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Positive associations with native shrubs are intense and important for an exotic invader but not the native annual community across an aridity gradient

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Abstract

Aim and Location: Positive interactions influence the assembly of plant communities globally, particularly in stressful environments such as deserts. However, few studies have measured the intensity and relative importance of positive interactions involving native and invasive species along aridity gradients. These measures are essential for predicting how dryland communities will respond to biological invasions and environmental change. Here, we measured the intensity and importance of positive associations formed between native shrubs and the annual plant community, which included highly invasive *Bromus madritensis* ssp. *rubens* ("*B. rubens*") and native neighbours, along an aridity gradient across the Mojave and San Joaquin Deserts.

Methods: Along the gradient, we sampled metrics of abundance and performance for invasive *B. rubens*, native annual species (pooled), exotic annual species (pooled) and all annual species (pooled) during peak flowering at 120 pairs of shrub and open microsites.

Results: Across the gradient, *B. rubens* occurred at far greater abundance, cover, biomass and fitness near shrubs than away from shrubs. When *Larrea tridentata* was the focal shrub, positive effects on *B. rubens* abundance and cover were least intense at the most arid sites under the shortest shrubs. The native annual community occurred at greater abundance, cover and species richness *away* from shrubs, regardless of relative aridity or shrub traits. Community-level species richness was greatest away from shrubs, but exotic species richness was similar in shrub and open microsites.

Main conclusions: Across two deserts, *B. rubens* formed intense and important positive associations with native shrubs that consistently improved its abundance, cover, biomass and fitness, and for abundance and cover, the intensity of *B. rubens*–*L. tridentata* associations depended upon relative aridity and shrub height. By strongly facilitating a dominant invader but not native- or community-level biodiversity, native shrubs provided the wrong kind of help to the annual plant community.

KEYWORDS

Bromus rubens, deserts, environmental gradients, facilitation, invasive species, positive interactions, shrubs, stress-gradient hypothesis

1 | INTRODUCTION

Positive interactions among species, or facilitation, play an important role in the organization of plant communities globally (Callaway, 2007; Holmgren & Scheffer, 2010) by enhancing biodiversity (Cavieres, Hernandez-Fuentes, Sierra-Almeida, & Kikvidze, 2015; McIntyre & Fajardo, 2014), ecosystem function (Cardinale, Palmer, & Collins, 2002) and multispecies coexistence (Gross, 2008; Losapio, De la Cruz, Escudero, Schmid, & Schob, 2018). Facilitation occurs when a foundation species (i.e. the facilitator) offsets biotic or abiotic stresses that would otherwise inhibit the performance, abundance or species richness of beneficiary species (mechanisms reviewed by Callaway, 2007; Filazzola & Lortie, 2014; Michalet & Pugnaire, 2016). Importantly, foundation plants are not always interchangeable—some foundation species are better facilitators than others (Callaway, 1998), and large plants can be better facilitators than small ones (Tewksbury & Lloyd, 2001). The strength and relative importance of facilitation can also depend upon environmental severity. The stress-gradient hypothesis (SGH) predicts that the frequency (Bertness & Callaway, 1994), intensity (le Roux & McGeoch, 2010) and importance (Bertness & Callaway, 1994; Callaway & Walker, 1997) of facilitation should increase with environmental stress such that positive interactions are most intense and most important in the most extreme environments. Here, intensity refers to the absolute impacts of biotic interactions, and importance refers to the impacts of biotic interactions relative to all other factors (Brooker et al., 2005). Positive interactions do occur even in mild environments (Holmgren & Scheffer, 2010), but there is relatively consistent empirical support for the SGH across taxa and biomes (see meta-analyses by Lortie & Callaway, 2006; He, Bertness, & Altieri, 2013; Romero, Goncalves-Souza, Vieira, & Koricheva, 2015; Dangles, Herrera, Caprio, & Lortie, 2018; but see Butterfield, Bradford, Armas, Prieto, & Pugnaire, 2016).

Evaluating positive interactions along stress gradients has particular relevance for explaining, predicting and managing the effects of biological invasions by exotic plant species in drylands. Plant invasions are a pervasive global change that can sharply reduce the biodiversity and function of native ecosystems (Bellard, Cassey, & Blackburn, 2016; Davis et al., 2019; Shah et al., 2014; Simberloff et al., 2013; Vila et al., 2011), including deserts (Balch, Bradley, D'Antonio, & Gomez-Dans, 2013; D'Anotonio & Vitousek, 1992). Most empirical studies of plant invasions have focused on negative interactions, that is competition and predation (reviewed by Jeschke et al., 2012; Maron & Vila, 2001; Mitchell et al., 2006; Roy, Lawson Handley, Schonrogge, Poland, & Purse, 2011), but positive interactions can also influence invasion trajectories (reviewed by Simberloff, 2006; Travaset & Richardson, 2014). In this context, native species in deserts can exacerbate plant invasions by strongly facilitating the abundance (Lucero et al., 2019; Schafer et al., 2012), performance (Holzapfel & Mahall, 1999) and population growth (Griffith, 2010) of invasive plant species, or by indirectly increasing the competitive effects of invasive species on native neighbours (Llambi, Hupp, Saez, & Callaway, 2018; Reisner, Doescher, & Pyke, 2015). There is some evidence that the intensity of positive interactions between native and invasive species can vary along environmental gradients (Badano, Villarroel, Bustamante, Marquet, & Cavieres, 2007; Saccone, Pages, Griel, & Michalet, 2010), but very few dryland studies have measured the intensity *and* importance of such interactions along an aridity gradient. This knowledge gap is significant because dryland ecosystems are predicted to become hotter and drier in the future (Abatzoglou & Kolden, 2011; Archer & Predick, 2008), which could favour the expansion of exotic plant species (Bradley, Blumenthal, Wilcove, & Ziska, 2010) and shift the frequency and importance of biotic interactions away from competition and towards facilitation (He et al., 2013).

In changing drylands, positive interactions can benefit exotic plant species more than their native competitors (Abella & Chiquione, 2018). For instance, Lucero et al. (2019) monitored associations between native shrubs and the annual plant community—including native and exotic taxa—over three years in a California desert and found that shrubs facilitated the abundance of exotic annual species 2.75 times stronger than native annual species. Interestingly, shrub–annual associations were least positive in the wettest years, which is consistent with the SGH. However, Lucero et al. (2019) explored a limited spatial scale that did not incorporate geographic variation in aridity and did not consider the *importance* of facilitation relative to other factors. Understanding variation in the intensity and importance of positive interactions involving native and invasive species along aridity gradients is essential for predicting how dryland communities will respond to biological invasions and environmental change (Badano et al., 2016; He et al., 2013).

The objective of this study was to investigate the extent that the highly invasive annual species *Bromus madritensis* ssp. *rubens* ("*B. rubens*" hereafter) and the co-occurring native annual community associate with native shrubs along an aridity gradient across the Mojave and San Joaquin Deserts—a large portion of the non-native range of *B. rubens*. Specifically, we examined the hypothesis that positive shrub-mediated interactions would be most intense and most important in the most arid environments. We tested the following predictions: (a) *B. rubens* achieves greater abundance, cover, biomass and fitness near native shrubs than away from shrubs, (b) the native annual community achieves greater abundance, cover, and species richness near native shrubs; (c) shrub-related effects on the annual plant community are influenced by the identity and size of shrubs; and (d) the intensity and importance of shrub–annual associations increase with relative aridity. To better understand interactions between *B. rubens* and the native annual community, we correlated the abundance of *B. rubens* with that of native annuals near and away from shrubs.

2 | METHODS

2.1 | Study area and species

We surveyed annual plant communities at peak flowering in April 2019 at six sites that spanned an aridity gradient (see Table A1 for site names, locations and aridity values) across the Mojave (n = 3) and San Joaquin (n = 3) Deserts, USA (Germano et al., 2011). Sites in the Mojave Desert were located near the cities of Mesquite, NV; Las Vegas, NV; and Mojave, 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 any major disturbance (e.g. fire). One site (Carrizo) was grazed by cattle during the study year, but all others were free from grazing. For each site, we calculated the de Martonne aridity index (A_{dM}) (de Martonne, 1920) during the study year as follows:

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

where P was the total precipitation (mm) from 1 May 2018 to 30 April 2019, and T was the mean annual temperature (°C) during the same interval. Thus, low A_{dM} values indicated high aridity. We chose this index because its components are recorded at practically all weather stations, which facilitates direct calculations of A_{dM} at fine spatio-temporal scales relevant to biotic interactions in local communities. We also calculated a 20-year A_{dM} value for each site by averaging yearly A_{dM} values over the last 20 years (2000–2019). Importantly, our statistical analyses used the A_{dM} of the study year (2018–2019), not the 20-year average, because long-term climatic trends are less relevant to the establishment and performance of *B. rubens* than current trends, as *B. rubens* seed banks persist less than two years in the field (Jurad, Abella, & Suazo, 2013).

Sites in the Mojave Desert were dominated primarily by the native shrub *Larrea tridentata*, but the native perennials *Ambrosia dumosa*, *Lycium andersonii*, *Yucca brevifolia* and *Y. utahensis* were also present at relatively low densities. Sites in the San Joaquin Desert were dominated almost exclusively by the native shrub *Ephedra californica*, but the native perennial *Agave americana* was present at low densities at one site (Cuyama). Here, we focused on the potential for native shrub species to act as facilitators because they are the dominant physiognomic class across our study area (Pan et al., 2015). All sites were invaded by the exotic annual species *B. rubens*, *Schismus* spp. and *Erodium cicutarium*. *Bromus diandrus* was present at low densities at the Cuyama and Carrizo sites. Among these exotic species, we chose to focus on *B. rubens* because it is reported as one of the region's most problematic invasive species (Hunter, 1991; Salo, 2004) due to strong negative impacts on community-level biodiversity (Brooks, 2000; Salo, 2005) and historic fire cycles (Abatzoglou & Kolden, 2011; Brooks et al., 2004; Fusco, Finn, Balch, Nagy, & Bradley, 2019). During the study year, annual precipitation, mean annual temperature and A_{dM} at the study sites ranged from 97.70 to 303.53 mm, 17.45 to 21.98°C and 3.56 to 10.25 (A_{dM} is generally expressed without units), respectively. Twenty-year A_{dM} values ranged from 3.45 to 11.70, a range similar to the study year. At each site, the A_{dM} for the study year fell within the 95% CI of the 20-year A_{dM}, except at the Las Vegas and Carrizo sites, which were more and less arid, respectively, than usual (Table A1). Importantly, our study sites represented a moderate sampling of A_{dM} values potentially experienced by *B. rubens* populations across the non-native range. For comparison, the 20-year A_{dM} near Death Valley, CA (the extreme arid end), is 1.71, and the 20-year A_{dM} near Cedar City, UT (the extreme mesic end), is 14.62. Twenty-year and current-year A_{dM} values for our study sites fell well within these extremes.

