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.
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’Antonio & 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; Travasset & 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, & Michelet, 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 interactions vary along an aridity gradient.
assessments 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:

\[
A_{dM} = \frac{P}{T + 10}
\]

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 phytosociologic 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-cm² frames (Pescador, Chacon-Labela, 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:

\[
RII = \frac{M_t - M_o}{M_t + M_o}
\]

where \(M_t\) 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:

\[
I_{imp} = \frac{N_{imp}}{N_{imp} + E_{imp}}
\]

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. 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

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.

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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 RII 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 RII 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 $I_{mp}$ 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.

![Graph showing 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.](image)
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
| RII measure          | Fixed factor | Shrub species | Shrub height | $A_{\text{adM}} \times \text{Species}$ | $A_{\text{adM}} \times \text{Height}$ | Species $\times$ Height | $A_{\text{adM}} \times \text{Species} \times \text{Height}$ |
|---------------------|--------------|---------------|--------------|---------------------------------------|--------------------------------------|------------------------|---------------------------------------------------|
| B. rubens biomass   | $F_{1,103.00} = 0.003$ | $F_{1,103.00} = 0.521$ | $F_{1,103.00} = 0.217$ | $F_{2,103.00} = 0.946$ | $F_{1,103.00} = 0.238$ | $F_{1,103.00} = 0.870$ | $F_{2,103.00} = 1.236$ |
|                     | $p = .956$   | $p = .669$    | $p = .391$   | $p = .627$                          | $p = .459$                          | $p = .295$                         |
| B. rubens spikelet  | $F_{1,84.94} = 0.720$ | $F_{1,84.94} = 1.009$ | $F_{3,90.46} = 0.521$ | $F_{2,90.46} = 0.873$ | $F_{1,90.46} = 1.321$ | $F_{3,90.46} = 1.247$ | $F_{2,90.46} = 0.292$ |
|                     | $p = .397$   | $p = .392$    | $p = .669$   | $p = .421$                          | $p = .253$                          | $p = .372$                         |
| B. rubens abundance | $F_{1,59.35} = 2.490$ | $F_{1,59.35} = 5.390$ | $F_{1,59.35} = 1.627$ | $F_{2,59.35} = 5.471$ | $F_{1,59.35} = 1.133$ | $F_{3,59.35} = 3.267$ | $F_{2,59.35} = 0.23$ |
|                     | $p = .120$   | $p = .002$    | $p = .205$   | $p = .006$                          | $p = .290$                          | $p = .023$                         | $p = .068$                        |
| B. rubens cover     | $F_{1,25.35} = 2.626$ | $F_{1,25.35} = 6.632$ | $F_{1,25.35} = 2.167$ | $F_{2,25.35} = 6.537$ | $F_{1,25.35} = 1.643$ | $F_{3,25.35} = 4.365$ | $F_{2,25.35} = 0.06$ |
|                     | $p = .117$   | $p = .001$    | $p = .142$   | $p = .004$                          | $p = .203$                          | $p = .006$                         | $p = .032$                        |
| Native abundance    | $F_{1,28.90} = 0.074$ | $F_{1,28.90} = 0.212$ | $F_{1,28.90} = 0.045$ | $F_{2,28.90} = 0.065$ | $F_{1,28.90} = 0.012$ | $F_{3,28.90} = 0.183$ | $F_{2,28.90} = 0.008$ |
|                     | $p = .787$   | $p = .888$    | $p = .833$   | $p = .938$                          | $p = .912$                          | $p = .908$                         | $p = .992$                        |
| Native cover        | $F_{1,39.42} = 0.036$ | $F_{1,39.42} = 0.137$ | $F_{1,39.42} = 0.089$ | $F_{2,39.42} = 0.050$ | $F_{1,39.42} = 0.041$ | $F_{3,39.42} = 0.127$ | $F_{2,39.42} = 0.015$ |
|                     | $p = .850$   | $p = .937$    | $p = .766$   | $p = .951$                          | $p = .840$                          | $p = .944$                         | $p = .985$                        |
| Native richness     | $F_{1,100.00} = 0.025$ | $F_{1,100.00} = 0.170$ | $F_{1,100.00} = 0.043$ | $F_{2,100.00} = 0.249$ | $F_{1,100.00} = 0.037$ | $F_{3,100.00} = 0.089$ | $F_{2,100.00} = 0.121$ |
|                     | $p = .622$   | $p = .917$    | $p = .837$   | $p = .780$                          | $p = .847$                          | $p = .966$                         | $p = .887$                        |
| Exotic richness     | $F_{1,105.00} = 0.420$ | $F_{1,105.00} = 0.701$ | $F_{1,105.00} = 0.293$ | $F_{2,105.00} = 0.643$ | $F_{1,105.00} = 0.281$ | $F_{3,105.00} = 0.498$ | $F_{2,105.00} = 0.367$ |
|                     | $p = .538$   | $p = .550$    | $p = .590$   | $p = .528$                          | $p = .597$                          | $p = .685$                         | $p = .694$                        |
| Total richness      | $F_{1,105.00} = 0.189$ | $F_{1,105.00} = 0.255$ | $F_{1,105.00} = 0.028$ | $F_{2,105.00} = 0.031$ | $F_{1,105.00} = 0.000$ | $F_{3,105.00} = 0.319$ | $F_{2,105.00} = 0.079$ |
|                     | $p = .665$   | $p = .858$    | $p = .868$   | $p = .970$                          | $p = .998$                          | $p = .812$                         | $p = .924$                        |

