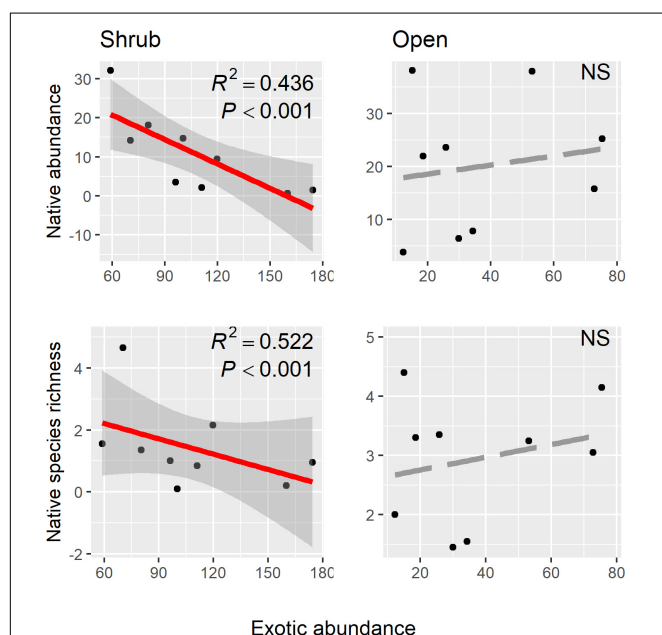


FIGURE 3 | Native abundance and native species richness (all native species combined) plotted against exotic abundance (all exotic species combined) in shrub and open microsites. Red regression lines ($\pm$ 95% CI) indicate significant native-exotic relationships.

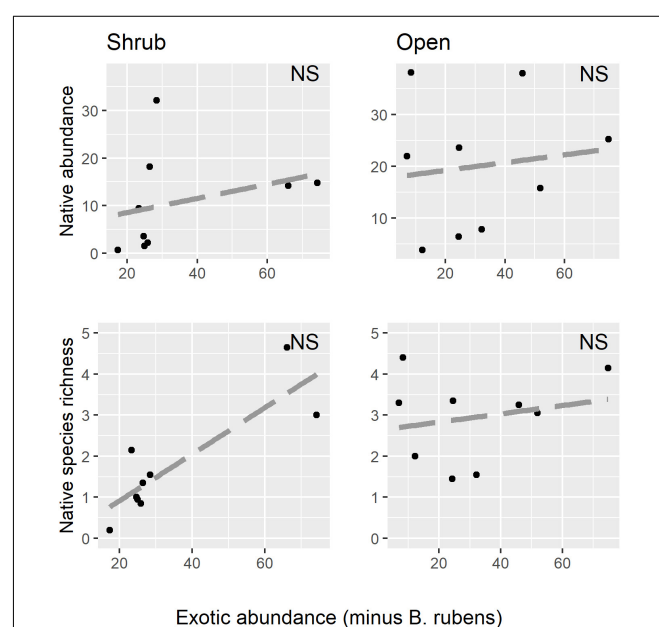


FIGURE 4 | Native abundance and native species richness (all native species combined) plotted against exotic abundance with *B. rubens* omitted from the data in shrub and open microsites. Note that there are no significant native-exotic relationships when *B. rubens* is omitted from the data.

they found that *B. rubens* formed stronger positive associations with native perennials than *Schismus* spp. or *E. cicutarium*. Our findings also coincide with reports that exotic annuals respond more strongly to positive interactions than native annuals at the provenance level. In a southern California rangeland, Lucero et al. (2019) found that exotic annuals as a group were facilitated over 2.75 times stronger in abundance than native annuals, and across the Mojave and San Joaquin Deserts, Lucero et al. (2020) found that positive associations were intense and important for invasive *B. rubens* but not the native annual community. By promoting plant invasions (Lortie et al., 2021), intense facilitation of invasive species can indirectly erode biodiversity and ecosystem functioning (Northfield et al., 2018). Thus, any community-level benefits of shrub facilitation may backfire when invasive species are strongly facilitated. Our work extends this literature to multiple invasive taxa interacting with native shrubs across a broad geographical scale that spans substantial environmental variability.