2.2 | Sampling

We sampled the annual plant community using a paired shrub–open microsite contrast with a 0.5 × 0.5 m quadrat subdivided into 100, 5-cm^2 frames (Pescador, Chacon-Labella, de la Cruz, & Escudero, 2014). Shrub microsites were defined as the area immediately beneath the canopy of a shrub, and open microsites were defined as interstitial spaces at least 1 m from any shrub canopy. For shrub microsites, sampling quadrats were placed midway between the shrub centre and dripline. We did not sample areas more than 5 m away from shrubs. A total of 120 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 height (m) and species of the shrub. Shrub–open pairs for sampling were chosen haphazardly at each site. In the Mojave, focal shrubs were *L. tridentata* (n = 44), *Ambrosia dumosa* (n = 13) and *Lycium andersonii* (n = 3). 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. of plants rooted inside the quadrat) and percentage cover (percentage of quadrat frames with a plant rooted inside) of *B. rubens* and native species (pooled), as well as the richness of native species, exotic species, and all species combined. Relationships among these particular measures are used to describe the invasiveness and impacts of exotic species in non-native communities (Pearson, Ortega, Ozkan, & Hierro, 2016). For all species, individual plants were easy to distinguish because asexual reproduction is absent. In addition, we haphazardly collected a single *B. rubens* individual from each quadrat and counted the number of spikelets produced on the longest inflorescence, as a proxy for fitness. We transported collected *B. rubens* plants back to the laboratory in individual paper sacks and measured the aboveground biomass (g) of each after drying to constant mass at 70°C for 72 hr, as a proxy for plant performance (Holzapfel & Mahall, 1999).

2.3 | Statistical analyses

Relative interaction indices (RIIs; Armas, Ordinales, & Pugnaire, 2004) were used to estimate the intensity of shrub-mediated effects on the annual plant community. We calculated RIIs as follows:

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

where M_s was a vegetation measure (e.g. *B. rubens* abundance, species richness) 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 (antagonistic) associations between shrubs and annuals, positive values indicate positive (facilitative) associations, and a value of 0 indicates no (neutral) association.

We estimated the importance of shrub-mediated effects on the annual plant community using the I_{imp} index (Seifan, Seifan, Ariza, & Tielbörger, 2010). We calculated I_{imp} as follows:

$$I_{\mathrm{imp}} = \frac{N_{\mathrm{imp}}}{\left|N_{\mathrm{imp}} + E_{\mathrm{imp}}\right|}$$

where N_{imp} was the contribution of shrub-mediated interactions to a particular vegetation measure (e.g. *B. rubens* abundance, species richness), and E_{imp} was the environmental contribution to the same measure. These components and their calculation are fully explained by Seifan et al. (2010). Like RII, I_{imp} values range from −1 to + 1. Negative I_{imp} values indicate that negative (antagonistic) interactions are relatively important drivers of a vegetation measure, positive values indicate that positive (facilitative) interactions are relatively important drivers of a vegetation measure, and a value of 0 indicates that shrub-mediated interactions are relatively unimportant. We used the I_{imp} index because it is symmetrical around zero and unbiased towards positive or negative interactions (Seifan & Seifan, 2015).

We used *t* tests and linear mixed-effects models to characterize associations between native shrubs and the annual plant community. To evaluate the direction and magnitude of the intensity and importance of shrub–annual associations across all study sites, we performed independent one-sample *t* tests with RII or I_{imp} (averaged at the site level) as the response variable. We evaluated the effects of aridity and shrub traits on the intensity and importance of shrub–annual associations using independent linear mixed-effects models with RII or I_{imp} as the response variable: A_{dM}, shrub species and shrub height as fixed factors; and study site as a random factor. To better understand the ability of *E. californica*, *L. tridentata* and *A. dumosa* to act as facilitators, we used independent linear mixed-effects models for each shrub species with RII as the response variable; A_{dM} and shrub height as fixed factors; and study site as a random factor. We could not explicitly consider *L. andersonii* because this shrub was surveyed at only one study site (Las Vegas). We contrasted the absolute magnitude of vegetation measures taken in shrub and open microsites at each study site using independent linear mixed-effects models with vegetation measure as the response variable; microsite (shrub vs. open) as a fixed factor; and shrub–open pair replicate as a random factor. We examined the effects of aridity on *B. rubens* invasion success using a linear mixed-effects model with absolute *B. rubens* abundance (log-transformed, a proxy for invasion success) as the response variable; microsite (open vs. shrub) and A_{dM} as fixed factors; and study site as a random factor. We inferred the effects of microsite (shrub vs. open) and aridity on biotic interactions between *B. rubens* and native annuals using a linear mixed-effects model with native abundance (all species combined; log-transformed) as the response variable; *B. rubens* abundance (log-transformed), microsite and A_{dM} as fixed factors; and study site as a random factor. In this analysis, negative line slopes suggest competitive *B. rubens*–native annual interactions, and positive line slopes suggest facilitative interactions.

All analyses were performed in R, version 3.5.1 (R Development Core Team, 2018). All linear mixed-effects models used the lmer function of the "lmerTest" package (Kuznetsova, Brockhoff, & Christensen, 2017), which uses Satterthwaite's method to calculate denominator degrees of freedom (*df* hereafter). Post hoc Tukey contrasts were estimated using the emmeans function of the "emmeans" package (Lenth, Singmann, Love, Buerkner, & Herve, 2018). We did *t* tests using the t.test function (R Development Core Team, 2018).

3 | RESULTS

Bromus rubens formed exceptionally intense (based on RII) and important (based on I_{imp}) positive associations with native shrubs. At each site, *B. rubens* abundance, cover, biomass and spikelet production (i.e. fitness) were at least 2.52 (and up to 70.47) times greater in shrub microsites than in open microsites (Table A2), and RII (Figure 1) and I_{imp} (Figure 2) values for these metrics were always positive. Exotic species richness (which included *B. rubens*) was consistently similar in shrub and open microsites (Table A2), and RII (Figure 1) and I_{imp} (Figure 2) values never differed from zero.

In contrast, the native annual community did not associate positively with native shrubs. At the site level, native abundance, cover and species richness did not always differ by microsite but were never greater in shrub microsites (Table A2). Hence, RII (Figure 1) and I_{imp} (Figure 2) values for native annuals varied by site but were never positive. Similarly, RII (Figure 1) and I_{imp} (Figure 2) values for total species richness (all species combined) varied by site but were never positive.

Shrub traits and relative aridity influenced the intensity of some shrub–annual associations (Table 1), but never importance (Table 2). When *L. tridentata* was the focal shrub (Table 3), RII values for *B. rubens* abundance and cover were least positive (though never negative) at the most arid sites when shrubs were shortest (Figure 3). No other RII (Table 1) or I_{imp} (Table 2) measurement was influenced by relative aridity, shrub species or shrub height.

We found no spatially based evidence of biotic interactions between *B. rubens* and the native annual community (Figure A2). *Bromus rubens* abundance had no relationship with native abundance in any microsite or aridity context (Table 4). However, we reemphasize that microsite had a strong effect on the absolute abundance of *B. rubens* across the entire aridity gradient (Table A3).

4 | DISCUSSION

Invasive *B. rubens* formed intense and important positive associations with native shrubs that consistently improved its abundance, cover, biomass and fitness across a large portion of the non-native range. The intensity of positive interactions for *B. rubens* abundance—a critical metric of invasion success (Pearson et al., 2016)—was exceptionally high, ranging from RIIs of 0.66 (Panoche Hills) to 0.97 (Cuyama) and averaging 0.83 across all sites. To put this in context, Cavieres et al. (2014) found RIIs that averaged 0.40 and did not exceed 0.80 in a global study of 78 alpine communities, systems characterized by intense facilitation. In addition, consistently positive I_{imp} values suggest that, relative to other factors, shrub-mediated interactions played an important role in increasing the local abundance of *B. rubens* across the entire aridity gradient. Interestingly, when *L. tridentata* was the focal shrub, the intensity (RII) of shrub-related effects on *B. rubens* abundance and cover was least positive (though never negative) under the shortest shrubs at the most arid sites. Otherwise, aridity did not predict the intensity or importance of *B. rubens*–native shrub associations. Hence, positive associations between *B. rubens* and native shrubs did not follow predictions derived from the SGH. In stark contrast to *B. rubens*, the native annual community generally formed *negative* associations with shrubs, regardless of aridity or shrub traits. Taken together, these findings suggest that native shrubs mediated biotic interactions that generally benefitted *B. rubens* but not the native annual community.