Note: RII was the response variable; de Martonne aridity ($A_{\text{adM}}$), 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.
| Fixed factor               | B. rubens biomass | B. rubens spikelet | B. rubens abundance | B. rubens cover | Native abundance | Native cover | Native richness | Exotic richness | Total richness |
|---------------------------|-------------------|--------------------|---------------------|----------------|-----------------|--------------|----------------|----------------|----------------|
| \( I_{\text{imp}} \) measure | \( A_{\text{dM}} \) | \( \text{Species} \) | \( \text{Height} \) | \( A_{\text{dM}} \times \text{Species} \) | \( A_{\text{dM}} \times \text{Height} \) | \( \text{Species} \times \text{Height} \) | \( A_{\text{dM}} \times \text{Species} \times \text{Height} \) |
| \( B. \text{rubens} \) biomass | \( F_{1,79.32} = 0.137 \) | \( F_{3.86.84} = 0.920 \) | \( F_{1,100.77} = 0.201 \) | \( F_{2.79.93} = 0.327 \) | \( F_{1,100.77} = 0.689 \) | \( F_{3,100.79} = 1.861 \) | \( F_{2,100.82} = 1.146 \) |
| \( p = .712 \) | \( p = .435 \) | \( p = .656 \) | \( p = .722 \) | \( p = .422 \) | \( p = .141 \) | \( p = .322 \) |
| \( B. \text{rubens} \) spikelet | \( F_{1,40.07} = 1.538 \) | \( F_{3.56.83} = 0.617 \) | \( F_{1,100.87} = 3.106 \) | \( F_{2.45.09} = 0.824 \) | \( F_{1,100.87} = 4.300 \) | \( F_{3,100.88} = 1.162 \) | \( F_{2,100.89} = 2.163 \) |
| \( p = .222 \) | \( p = .607 \) | \( p = .081 \) | \( p = .445 \) | \( p = .061 \) | \( p = .328 \) | \( p = .120 \) |
| \( B. \text{rubens} \) abundance | \( F_{1,6.092} = 0.168 \) | \( F_{3.14.565} = 0.695 \) | \( F_{1,102.99} = 0.590 \) | \( F_{2,10.56} = 0.453 \) | \( F_{1,102.99} = 0.250 \) | \( F_{3,102.99} = 0.368 \) | \( F_{2,103.00} = 0.567 \) |
| \( p = .696 \) | \( p = .570 \) | \( p = .444 \) | \( p = .647 \) | \( p = .620 \) | \( p = .777 \) | \( p = .945 \) |
| \( B. \text{rubens} \) cover | \( F_{1,5.00} = 0.560 \) | \( F_{3.13.22} = 0.917 \) | \( F_{1,102.99} = 1.724 \) | \( F_{2,9.65} = 0.708 \) | \( F_{1,102.99} = 0.841 \) | \( F_{3,102.99} = 0.424 \) | \( F_{2,103.00} = 0.169 \) |
| \( p = .488 \) | \( p = .459 \) | \( p = .192 \) | \( p = .517 \) | \( p = .361 \) | \( p = .736 \) | \( p = .845 \) |
| \( \text{Native abundance} \) | \( F_{1,36.25} = 0.707 \) | \( F_{3.13.20} = 0.027 \) | \( F_{1,98.15} = 0.213 \) | \( F_{2,24.29} = 0.087 \) | \( F_{1,98.15} = 0.308 \) | \( F_{3,98.15} = 0.141 \) | \( F_{2,98.20} = 0.042 \) |
| \( p = .406 \) | \( p = .994 \) | \( p = .646 \) | \( p = .917 \) | \( p = .580 \) | \( p = .935 \) | \( p = .959 \) |
| \( \text{Native cover} \) | \( F_{1,44.37} = 0.354 \) | \( F_{3.60.65} = 0.019 \) | \( F_{1,98.15} = 0.070 \) | \( F_{2,50.84} = 0.017 \) | \( F_{1,98.18} = 0.127 \) | \( F_{3,98.17} = 0.156 \) | \( F_{2,98.23} = 0.088 \) |
| \( p = .850 \) | \( p = .937 \) | \( p = .766 \) | \( p = .951 \) | \( p = .840 \) | \( p = .944 \) | \( p = .985 \) |
| \( \text{Native richness} \) | \( F_{1,85.45} = 2.829 \) | \( F_{3.90.41} = 1.346 \) | \( F_{1,99.34} = 0.237 \) | \( F_{2,86.30} = 1.887 \) | \( F_{1,99.37} = 0.458 \) | \( F_{3,99.36} = 0.616 \) | \( F_{2,99.46} = 0.459 \) |
| \( p = .096 \) | \( p = .264 \) | \( p = .627 \) | \( p = .158 \) | \( p = .492 \) | \( p = .606 \) | \( p = .633 \) |
| \( \text{Exotic richness} \) | \( F_{1,105.00} = 0.000 \) | \( F_{3.105.00} = 0.885 \) | \( F_{1,105.00} = 0.032 \) | \( F_{2,105.00} = 0.628 \) | \( F_{1,105.00} = 0.002 \) | \( F_{3,99.37} = 0.895 \) | \( F_{2,105.00} = 0.450 \) |
| \( p = .991 \) | \( p = .452 \) | \( p = .858 \) | \( p = .536 \) | \( p = .961 \) | \( p = .447 \) | \( p = .639 \) |
| \( \text{Total richness} \) | \( F_{1,105.00} = 0.508 \) | \( F_{3.105.00} = 0.568 \) | \( F_{1,105.00} = 0.000 \) | \( F_{2,105.00} = 0.346 \) | \( F_{1,105.00} = 0.038 \) | \( F_{3,105.00} = 0.499 \) | \( F_{2,105.00} = 0.165 \) |
| \( p = .478 \) | \( p = .638 \) | \( p = .995 \) | \( p = .708 \) | \( p = .845 \) | \( p = .686 \) | \( p = .848 \) |