Our study highlights the precocious ability of invasive *Bromus* species to capitalize on native facilitators. Native shrubs, trees, and grasses across the Great Basin, Mojave, San Joaquin, and Colorado Plateau Deserts can increase the abundance, biomass, fitness, and population growth of *B. tectorum* (Belnap and Sherrod, 2008; Griffith, 2010; Kane et al., 2011; Lucero et al., 2021). Across the Mojave and San Joaquin Deserts, native perennials often strongly facilitate *B. rubens* (reviewed by Abella and Smith, 2013). In central California, invasive *B. diandrus* and *B. mollis* can be facilitated by native *Quercus douglasii* (Callaway et al., 1991). In this study, each invasive *Bromus* species we encountered (*B. rubens*, *B. tectorum*, *B. diandrus*) formed intense positive associations with native shrubs, regardless of environmental context. Taken together, this literature suggests that invasive *Bromus* species are broadly facilitated by native plants from a variety of functional groups and environments. We suggest that disrupting positive interactions from native facilitators may be a useful strategy for controlling *Bromus* invasions across western North America. For instance, herbicide applications to reduce invasive *Bromus* densities could be most cost-effective when focused under shrub canopies. Importantly, we acknowledge that invasive *Bromus* species do not necessarily need native facilitators to establish (Holzapfel and Mahall, 1999; Brooks and Berry, 2006; Lucero et al., 2021) or spread (Reid et al., 2006). Rather, our findings suggest that native shrubs can aggravate *Bromus* invasions by increasing their local densities and impacts.

Biotic interactions do not always become more positive as aridity increases. Meta-analyses across taxa and biomes have returned broad support for the prediction derived from the SGH that positive interactions become more important as environmental severity increases (Bertness and Callaway, 1994; Lortie and Callaway, 2006; He et al., 2013; Romero et al., 2015; Adams et al., 2022). However, with respect to aridity gradients in drylands, and especially with exotic species, support for the SGH has varied (Butterfield et al., 2016; Bashirzadeh et al., 2022). For instance, Lucero et al. (2021) showed that invasive *B. tectorum* formed strong positive associations with native shrubs along a substantial aridity gradient across the Great Basin, Mojave,

and San Joaquin Deserts, but relative aridity did not predict the intensity of these associations. Similarly, our analyses found no support for the SGH for any vegetation measure along our aridity gradient. It is possible that our gradient was too shallow to detect significant aridity-RII relationships, but our findings over a single growing season coincide with similar studies across much steeper aridity gradients (Lucero et al., 2021). We hypothesize that the intensity of shrub-invasive annual associations may not closely track aridity if invasive annuals are less limited by water than other resources, such as nutrients (Rao and Allen, 2010; Suazo et al., 2012; Bansal et al., 2014; Gill et al., 2018; see discussion below). In this context, an exciting next step would be to experimentally evaluate shrub facilitation of invasive species along multiple, interacting stress gradients.

Our findings indicate that desert shrubs can alter biotic interactions between invasive plants and their neighbors. Invasive species in deserts can inhibit native species in both shrub and open microsites (Brooks, 2000; Bishop et al., 2019), and many studies have investigated the potential for environmental factors to shift competitive outcomes (Hart and Marshall, 2013). Our study reinforces this literature by highlighting the potential for native shrubs to indirectly facilitate plant invasions by increasing the competitive impacts of invasive species (Lortie et al., 2021). We hypothesize that negative *B. rubens*-herbaceous neighbor relationships (evidence for competition) arose near but not away from shrubs due to relatively fertile soils near shrubs (Schlesinger et al., 1996) that ameliorated nutrient limitation and favored the performance of *B. rubens* over neighbors. Across the literature, nutrient enrichment almost always promotes the local dominance of invasive species (Brooks, 2003; Levine et al., 2004; Davis and Pelsor, 2008; Besaw et al., 2011). Of course, we do not discount the possibility that enhanced soil water near shrubs relative to open areas (Segoli et al., 2012) also bolstered the competitive impacts of *B. rubens* because water and nutrient availability act synergistically to affect plant performance (Rao and Allen, 2010; Suazo et al., 2012; Plett et al., 2020). These possibilities underscore the need to experimentally manipulate shrub-invasive annual interactions along mixed water and nutrient gradients. Importantly, this pattern arose only for *B. rubens*, suggesting that the risk of facilitated invasion (both directly *via* increased abundance and indirectly *via* increased impacts) is particularly high for this species across our study area. All of the invasive species we examined can negatively impact natives, but in our system, *B. rubens* appears to be the invader most responsible for displacing native annuals under shrubs, though experimentation is needed to confirm this.