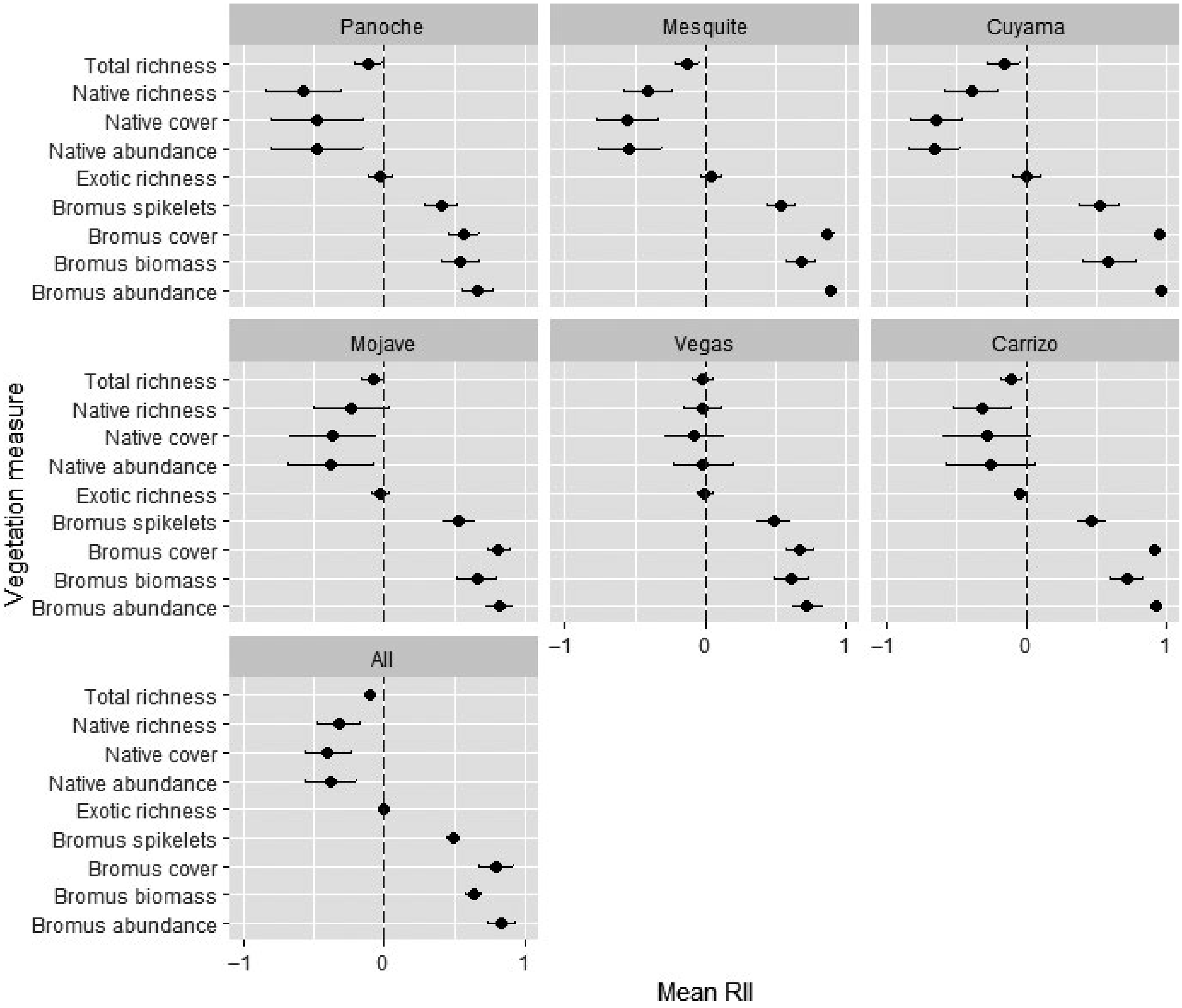

FIGURE 1 Mean intensity (RII ± 95% CI) of shrub-mediated effects on the annual plant community at each of six study sites spanning an aridity gradient across the Mojave and San Joaquin Deserts, and averaged across all sites ("All"), according to independent one-sample *t* tests with RII as the response variable. RII > 0 suggests positive (i.e. facilitative) effects, and RII < 0 suggests negative (i.e. antagonistic) effects. Study sites are arranged from the least arid (Panoche) to the most arid (Carrizo). See Table A6 for complete statistics

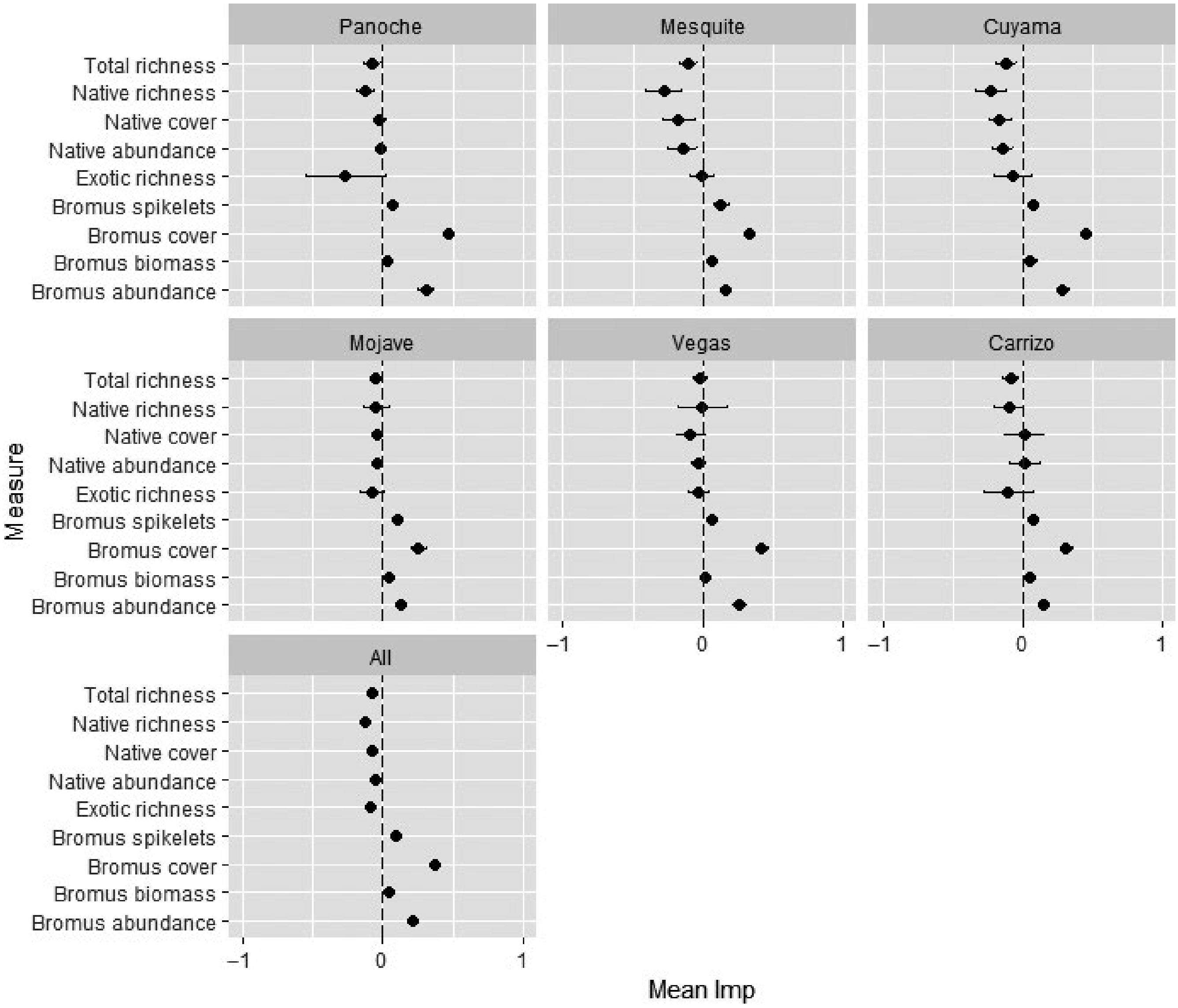

FIGURE 2 Mean importance (I_{imp} ± 95% CI) ("Imp") of shrub-mediated effects on the annual plant community at each of six study sites spanning an aridity gradient across the Mojave and San Joaquin Deserts, and averaged across all sites ("All"), according to independent one-sample *t* tests with I_{imp} as the response variable. $I_{imp} > 0$ suggests that positive (i.e. facilitative) shrub-mediated interactions are important, and $I_{imp} < 0$ suggests that negative (i.e. antagonistic) shrub-mediated interactions are important. Panel arrangement follows Figure 1. See Table A6 for complete statistics

Our findings coincide with a growing number of studies reporting strong facilitation of exotic plant species by native species. Positive interactions among exotic species are common (reviewed by Simberloff, 2006), and such "invasional meltdown" (Simberloff & Von Holle, 1999) is a key concept in invasion biology (Jeschke et al., 2012). The potential for native plant species to facilitate invasive species has received surprisingly little attention (Gallien & Carboni, 2017), but there are striking examples in the genus *Bromus*. Griffith (2010) experimentally showed that the native shrub species *Artemisia tridentata* strongly facilitated the population growth of *B. tectorum*, a highly invasive congener of *B. rubens*, in the Great Basin Desert. In central California, Callaway, Nadkarni, and Mahall (1991) found that under certain circumstances, native *Quercus douglasii* facilitated invasive *B. diandrus* and *B. mollis*. In the San Joaquin Desert, near one of our study sites (Carrizo), Lucero et al. (2019) showed that native shrubs generally facilitated the abundance of exotic annual species, including *B. rubens*, much more than native annual species, and Abella and Chiquione (2018) reported a similar pattern in a long-term experimental study in the Mojave Desert. The present study provides further evidence that exotic invaders can capitalize on positive interactions to a greater extent than native competitors, and extends this evidence to a regional scale. In addition to describing the intensity of such positive interactions, we also evaluated their relative importance. Measuring the intensity *and* importance of biotic interactions is essential for understanding the capacity of competition and facilitation to influence community assembly in general (Brooker et al., 2005) and the trajectory of biological invasions in particular. In this context, we suggest

TABLE 1 Results of independent linear mixed-effects models testing the influence of relative aridity and shrub traits on the intensity of shrub–annual associations along an aridity gradient spanning the Mojave and San Joaquin Deserts