Note: \( I_{\text{imp}} \) was the response variable; de Martonne aridity (\( A_{\text{dM}} \)), 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 | Height | $A_{BM}$ | $A_{BM} \times$ Height |
|-------------|---------------|--------------|--------|----------|-------------------------|
| *B. rubens* abundance | *E. californica* | $F_{1,13.93} = 3.600$; $p = .079$ | $F_{1,55.00} = 0.134$; $p = .716$ | $F_{1,55.04} = 0.340$; $p = .563$ |
|               | *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* | $F_{1,13.56} = 3.120$; $p = .190$ | $F_{1,55.01} = 0.002$; $p = .990$ | $F_{1,55.02} = 0.001$; $p = .971$ |
|               | *L. tridentata* | $F_{1,35.46} = 10.561$; $p = .005$ | $F_{1,38.02} = 12.513$; $p = .001$ | $F_{1,39.01} = 9.446$; $p = .004$ |
|               | *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 ($A_{BM}$) 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, Bertain, & Silliman, 2010), sand dune (Cushman, Lortie, & Christian, 2011) and forest (Saccone et al., 2010) ecosystems, suggesting that native-facilitated invasions may be widespread.

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 $I_{max}$ 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 neighbors, especially where environmental stress was highest. Similarly, strong facilitation of *B. rubens* may threaten the stability of plant communities across

**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.

![Graph showing the relationship between Bromus abundance and cover with RII values](image-url)
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, García-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-arid 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 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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**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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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 of Vicinity Desert Coordinates TAP 2018–19 MAT 2018–19 \(A_{DM}\) 2018–19 TAP 20-yr MAT 20-yr \(A_{DM}\) 20-yr

| Site               | 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) \(^f\) |
| Pancho 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, 19.00 | 79.377  | <.001      |
|                    | Native cover       | 11.40 4.12| 9.65 2.92 | 1, 19.00 | 79.377  | <.001      |
|                    | Native richness    | 2.05 0.18 | 1.30 0.23 | 1, 19.00 | 79.377  | <.001      |
|                    | Exotic richness    | 2.38 0.15 | 2.38 0.15| 1, 19.00 | 79.377  | <.001      |
|                    | Total richness     | 5.75 0.29 | 4.65 0.27 | 1, 19.00 | 79.377  | <.001      |
| 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, 19.00 | 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, 19.00 | 14.155  | <.001      |
|                    | Native cover       | 17.75 3.65| 2.80 0.67 | 1, 19.00 | 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, 19.00 | 0.059   | .086       |