This observational study did not test for mechanisms of species-specific facilitation, but the functional traits of our focal species may provide some clues (Funk et al., 2017). Facilitation in plant communities can arise *via* a number of pathways, including abiotic stress amelioration, herbivore protection, pollinator attraction, substrate modification, seed trapping, soil moisture retention, and soil nutrient enhancement (Flores and Jurado, 2003; Filazzola and Lortie, 2014). Not all shrub species are equal facilitators because not all shrub species have equal traits (McAuliffe, 1988). For instance, *Larrea tridentata*, the dominant shrub species across our Mojave Desert

sites, can be a relatively poor facilitator compared to other shrub species due to strong competitive effects and allelopathy (reviewed by Callaway, 2007), though we found limited evidence for this. A key mechanism that determines whether shrub-neighbor interactions are positive or negative is the match between what the shrub offers and what the beneficiary species requires (Paterno et al., 2016). Importantly, the offerings and requirements of species depend upon their functional traits (Funk et al., 2017). Thus, species-specific patterns of shrub-annual associations in our study likely reflect the unique functional traits of our focal species. In this context, our three most commonly encountered invasive annual species—*B. rubens*, *Schismus* spp., and *E. cicutarium*—have distinct physiological characteristics. Relative to other Mojave Desert species, *B. rubens* uses water very rapidly, has high N uptake, and high net assimilation; *Schismus* spp. has thin leaves, low leaf mass per area, and low leaf N content; and *E. cicutarium* may be less physiologically specialized than *B. rubens* or *Schismus* spp. (DeFalco et al., 2003; Steers et al., 2011). These trait sets suggest that *B. rubens* can rapidly capitalize on water and nutrient additions, *Schismus* spp. has relatively low N requirements, and *E. cicutarium* may have less specialized physiological requirements than *B. rubens* or *Schismus* spp. (DeFalco et al., 2003; Steers et al., 2011). These functional trait syndromes coincide nicely with our species-specific findings: *B. rubens* associated strongly and consistently with shrubs, perhaps due to its ability to rapidly capitalize on shrub-mediated resource additions; *Schismus* spp. consistently formed negative associations with shrubs, perhaps due to its relatively low requirements for shrub-mediated nutrient additions; and *E. cicutarium* varied in its spatial association with shrubs, perhaps due to its intermediate or facultative requirements for shrub-mediated resources. These possibilities present exciting avenues for future experimentation.

We found a pattern consistent with invasional meltdown in open microsites. Invasional meltdown, or positive interactions among exotic species (Simberloff and Von Holle, 1999), can accelerate the transformation of communities by exotic invaders (Braga et al., 2018). In this context, we found positive relationships between *B. rubens* abundance and exotic species richness in open microsites across the study area. This finding closely coincides with that of Lucero et al. (2021), which reported a positive relationship between *B. tectorum* abundance and exotic species richness in open microsites across the Great Basin Desert. Because our findings were based on abundance relationships, it is unclear if *B. rubens* directly facilitated exotic species richness, or if *B. rubens* and the broader exotic community capitalized on similar advantageous microsites away from shrubs. Experimentation is necessary to disentangle these possibilities and explain why these patterns emerged in open, not shrub, microsites. Again, we emphasize that we only detected this pattern for *B. rubens*.

CONCLUSION

Along an aridity gradient across the Mojave and San Joaquin Deserts, invasive annual species formed highly species-specific associations with native shrubs that varied from positive to negative. Interestingly, the direction and intensity of these associations were unaffected by shrub size or relative aridity, and we found correlative evidence that native shrubs exacerbated the negative impacts of *B. rubens* (but no other invader) on neighboring annuals. We conclude that native shrubs have considerable potential to increase the abundance and impacts of invasive plant species across broad spatial scales, but this potential may depend more upon invader identity than environmental severity.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

JL, CL, RC, and AF conceived the idea. JL collected the data, analyzed the data, and wrote the manuscript. RC, CL, and AF contributed to editorial input. All authors contributed substantially to the development of this manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.886690/full#supplementary-material>

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