	Fixed factor						
RII measure	**A_{dM}**	**Shrub species**	**Shrub height**	**A_{dM} × Species**	**A_{dM} × Height**	**Species × Height**	**A_{dM} × Species ×Height**
B. rubens biomass	$F_{1,103.00} = 0.003$ $p = .956$	$F_{3,103.00} = 0.521$ $p = .669$	$F_{1,103.00} = 0.217$ $p = .642$	$F_{2,103.00} = 0.946$ $p = .391$	$F_{1,103.00} = 0.238$ $p = .627$	$F_{3,103.00} = 0.870$ $p = .459$	$F_{2,103.00} = 1.236$ $p = .295$
B. rubens spikelet	$F_{1,84.94} = 0.720$ $p = .397$	$F_{3,90.46} = 1.009$ $p = .392$	$F_{1,100.86} = 0.668$ $p = .416$	$F_{2,84.96} = 0.873$ $p = .421$	$F_{1,100.87} = 1.321$ $p = .253$	$F_{3,100.89} = 1.056$ $p = .372$	$F_{2,100.92} = 1.247$ $p = .292$
B. rubens abundance	$F_{1,59.35} = 2.490$ $p = .120$	**$F_{3,73.39} = 5.390$** **$p = .002$**	$F_{1,103.16} = 1.627$ $p = .205$	**$F_{2,62.93} = 5.471$** **$p = .006$**	$F_{1,103.17} = 1.133$ $p = .290$	**$F_{3,103.17} = 3.267$** **$p = .023$**	$F_{2,103.18} = 2.761$ $p = .068$
B. rubens cover	$F_{1,25.35} = 2.626$ $p = .117$	**$F_{3,41.16} = 6.632$** **$p = .001$**	$F_{1,103.03} = 2.167$ $p = .142$	**$F_{2,31.01} = 6.537$** **$p = .004$**	$F_{1,103.04} = 1.643$ $p = .203$	**$F_{3,103.04} = 4.365$** **$p = .006$**	**$F_{2,103.05} = 3.572$** **$p = .032$**
Native abundance	$F_{1,28.90} = 0.074$ $p = .787$	$F_{3,45.27} = 0.212$ $p = .888$	$F_{1,97.99} = 0.045$ $p = .833$	$F_{2,35.77} = 0.065$ $p = .938$	$F_{1,98.00} = 0.012$ $p = .912$	$F_{3,98.00} = 0.183$ $p = .908$	$F_{2,98.05} = 0.008$ $p = .992$
Native cover	$F_{1,39.42} = 0.036$ $p = .850$	$F_{3,55.92} = 0.137$ $p = .937$	$F_{1,98.00} = 0.089$ $p = .766$	$F_{2,46.01} = 0.050$ $p = .951$	$F_{1,98.02} = 0.041$ $p = .840$	$F_{3,98.02} = 0.127$ $p = .944$	$F_{2,98.08} = 0.015$ $p = .985$
Native richness	$F_{1,100.00} = 0.025$ $p = .622$	$F_{3,100.00} = 0.170$ $p = .917$	$F_{1, 100.00} = 0.043$ $p = .837$	$F_{2,100.00} = 0.249$ $p = .780$	$F_{1,100.00} = 0.037$ $p = .847$	$F_{3,100.00} = 0.089$ $p = .966$	$F_{2,100.00} = 0.121$ $p = .887$
Exotic richness	$F_{1,105.00} = 0.420$ $p = .518$	$F_{3,105.00} = 0.701$ $p = .550$	$F_{1,105.00} = 0.293$ $p = .590$	$F_{2,105.00} = 0.643$ $p = .528$	$F_{1,105.00} = 0.281$ $p = .597$	$F_{3,105.00} = 0.498$ $p = .685$	$F_{2,105.00} = 0.367$ $p = .694$
Total richness	$F_{1,105.00} = 0.189$ $p = .665$	$F_{3,105.00} = 0.255$ $p = .858$	$F_{1,105.00} = 0.028$ $p = .868$	$F_{2,105.00} = 0.031$ $p = .970$	$F_{1,105.00} = 0.000$ $p = .998$	$F_{3,105.00} = 0.319$ $p = .812$	$F_{2,105.00} = 0.079$ $p = .924$

Note: RII was the response variable; de Martonne aridity (A_{dM}), shrub species ("Species") and shrub height ("Height") were fixed factors; and study site was a random factor (not shown). Significant (i.e. $p < .05$) effects appear in bold.

TABLE 2 Results of independent linear mixed-effects models testing the influence of relative aridity and shrub traits on the importance of shrub–annual associations along an aridity gradient spanning the Mojave and San Joaquin Deserts

	Fixed factor						
I_{imp} measure	A_{dM}	Shrub species	Shrub height	A_{dM} × Species	A_{dM} × Height	Species × Height	A_{dM} × Species ×Height
B. rubens biomass	$F_{1,79.32} = 0.137$ $p = .712$	$F_{3,86.84} = 0.920$ $p = .435$	$F_{1,100.77} = 0.201$ $p = .656$	$F_{2,79.93} = 0.327$ $p = .722$	$F_{1,100.77} = 0.689$ $p = .422$	$F_{3,100.79} = 1.861$ $p = .141$	$F_{2,100.82} = 1.146$ $p = .322$
B. rubens spikelet	$F_{1,40.07} = 1.538$ $p = .222$	$F_{3,56.81} = 0.617$ $p = .607$	$F_{1,100.87} = 3.106$ $p = .081$	$F_{2,45.08} = 0.824$ $p = .445$	$F_{1,100.87} = 4.300$ $p = .061$	$F_{3,100.88} = 1.162$ $p = .328$	$F_{2,100.89} = 2.163$ $p = .120$
B. rubens abundance	$F_{1,6.092} = 0.168$ $p = .696$	$F_{3,14.565} = 0.695$ $p = .570$	$F_{1,102.99} = 0.590$ $p = .444$	$F_{2,10.56} = 0.453$ $p = .647$	$F_{1,102.99} = 0.250$ $p = .620$	$F_{3,102.99} = 0.368$ $p = .777$	$F_{2,103.00} = 0.567$ $p = .945$
B. rubens cover	$F_{1,5.00} = 0.560$ $p = .488$	$F_{3,13.22} = 0.917$ $p = .459$	$F_{1,102.99} = 1.724$ $p = .192$	$F_{2,9.65} = 0.708$ $p = .517$	$F_{1,102.99} = 0.841$ $p = .361$	$F_{3,102.99} = 0.424$ $p = .736$	$F_{2,103.00} = 0.169$ $p = .845$
Native abundance	$F_{1,36.35} = 0.707$ $p = .406$	$F_{3,53.20} = 0.027$ $p = .994$	$F_{1,98.13} = 0.213$ $p = .646$	$F_{2,43.29} = 0.087$ $p = .917$	$F_{1,98.15} = 0.308$ $p = .580$	$F_{3,98.15} = 0.141$ $p = .935$	$F_{2,98.20} = 0.042$ $p = .959$
Native cover	$F_{1,44.37} = 0.354$ $p = .850$	$F_{3,60.63} = 0.019$ $p = .937$	$F_{1,98.15} = 0.070$ $p = .766$	$F_{2,50.84} = 0.017$ $p = .951$	$F_{1,98.18} = 0.127$ $p = .840$	$F_{3,98.17} = 0.156$ $p = .944$	$F_{2,98.23} = 0.088$ $p = .985$
Native richness	$F_{1,85.45} = 2.829$ $p = .096$	$F_{3,90.41} = 1.346$ $p = .264$	$F_{1, 99.34} = 0.237$ $p = .627$	$F_{2,86.30} = 1.887$ $p = .158$	$F_{1,99.37} = 0.458$ $p = .492$	$F_{3,99.36} = 0.616$ $p = .606$	$F_{2,99.46} = 0.459$ $p = .633$
Exotic richness	$F_{1,105.00} = 0.000$ $p = .991$	$F_{3,105.00} = 0.885$ $p = .452$	$F_{1,105.00} = 0.032$ $p = .858$	$F_{2,105.00} = 0.628$ $p = .536$	$F_{1,105.00} = 0.002$ $p = .961$	$F_{3,99.37} = 0.895$ $p = .447$	$F_{2,105.00} = 0.450$ $p = .639$
Total richness	$F_{1,105.00} = 0.508$ $p = .478$	$F_{3,105.00} = 0.568$ $p = .638$	$F_{1,105.00} = 0.000$ $p = .995$	$F_{2,105.00} = 0.346$ $p = .708$	$F_{1,105.00} = 0.038$ $p = .845$	$F_{3,105.00} = 0.499$ $p = .686$	$F_{2,105.00} = 0.165$ $p = .848$

Note: I_{imp} was the response variable; de Martonne aridity (A_{dM}), shrub species ("Species"), and shrub height ("Height") were fixed factors; and study site was a random factor (not shown). Note that there are no significant effects.

TABLE 3 Results of independent linear mixed-effects models testing the influence of relative aridity and shrub height on the intensity of associations between *Bromus rubens* and the native shrubs *Ephedra californica*, *Larrea tridentata* or *Ambrosia dumosa* along an aridity gradient that spanned the Mojave Desert portion of the study

RII measure	Shrub species	Fixed factor		
		A_{dM}	Height	A_{dM} × Height
B. rubens abundance	*E. californica*	$F_{1,13.93} = 3.600$; $p = .079$	$F_{1,55.01} = 0.134$; $p = .716$	$F_{1,55.04} = 0.340$; $p = .563$
	L. tridentata	**$F_{1,39.00} = 6.120$; $p = .017$**	**$F_{1,39.00} = 6.087$; $p = .018$**	**$F_{1,39.00} = 4.791$; $p = .035$**
	A. dumosa	$F_{1,9.00} = 1.682$; $p = .227$	$F_{1,9.00} = 0.670$; $p = .434$	$F_{1,9.00} = 0.143$; $p = .714$
B. rubens cover	*E. californica*	$F_{1,8.56} = 3.120$; $p = .190$	$F_{1,55.01} = 0.002$; $p = .990$	$F_{1,55.02} = 0.001$; $p = .971$
	L. tridentata	**$F_{1,15.48} = 10.561$; $p = .005$**	**$F_{1,38.02} = 12.513$; $p = .001$**	**$F_{1,39.01} = 9.446$; $p = .004$**
	A. dumosa	$F_{1,9.00} = 1.094$; $p = .323$	$F_{1,9.00} = 0.211$; $p = .664$	$F_{1,9.00} = 0.000$; $p = .999$

Note: RII for *B. rubens* abundance (log-transformed) or cover was the response variable; de Martonne aridity (A_{dM}) and shrub height ("Height") were fixed factors; and study site was a random factor (not shown). Significant (i.e. $p < .05$) effects appear in bold. RII for other vegetation measures did not vary with respect to shrub species (Table 1), and are thus not shown. Results specific to *L. tridentata* are displayed in Figure 3.

that positive interactions mediated by native shrubs can play an important role in increasing the abundance, cover, biomass and fitness of *B. rubens* in the non-native range. Beyond deserts, examples of native-facilitated plant invasions come from alpine (Cavieres, Quiroz, & Molina-Montenegro, 2008; Hupp, Llambi, Ramirez, & Callaway, 2017), coastal (Altieri, van Wesenbeeck, Bertness, & Silliman, 2010), sand dune (Cushman, Lortie, & Christian, 2011) and forest (Saccone et al., 2010) ecosystems, suggesting that native-facilitated invasions may be widespread.

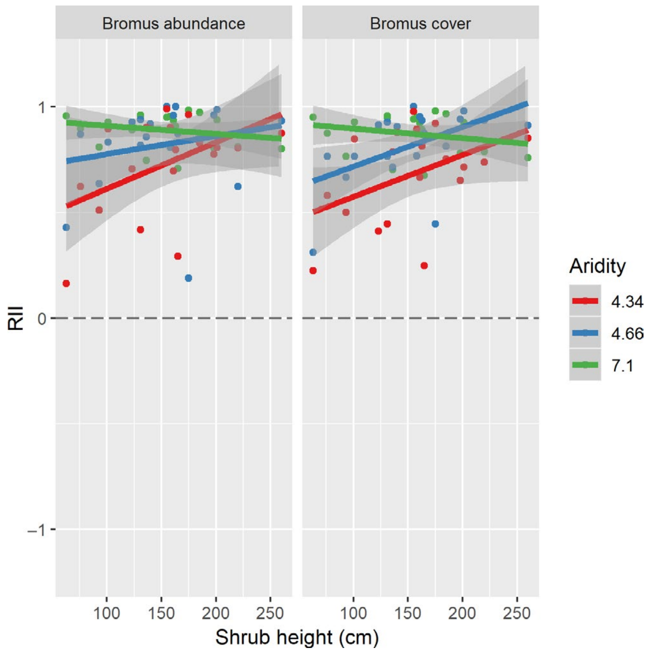

FIGURE 3 Results of independent linear mixed-effects models testing the influence of shrub height and relative aridity on the intensity of associations between *Bromus rubens* ("*Bromus*") and the native shrub *Larrea tridentata* at three sites spanning an aridity gradient across the Mojave Desert portion of our study. RII for *Bromus* abundance (log-transformed) or cover was the response variable; shrub height (cm) and de Martonne aridity ("Aridity"; low values indicate high aridity) were fixed factors; and study site was a random factor. See Table 3 for complete statistics. Regressions show ± 95% CI. Table A1 links aridity values to site locations

Our main findings challenge the paradigm that positive interactions in deserts always act as an insurance for maintaining species diversity—it depends on the species or functional role that is being facilitated (He et al., 2013). Numerous studies in deserts have shown that positive interactions enhance the abundance, performance or species richness of the annual plant community (reviewed by Callaway, 2007). Such facilitation can potentially buffer desert communities against current and future environmental change (He et al., 2013), which may include increased aridity and invasion by exotic plant species (Abatzoglou & Kolden, 2011; Archer & Predick, 2008; Bradley et al., 2010; Curtis & Bradley, 2015). Accordingly, positive interactions mediated by trees, shrubs and cacti have been touted as an "insurance" (Michalet, 2006) for dryland biodiversity (see also Cavieres et al., 2015). This may often be the case, but we found that shrubs did not facilitate any community-level measure of biodiversity considered here (i.e. native species richness, exotic species richness, whole-community species richness) and actually appeared to reduce the species richness of the annual plant community across all sites. Crucially however, we hypothesize that negative RII and I_{imp} values for native annuals arose indirectly via the competitive effects of shrub-facilitated *B. rubens* rather than any direct effects of shrubs themselves, although our current spatial data cannot support this (see Discussion below). In this context, Reisner et al. (2015) found that shrub facilitation by *A. tridentata* destabilized Great Basin plant communities by enhancing the ability of invasive *B. tectorum* to competitively exclude native neighbours, especially where environmental stress was highest. Similarly, strong facilitation of *B. rubens* may threaten the stability of plant communities across

TABLE 4 Results of a linear mixed-effects model testing the influence of *Bromus rubens* abundance, microsite (shrub vs. open) and relative aridity on the abundance of native annuals along an aridity gradient spanning the Mojave and San Joaquin Deserts

Response	Fixed factor						
	Bromus abundance	Microsite	A_{dM}	*Bromus* × Microsite	*Bromus* × A_{dM}	Microsite × A_{dM}	*Bromus* × Microsite × A_{dM}
Native abundance	$F_{1,203.51} = 0.834$ $p = .363$	$F_{1,229.128} = 0.621$ $p = .431$	$F_{1,67.32} = 1.361$ $p = .248$	$F_{1,229.70} = 0.800$ $p = .3723$	$F_{1,198.56} = 0.211$ $p = .647$	$F_{1,228.98} = 0.861$ $p = .354$	$F_{1,229.70} = 0.707$ $p = .402$

Note: Absolute native abundance (pooled across all species; log-transformed) was the response variable; absolute *B. rubens* ("*Bromus*") abundance (log-transformed), microsite and de Martonne aridity (A_{dM}) were fixed factors; and study site was a random factor (not shown). Note that there are no significant effects.

the Mojave and San Joaquin Deserts (see Bishop, Gill, McMillan, & St. Clair, 2019). Thus, positive interactions involving strong invaders do not necessarily promote community-level biodiversity and can indirectly erode it.

As noted above, intense and important facilitation of *B. rubens* may have disrupted the ability of the native annual community to form positive associations with shrubs. A rich literature documents the ability of invasive plant species to degrade native communities by disrupting mutualisms (reviewed by Travaset & Richardson, 2014). To this point, over twenty years ago, Holzapfel and Mahall (1999) quantified associations between the native shrub *L. tridentata* and the annual plant community in the Mojave Desert and, contrary to our findings, reported that the annual plant community, including *B. rubens* and native species, generally formed positive associations with this shrub species. Importantly, the relative abundance of *B. rubens* was much lower in the study of Holzapfel and Mahall (1999) than in our study, hinting that high levels of *B. rubens* invasion might be necessary to disrupt positive shrub–native annual associations. If so, we might expect strong competitive interactions between *B. rubens* and the native annual community under shrubs (Salo, 2005), as experimentally demonstrated by Brooks (2000). However, we found no evidence for this, regardless of relative aridity. There are several potential explanations for this. First, we observed relatively little variation in native abundance under shrubs, which may have reduced our ability to detect evidence for competitive interactions via spatial abundance relationships. Alternatively, our study may not have been conducted at the appropriate temporal stage of invasion to find evidence for competition in action. Said differently, the damage of *B. rubens* competition under shrubs—the depletion of the native annual community—may have already been done (note that there were no shrubs without *B. rubens* beneath them; Figure A2). Furthermore, the effects of exotic annuals on native neighbours can fluctuate year to year, ranging from negative in some years to positive in others (Lucero et al., 2019; see also Brooks, 2000), and we may have simply missed strong competition. Finally, *B. rubens* is not the only invasive annual that could disrupt positive associations between shrubs and native annuals. All study sites were invaded by exotic *Schismus* spp. and *E. cicutarium*. Both can be facilitated by native shrubs (Holzapfel & Mahall, 1999; Lucero et al., 2019; but see Brooks & Berry, 2006), and both can impose competitive effects on native annuals (Bishop et al., 2019; Schutzenhofer & Valone, 2006). Thus, besides or in addition to *B. rubens*, *Schismus* spp. and *E. cicutarium* could potentially influence the outcome of shrub–native annual interactions and contribute to depauperate native annual communities under shrubs. Experimental addition or removal of these exotic annual species to shrub and open microsites where native annuals are established (sensu Brooks, 2000) could more clearly elucidate how exotic invaders influence the outcome of associations between shrubs and native annuals.

Our data reinforce the idea that the SGH does not uniformly "hold water" (Butterfield et al., 2016). Recently, Butterfield et al. (2016) drew attention to the mixed empirical support the SGH has received along aridity gradients in drylands. To date, most studies have examined facilitation using coarse biodiversity metrics, especially species richness at the community level (Vega-Alvarez, Garcia-Rodriguez, & Cayuela, 2019), a very conservative approach. We found little evidence for the SGH, but like most studies, our surveys included coarse biodiversity metrics, with the exception of more-detailed surveys of *B. rubens* performance. Furthermore, our study area sampled a modest range of aridity values potentially experienced by *B. rubens* populations across the non-native range, and our results may have differed had we included more arid or mesic locations in our surveys. Finally, RII values for *B. rubens* were exceptionally high and varied relatively little along our aridity gradient (see Cavieres et al., 2014, for an example of wider-ranging RII values), which may have reduced the power of our regressions (but see results specific to *B. rubens*–*L. tridentata* associations; Table 3). Given these considerations, it may not be particularly surprising that the SGH did not “hold water” here (see also Metz & Tielbörger, 2016).

It is unclear why RII values for *B. rubens* abundance and cover became less positive with aridity when *L. tridentata* shrubs were shortest. Compared to other shrub species, *L. tridentata* can be a poor facilitator (Hutto, McAuliffe, & Hogan, 1986; reviewed by Callaway, 2007) due to relatively strong competitive effects and allelopathy (Mahall & Callaway, 1992), but we found limited evidence for this. Across all sites, RII values for *B. rubens* abundance and cover (the only vegetation measures with RII values affected by shrub species; Table 1) were no different under *L. tridentata* than any other shrub species (Table A4). That said, *L. tridentata* was the only shrub species whose positive effects on *B. rubens* appeared to decline with aridity (especially when shrubs were short)—the opposite pattern predicted by the SGH. This pattern could arise if *B. rubens* became relatively less abundant under *L. tridentata* or relatively more abundant in the open as aridity increased, but it is unclear which occurred (Table A5; note the lack of a significant microsite × aridity interaction). The former could occur if the quantity, quality or availability of soil resources concentrated under *L. tridentata* canopies (Schlesinger, Raikes, Hartley, & Cross, 1996) declined with aridity, or if the competitive/allelopathic effects of *L. tridentata* increased with aridity. Regardless, our findings underscore the potential for shrub traits (species identity and height in this case) to mediate the effects of aridity on shrub–annual associations (reviewed by Callaway, 2007), though not necessarily as predicted by the SGH. However, we emphasize that *L. tridentata* canopies were surveyed at only three study sites, all in the Mojave Desert. Thus, RII–aridity relationships under *L. tridentata* canopies were based on a small sample size (n = 3 sites) that spanned a narrow aridity gradient. Accordingly, we urge caution in interpreting these patterns.

This observational study did not test for mechanisms of facilitation. Facilitation can arise via amelioration of abiotic stress, improvement of plant–pollinator relations, seed trapping, enhancement of soil biogeochemical processes, or herbivore protection (reviewed by Michalet & Pugnaire, 2016), and can be influenced by the spatial structure of vegetation (Berdugo, Soliveres, Kéfi, & Maestre, 2019). It is clear that desert shrubs can facilitate both native and exotic annuals (Abella & Chiquione, 2018; Lucero et al., 2019; Schafer et al., 2012), but we do not know whether native and exotic taxa are generally facilitated via the same mechanisms. If native and exotic species generally capitalize on different mechanisms, plant invasions could potentially be managed by disrupting pathways specific to exotics. However, no differences in the importance of positive effects among shrub species suggest a relatively simple and consistent mechanism such as shade or soil fertility (Schlesinger et al., 1996).

Our findings have practical implications. First, shrub canopies may be critical targets for management efforts aimed at controlling *B. rubens*. For example, herbicide applications to reduce *B. rubens* density and subsequent reseeding efforts to promote the establishment of native species (Clements, Harmon, Blank, & Weltz, 2017; Hulvey et al., 2017; Rowe, 2010) might be most productive when focused under shrub canopies. In addition, bioclimatic envelope modelling has predicted substantial expansion of *B. rubens* across the south-western USA (Curtis & Bradley, 2015), but most models have not considered the role of positive interactions (but see Filazzola, Sotomayor, & Lortie, 2018). We found little evidence that shrub facilitation could interact with environmental severity to exacerbate *B. rubens* expansion, but we do suggest that current models may underestimate the future extent of *B. rubens* invasion by ignoring the potentially strong, important and geographically widespread role of shrub-mediated interactions in promoting the success of this exotic invader. Furthermore, our findings suggest caution in using shrub facilitation as a tool for restoring native biodiversity. Facilitation by native shrubs can help restore native biodiversity to drylands degraded by biological invasions and other anthropogenic disturbances (Padilla & Pugnaire, 2006; Lortie, Filazzola, Kelsey, Hart, & Butterfield, 2018; Liczner, Sotomayor, Filazzola, & Lortie, 2017). However, Abella and Chiquione (2018) recently showed that efforts to use positive interactions to restore native biodiversity benefitted exotic species more than native species. Similarly, we found that shrub-mediated interactions greatly benefitted *B. rubens* but not the native annual community, underscoring the potential for strong facilitation of invasive species to confound restoration efforts.

5 | CONCLUSIONS

We found evidence that spatial association with native shrubs strongly and consistently increased the abundance, cover, biomass and fitness of *B. rubens* across a broad spatial scale and across a variety of biotic and abiotic factors. Thus, the risk of shrub-facilitated *B. rubens* invasion may be high across large portions of the Mojave and San Joaquin Deserts. By mediating positive interactions that benefitted a dominant invader but not native- or community-level biodiversity, native shrubs provided the wrong kind of help to the annual plant community.

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DATA AVAILABILITY STATEMENT

Data for this article have been archived in the Dryad repository: https://doi.org/10.5061/dryad.fttdz08qb.

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BIOSKETCH

Jacob E. Lucero is a plant ecologist who spends too much time sampling aquatic vertebrates. Author contributions: J.E.L., M.S., R.M.C. and C.J.L. conceived the idea and designed the study; and J.E.L. collected the data, analysed the data and led the writing.

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APPENDIX

The appendix for this article consists of two supplementary figures (Figures A1–A2) and six supplementary tables (Tables A1–A6).

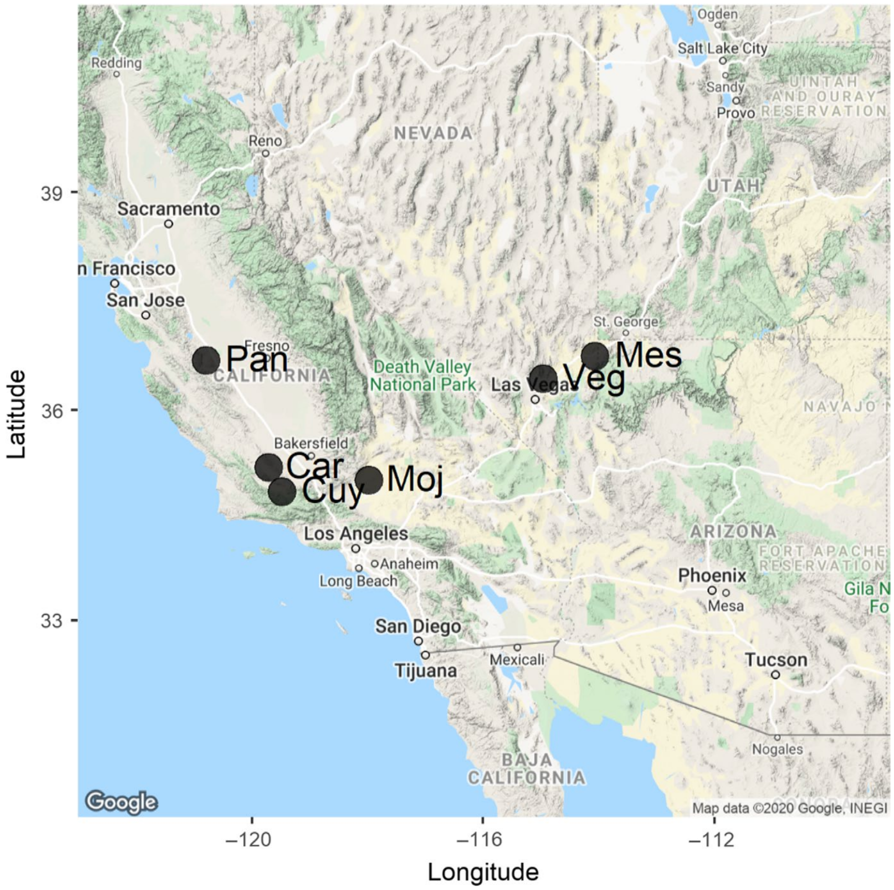

FIGURE A1 Locations of six study sites that spanned an aridity gradient across the Mojave and San Joaquin Deserts, courtesy of Google via the ggmap R package (Kahle & Wickham, 2013). Site names are abbreviated by their first three letters. Table A1 provides full site names

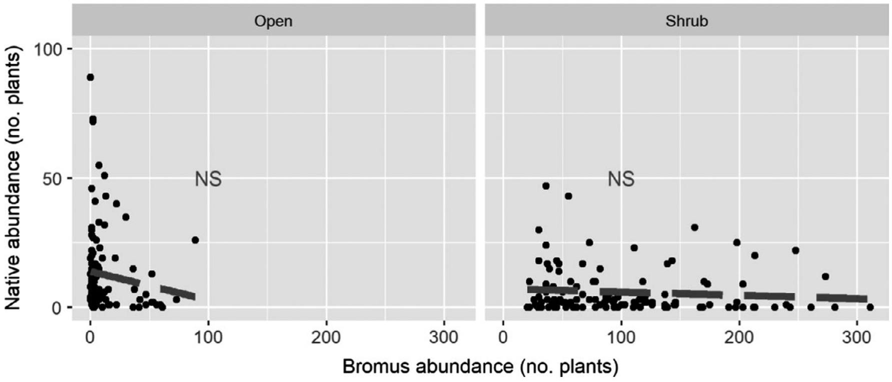

FIGURE A2 Results of a linear mixed-effects model testing the influence of *Bromus rubens* abundance, microsite (shrub vs. open) and relative aridity on the abundance of native annuals along an aridity gradient spanning the Mojave and San Joaquin Deserts. Absolute native abundance (pooled across all species; log-transformed) was the response variable; absolute *B. rubens* abundance ("*Bromus*"; log-transformed), microsite and de Martonne aridity (A_{dM}) were fixed factors; and study site was a random factor. See Table 4 for complete statistics

TABLE A1 Location, total annual precipitation (TAP) (mm), mean annual temperature (MAT ± *SE*) (°C) and the de Martonne aridity index (A_{dM}; formula given in main manuscript) for each study site during the study year (2018–19) and over the past 20 years (± *SE*). Sites spanned an aridity gradient across the Mojave and San Joaquin Deserts. Low A_{dM} values indicate high aridity. Study sites with 2018–19 A_{dM} values that fell outside the 95% CI of the 20-yr A_{dM} are marked with asterisks (*). Superscripts give the source of climate data. See Figure A1 for a map

Vicinity	Desert	Coordinates	TAP 2018–19	MAT 2018–19	A_{dM} 2018–19	TAP 20-yr	MAT 20-yr	A_{dM} 20-yr
Las Vegas, NV	Mojave	36.4460, −114.9599	138.43^{b}	21.88 (2.91)^{b}	4.34	105.92 (9.62)^{b}	20.72 (2.64)^{b}	3.45 (0.51)^{b}
Mojave, CA	Mojave	35.0172, −117.9778	130.56^{c}	18.01 (2.66)^{d}	*4.66	170.18 (9.89)^{d}	16.94 (2.26)^{d}	6.32 (0.46)^{d}
Mesquite, NV	Mojave	36.7599, −114.0705	226.31^{a}	21.88 (2.93)^{a}	7.10	230.38 (8.99)^{a}	20.30 (2.70)^{a}	7.60 (0.36)^{a}
Carrizo Plain, CA	San Joaquin	35.2015, −119.7237	97.70^{e}	17.45 (2.21)^{e}	*3.56	123.64 (9.84)^{e}	17.42 (0.15)^{e}	4.52 (0.38)^{e}
Cuyama, CA	San Joaquin	34.8551, −119.4861	152.91^{f}	19.84 (2.22)^{f}	5.12	163.83 (9.99)^{f}	18.40 (2.09)^{f}	5.77 (0.52)^{f}
Panoche Hills, CA	San Joaquin	36.7002, −120.8018	303.53^{g}	19.61 (2.19)^{g}	10.25	325.88 (10.02)^{g}	17.85 (2.03)^{g}	11.70 (0.82)^{g}

[a] https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:US1NVCK0017/detail; accessed 6-1-19.
[b] https://www.usclimatedata.com/climate/las-vegas/nevada/united-states/usnv0049; accessed 6-1-19.
[c] https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00045756/detail; accessed 6-1-19.
[d] https://www.usclimatedata.com/climate/mojave/california/united-states/usca0715/2019/1; accessed 6-1-19.
[e] http://ipm.ucanr.edu/calludt.cgi/WXSTATIONDATA?%20MAP=&STN=BLACKWLL.A; accessed 6-1-19.
[f] https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USW00023155/detail; accessed 6-1-19.
[g] https://www.ncdc.noaa.gov/cdo-web/quickdata; accessed 6-1-19.

TABLE A2 Mean (SE) values of vegetation measures taken in paired open and shrub microsites at each of six study sites along an aridity gradient spanning the Mojave and San Joaquin Deserts, and whether means differed (i.e. $p < .05$) was tested according to independent linear mixed-effects models with vegetation measure as the response variable; microsite (open vs. shrub) as a fixed factor; and replicate ($n = 20$ per site) as a random factor. Numerator and denominator degrees of freedom ("*df*") are separated by commas. Note that significant open–shrub contrasts here are reflected in RII values with 95% CI that do not overlap zero in Figure 1

Site	Vegetation measure	Open	*SE*	Shrub	*SE*	*df*	F-value	*p*-Value
Carrizo	*Bromus* biomass	0.05	0.01	0.34	0.04	1, 17.14	54.779	<.001
	Bromus spikelet	13.41	1.12	33.94	1.86	1, 16.99	95.096	<.001
	Bromus abundance	1.95	0.39	58.55	6.57	1, 19.00	75.003	<.001
	Bromus cover	1.95	0.39	49.55	5.41	1, 19.00	79.377	<.001
	Native abundance	7.40	1.08	2.80	1.53	1, 38.00	79.377	<.001
	Native cover	11.40	4.12	9.65	2.92	1, 38.00	0.120	.731
	Native richness	2.05	0.18	1.30	0.23	1, 38.00	6.448	.015
	Exotic richness	2.38	0.15	2.38	0.15	1, 19.00	3.199	.090
	Total richness	5.75	0.29	4.65	0.27	1, 19.00	7.956	.011
Cuyama	*Bromus* biomass	0.06	0.01	0.50	0.28	1, 19.49	49.568	<.001
	Bromus spikelet	11.59	1.67	30.25	3.00	1, 19.22	30.226	<.001
	Bromus abundance	1.90	0.40	133.90	12.64	1, 38.00	108.890	<.001
	Bromus cover	1.90	0.40	87.00	4.55	1, 19.00	350.940	<.001
	Native abundance	20.05	4.54	2.80	0.67	1, 38.00	14.155	<.001
	Native cover	17.75	3.65	2.80	0.67	1, 38.00	16.242	<.001
	Native richness	2.50	0.30	1.10	0.19	1, 19.00	18.255	<.001
	Exotic richness	2.50	0.14	2.55	0.15	1, 38.00	0.059	.086

(Continues)

Table A2 (Continued)

Site	Vegetation measure	Open	*SE*	Shrub	*SE*	*df*	*F*-value	*p*-Value
	Total richness	5.00	0.33	3.65	0.29	1, 38.00	9.289	<.001
Mesquite	*Bromus* biomass	0.05	0.01	0.48	0.13	1, 38.00	10.441	.002
	Bromus spikelet	13.00	2.04	57.30	12.48	1, 38.00	12.278	.001
	Bromus abundance	3.60	0.67	64.30	6.28	1, 19.00	99.170	<.001
	Bromus cover	3.60	0.67	54.65	5.18	1, 19.00	105.86	<.001
	Native abundance	22.65	6.58	4.95	1.27	1, 19.00	7.105	.015
	Native cover	19.85	5.23	4.00	0.91	1, 19.00	9.122	.007
	Native richness	2.90	0.38	1.40	0.24	1, 19.00	23.108	.001
	Exotic richness	2.70	0.15	2.90	0.12	1, 19.00	1.152	.297
	Total richness	5.60	0.39	4.30	0.29	1, 19.00	10.668	.004
Mojave	*Bromus* biomass	0.09	0.02	0.37	0.06	1, 19.05	22.302	.001
	Bromus spikelet	16.68	2.57	45.00	3.43	1, 18.69	72.772	<.001
	Bromus abundance	4.25	0.94	54.55	7.88	1, 38.00	40.156	<.001
	Bromus cover	3.05	0.56	40.10	5.65	1, 38.00	42.607	<.001
	Native abundance	7.40	1.30	2.80	0.80	1, 38.00	9.055	.005
	Native cover	7.00	1.23	2.80	0.80	1, 38.00	8.223	.007
	Native richness	1.55	0.23	1.15	0.23	1, 19.00	2.267	.149
	Exotic richness	2.30	0.11	2.15	0.11	1, 38.00	0.977	.329
	Total richness	3.85	0.23	3.30	0.24	1, 19.00	4.265	.053
Panoche	*Bromus* biomass	0.06	0.01	0.22	0.03	1, 38.00	33.118	<.001
	Bromus spikelet	13.95	1.52	33.25	3.20	1, 19.00	33.764	<.001
	Bromus abundance	32.30	4.96	167.60	15.53	1, 19.00	70.805	<.001
	Bromus cover	28.45	4.14	92.75	2.43	1, 19.00	70.805	<.001
	Native abundance	3.85	1.28	1.80	1.25	1, 19.00	1.427	.247
	Native cover	3.85	1.28	1.80	1.25	1, 19.00	11.494	.003
	Native richness	1.00	0.19	0.30	0.11	1, 19.00	11.494	.003
	Exotic richness	3.10	0.16	2.95	0.18	1, 38.00	0.376	.544
	Total richness	4.10	0.25	3.25	0.24	1, 38.00	6.027	.019
Vegas	*Bromus* biomass	0.04	0.01	0.16	0.03	1, 18.14	16.582	<.001
	Bromus spikelet	10.11	1.36	27.95	2.36	1, 35.00	41.09	<.001
	Bromus abundance	20.84	5.22	133.47	15.70	1, 35.00	70.805	<.001
	Bromus cover	17.32	3.75	80.53	5.24	1, 18.00	128.150	<.001
	Native abundance	16.95	3.28	13.32	2.01	1, 18.00	1.390	.254
	Native cover	17.79	4.58	10.68	1.61	1, 18.00	2.881	.106
	Native richness	2.63	0.30	2.42	0.22	1, 18.00	0.408	.531
	Exotic richness	2.37	0.14	2.37	0.16	1, 18.00	0.000	1.000
	Total richness	5.00	0.33	4.79	0.26	1, 18.00	0.308	.586

TABLE A3 Results of a linear mixed-effects model testing the influence of microsite (open versus. shrub) and relative aridity on the abundance of *Bromus rubens* along an aridity gradient spanning the Mojave and San Joaquin Deserts. Absolute *B. rubens* abundance (log-transformed) was the response variable; microsite and de Martonne aridity (A_{dM}) were fixed factors; and study site was a random factor (not shown). Significant (i.e. $p < .05$) effects appear in bold

	Fixed factor		
Response	Microsite	A_{dM}	Microsite × A_{dM}
B. rubens abundance	**$F_{1,229.99} = 133.043$; $p < .001$**	$F_{1,4.00} = 2.684$; $p = .180$	$F_{1,229.99} = 0.724$; $p = .366$

TABLE A4 Pairwise contrasts of RII values for *Bromus rubens* abundance and cover under *Ambrosia dumosa*, *Ephedra californica*, and *Larrea tridentata* canopies, according to the emmeans function (Lenth et al., 2018) applied to the linear mixed-effects models described in Table 1. We could not calculate pairwise contrasts for interactions mediated by *Lycium andersonii* because this was a focal shrub at only one site. Across all sites, mean RII (SE) values for *B. rubens* abundance and cover under *A. dumosa*, *E. californica* and *L. tridentata* canopies were 0.771 (0.058), 0.880 (0.037) and 0.383 (0.042), respectively; and 0.761 (0.067), 0.840 (0.497) and (0.808 (0.055), respectively

RII Measure	Contrast	Δ RII	*SE*	*df*	*t*-ratio	*p*-value
B. rubens abundance	*Ambrosia–Ephedra*	−0.108	0.069	6.25	−1.570	.458
	Ambrosia–Larrea	−0.067	0.060	102.56	−1.122	.677
	Ephedra–Larrea	0.041	0.056	2.97	0.734	.878
B. rubens cover	*Ambrosia–Ephedra*	−0.079	0.083	3.73	−0.950	.783
	Ambrosia–Larrea	−0.047	0.057	105.00	−0.835	.838
	Ephedra–Larrea	0.032	0.074	2.38	0.428	.968

TABLE A5 Results of a linear mixed-effects model testing the influence of microsite (open vs. shrub) and relative aridity on the abundance of *Bromus rubens* along an aridity gradient spanning the Mojave Desert portion of our study. The model only considered shrub–open pairs with *Larrea tridentata* as the shrub species. Absolute *B. rubens* abundance (log-transformed) was the response variable; microsite and de Martonne aridity (A_{dM}) were fixed factors; and study site was a random factor (not shown). Significant (i.e. $p < .05$) effects appear in bold. See Table A3 for results across all shrub species

	Fixed factor		
Response	**Microsite**	A_{dM}	**Microsite ×** A_{dM}
B. rubens abundance	**$F_{1,113.00} = 14.749$; $p < .001$**	$F_{1,1.00} = 0.333$; $p = .667$	$F_{1,113.00} = 0.341$; $p = .561$

TABLE A6 Mean (± 95% CI), intensity (RII) and importance (I_{imp}) of shrub-mediated effects on the annual plant community at each of six study sites ($n = 20$ shrub–open pairs at each site) that spanned an aridity gradient across the Mojave and San Joaquin Deserts, and averaged across all sites ("All"; $n = 6$). Whether means differed from zero (i.e. $p < .05$) was tested with independent one-sample *t* tests with RII or I_{imp} as the response variable. Means (± 95% CI) are plotted in Figures 1 and 2 in the main manuscript

Site	Index	Vegetation measure	Mean	95% CI	*df*	*t*-value	*p*-Value
Carrizo	RII	*B. rubens* abundance	0.928	0.024	19	75.651	<.001
	RII	*B. rubens* biomass	0.717	0.112	19	11.843	<.001
	RII	*B. rubens* cover	0.918	0.027	19	65.928	<.001
	RII	*B. rubens* spikelets	0.466	0.095	19	9.081	<.001
	RII	Exotic richness	−0.041	0.045	19	−1.786	.091
	RII	Native abundance	−0.255	0.317	19	−1.576	.132
	RII	Native cover	−0.280	0.313	19	−1.754	.095
	RII	Native richness	−0.313	0.211	19	−2.905	.009
	RII	Total richness	−0.109	0.069	19	−3.07	.006
	I_{imp}	*B. rubens* abundance	0.150	0.027	19	10.709	<.001
	I_{imp}	*B. rubens* biomass	0.048	0.011	19	7.977	<.001
	I_{imp}	*B. rubens* cover	0.311	0.044	19	13.83	<.001
	I_{imp}	*B. rubens* spikelets	0.078	0.014	19	10.083	<.001
	I_{imp}	Exotic richness	−0.105	0.177	19	−1.161	.261
	I_{imp}	Native abundance	0.013	0.106	19	0.244	.811
	I_{imp}	Native cover	0.012	0.139	19	0.167	.869
	I_{imp}	Native richness	−0.101	0.105	19	−1.884	.075
	I_{imp}	Total richness	−0.088	0.057	19	−3.036	.007

(Continues)

Table A6 (Continued)

Site	Index	Vegetation measure	Mean	95% CI	*df*	*t*-value	*p*-Value
Cuyama	RII	*B. rubens* abundance	0.968	0.017	19	113.85	<.001
	RII	*B. rubens* biomass	0.589	0.190	19	6.080	<.001
	RII	*B. rubens* cover	0.957	0.021	19	89.903	<.001
	RII	*B. rubens* spikelets	0.520	0.144	19	7.089	<.001
	RII	Exotic richness	0.007	0.096	19	0.145	.886
	RII	Native abundance	−0.651	0.185	19	−6.901	<.001
	RII	Native cover	−0.641	0.184	19	−6.839	<.001
	RII	Native richness	−0.392	0.188	19	−4.051	<.001
	RII	Total richness	−0.161	0.110	19	−2.859	.010
	I_{imp}	*B. rubens* abundance	0.289	0.039	19	14.443	<.001
	I_{imp}	*B. rubens* biomass	0.054	0.048	19	2.167	.042
	I_{imp}	*B. rubens* cover	0.456	0.035	19	25.214	<.001
	I_{imp}	*B. rubens* spikelets	0.073	0.022	19	6.476	<.001
	I_{imp}	Exotic richness	−0.069	0.131	19	−1.034	.314
	I_{imp}	Native abundance	−0.139	0.074	19	−3.701	.005
	I_{imp}	Native cover	−0.162	0.081	19	−3.937	<.001
	I_{imp}	Native richness	−0.230	0.107	19	−4.222	<.001
	I_{imp}	Total richness	−0.120	0.078	19	−3.027	.007
Panoche Hills	RII	*B. rubens* abundance	0.664	0.110	19	11.872	<.001
	RII	*B. rubens* biomass	0.540	0.131	19	8.059	<.001
	RII	*B. rubens* cover	0.563	0.108	19	10.246	<.001
	RII	*B. rubens* spikelets	0.403	0.111	19	7.123	<.001
	RII	Exotic richness	−0.030	0.084	19	−0.686	.499
	RII	Native abundance	−0.478	0.326	19	−2.491	.026
	RII	Native cover	−0.478	0.326	19	−2.491	.026
	RII	Native richness	−0.578	0.267	19	−3.667	.003
	RII	Total richness	−0.116	0.092	19	−2.465	.023
	I_{imp}	*B. rubens* abundance	0.305	0.054	19	11.094	<.001
	I_{imp}	*B. rubens* biomass	0.028	0.009	19	5.802	<.001
	I_{imp}	*B. rubens* cover	0.468	0.021	19	42.924	<.001
	I_{imp}	*B. rubens* spikelets	0.070	0.022	19	6.149	<.001
	I_{imp}	Exotic richness	−0.271	0.285	19	−1.869	.078
	I_{imp}	Native abundance	−0.019	0.033	19	−0.976	.346
	I_{imp}	Native cover	−0.024	0.047	19	−0.883	.392
	I_{imp}	Native richness	−0.126	0.062	19	−0.3597	.003
	I_{imp}	Total richness	−0.077	0.060	19	−2.517	.021
Mojave	RII	*B. rubens* abundance	0.820	0.090	19	17.763	<.001
	RII	*B. rubens* biomass	0.660	0.143	19	9.073	<.001
	RII	*B. rubens* cover	0.814	0.078	19	20.461	<.001
	RII	*B. rubens* spikelets	0.528	0.109	19	9.476	<.001
	RII	Exotic richness	−0.033	0.061	19	−1.070	.298
	RII	Native abundance	−0.383	0.307	19	−2.442	.025
	RII	Native cover	−0.373	0.306	19	−2.388	.027
	RII	Native richness	−0.240	0.267	19	−1.765	.094

(Continues)

Table A6 (Continued)

Site	Index	Vegetation measure	Mean	95% CI	*df*	*t*-value	*p*-Value
	RII	Total richness	−0.084	0.074	19	−2.232	.038
	I_{imp}	*B. rubens* abundance	0.133	0.034	19	7.647	<.001
	I_{imp}	*B. rubens* biomass	0.047	0.018	19	5.193	<.001
	I_{imp}	*B. rubens* cover	0.254	0.054	19	9.147	<.001
	I_{imp}	*B. rubens* spikelets	0.104	0.021	19	9.819	<.001
	I_{imp}	Exotic richness	−0.077	0.081	19	−1.862	.078
	I_{imp}	Native abundance	−0.036	0.028	19	−2.546	.0197
	I_{imp}	Native cover	−0.044	0.037	19	−2.340	.030
	I_{imp}	Native richness	−0.050	0.088	19	−1.123	.275
	I_{imp}	Total richness	−0.050	0.044	19	−2.232	.038
Mesquite	RII	*B. rubens* abundance	0.890	0.036	19	48.986	<.001
	RII	*B. rubens* biomass	0.680	0.106	19	12.573	<.001
	RII	*B. rubens* cover	0.873	0.041	19	41.653	<.001
	RII	*B. rubens* spikelets	0.538	0.101	19	10.441	<.001
	RII	Exotic richness	0.042	0.073	19	1.119	.277
	RII	Native abundance	−0.540	0.226	19	−4.681	<.001
	RII	Native cover	−0.558	0.218	19	−5.019	<.001
	RII	Native richness	−0.406	0.170	19	−4.686	<.001
	RII	Total richness	−0.128	0.088	19	−2.859	.010
	I_{imp}	*B. rubens* abundance	0.161	0.026	19	12.181	<.001
	I_{imp}	*B. rubens* biomass	0.064	0.035	19	3.595	.002
	I_{imp}	*B. rubens* cover	0.333	0.042	19	15.475	<.001
	I_{imp}	*B. rubens* spikelets	0.130	0.052	19	4.851	<.001
	I_{imp}	Exotic richness	−0.005	0.085	19	−0.113	.911
	I_{imp}	Native abundance	−0.145	0.106	19	−2.676	.015
	I_{imp}	Native cover	−0.175	0.113	19	−3.0338	.007
	I_{imp}	Native richness	−0.281	0.131	19	−4.199	<.001
	I_{imp}	Total richness	−0.104	0.060	19	−3.416	.003
Las Vegas	RII	*B. rubens* abundance	0.728	0.101	19	13.773	<.001
	RII	*B. rubens* biomass	0.618	0.121	19	9.783	<.001
	RII	*B. rubens* cover	0.679	0.098	19	13.287	<.001
	RII	*B. rubens* spikelets	0.486	0.114	19	8.175	<.001
	RII	Exotic richness	−0.003	0.057	19	−0.102	.920
	RII	Native abundance	−0.016	0.212	19	−0.148	.889
	RII	Native cover	−0.081	0.207	19	−0.742	.467
	RII	Native richness	−0.017	0.133	19	−0.249	.806
	RII	Total richness	−0.014	0.073	19	−0.374	.713
	I_{imp}	*B. rubens* abundance	0.260	0.053	19	9.422	<.001
	I_{imp}	*B. rubens* biomass	0.021	0.009	19	4.511	<.001
	I_{imp}	*B. rubens* cover	0.422	0.043	19	18.967	<.001
	I_{imp}	*B. rubens* spikelets	0.066	0.018	19	7.072	<.001
	I_{imp}	Exotic richness	−0.033	0.076	19	−0.8337	.415
	I_{imp}	Native abundance	−0.030	0.052	19	−1.111	.281
	I_{imp}	Native cover	−0.087	0.100	19	−1.653	.116
	I_{imp}	Native richness	−0.002	0.172	19	−0.019	.985

(Continues)

Table A6 (Continued)

Site	Index	Vegetation measure	Mean	95% CI	*df*	*t*-value	*p*-Value
	I_{imp}	Total richness	−0.020	0.051	19	−0.736	.471
All	RII	*B. rubens* abundance	0.833	0.095	5	17.230	<.001
	RII	*B. rubens* biomass	0.634	0.052	5	24.094	<.001
	RII	*B. rubens* cover	0.801	0.121	5	12.939	<.001
	RII	*B. rubens* spikelets	0.490	0.040	5	23.775	<.001
	RII	Exotic richness	−0.010	0.025	5	−0.754	.485
	RII	Native abundance	−0.387	0.181	5	−4.187	.009
	RII	Native cover	−0.402	0.163	5	−4.843	.005
	RII	Native richness	−0.324	0.150	5	−4.223	.008
	RII	Total richness	−0.102	0.040	5	−5.017	.004
	I_{imp}	*B. rubens* abundance	0.216	0.005	5	6.904	<.001
	I_{imp}	*B. rubens* biomass	0.043	0.007	5	6.665	.001
	I_{imp}	*B. rubens* cover	0.374	0.004	5	10.533	<.001
	I_{imp}	*B. rubens* spikelets	0.087	0.006	5	8.500	<.001
	I_{imp}	Exotic richness	−0.093	0.033	5	−2.443	.058
	I_{imp}	Native abundance	−0.059	0.014	5	−2.200	.079
	I_{imp}	Native cover	−0.080	0.016	5	−2.589	.049
	I_{imp}	Native richness	−0.132	0.015	5	−3.038	.029
	I_{imp}	Total richness	−0.076	0.005	5	−5.120	.004