(Continues)
Table A2 (Continued)

| Site   | Vegetation measure          | Open | SE  | Shrub  | SE  | df | F-value | p-Value |
|--------|-----------------------------|------|-----|--------|-----|----|---------|---------|
| Mesquite | Total richness              | 5.00 | 0.33| 3.65   | 0.29| 1  | 138.00  | 9.289   | <.001   |
|        |  B. rubens biomass          | 0.05 | 0.01| 0.48   | 0.13| 1  | 138.00  | 10.441  | .002    |
|        |  B. rubens spikelet         | 13.00| 2.04| 57.30  | 12.48| 1  | 138.00  | 12.278  | .001    |
|        |  B. rubens abundance        | 3.60 | 0.67| 64.30  | 6.28| 1  | 19.00   | 99.170  | <.001   |
|        |  B. rubens 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  | 19.00   | 22.302  | .001    |
|        |  B. rubens spikelet         | 16.68| 2.57| 45.00  | 3.43| 1  | 18.69   | 72.772  | <.001   |
|        |  B. rubens abundance        | 4.25 | 0.94| 54.55  | 7.88| 1  | 138.00  | 40.156  | <.001   |
|        |  B. rubens cover            | 3.05 | 0.56| 40.10  | 5.65| 1  | 138.00  | 42.607  | <.001   |
|        |  Native abundance           | 7.40 | 1.30| 2.80   | 0.80| 1  | 138.00  | 9.055   | .005    |
|        |  Native cover               | 7.00 | 1.23| 2.80   | 0.80| 1  | 138.00  | 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  | 19.00   | 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  | 138.00  | 33.118  | <.001   |
|        |  B. rubens spikelet         | 13.95| 1.52| 33.25  | 3.20| 1  | 19.00   | 33.764  | <.001   |
|        |  B. rubens abundance        | 32.30| 4.96| 167.60 | 15.53| 1  | 19.00   | 70.805  | <.001   |
|        |  B. rubens cover            | 28.45| 4.14| 92.75  | 3.20| 1  | 19.00   | 70.805  | <.001   |
|        |  Native abundance           | 3.85 | 1.28| 1.80   | 1.25| 1  | 138.00  | 1.427   | .247    |
|        |  Native cover               | 3.85 | 1.28| 1.80   | 1.25| 1  | 138.00  | 11.494  | .003    |
|        |  Native richness            | 1.00 | 0.19| 0.30   | 0.11| 1  | 138.00  | 11.494  | .003    |
|        |  Exotic richness            | 3.10 | 0.16| 2.95   | 0.18| 1  | 138.00  | 0.376   | .544    |
|        |  Total richness             | 4.10 | 0.25| 3.25   | 0.24| 1  | 138.00  | 6.027   | .019    |
| Vegas  | Bromus biomass              | 0.04 | 0.01| 0.16   | 0.03| 1  | 18.14   | 16.582  | <.001   |
|        |  B. rubens spikelet         | 10.11| 1.36| 27.95  | 2.36| 1  | 135.00  | 41.09   | <.001   |
|        |  B. rubens abundance        | 20.84| 5.22| 133.47 | 15.70| 1  | 135.00  | 70.805  | <.001   |
|        |  B. rubens cover            | 17.32| 3.75| 80.53  | 5.24| 1  | 138.00  | 128.150 | <.001   |
|        |  Native abundance           | 16.95| 3.28| 13.32  | 2.01| 1  | 138.00  | 1.390   | .254    |
|        |  Native cover               | 17.79| 4.58| 10.68  | 1.61| 1  | 138.00  | 2.881   | .106    |
|        |  Native richness            | 2.63 | 0.30| 2.42   | 0.22| 1  | 138.00  | 0.408   | .531    |
|        |  Exotic richness            | 2.37 | 0.14| 2.37   | 0.16| 1  | 138.00  | 0.000   | 1.000   |
|        |  Total richness             | 5.00 | 0.33| 4.79   | 0.26| 1 | 18.00   | 3.038   | .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 B. 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\text{dM}) were fixed factors; and study site was a random factor (not shown). Significant (i.e. \( p < .05 \)) effects appear in bold.

| Response       | Fixed factor | Microsite | A\text{dM} | Microsite \times A\text{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 | .968    |
|              | Ephedra–Larrea    | 0.032  | 0.074 | 2.38  | 0.428  | .683    |

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*R) 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.

| Response       | Fixed factor               |
|----------------|---------------------------|
| *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)
| 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    |
| Panoche Hills | RII   | B. rubens abundance| 0.289 | 0.039  | 19  | 14.443  | <.001   |
|            | RII   | B. rubens biomass  | 0.054 | 0.048  | 19  | 2.167   | .042    |
|            | RII   | B. rubens cover    | 0.456 | 0.035  | 19  | 25.214  | <.001   |
|            | RII   | B. rubens spikelets| 0.073 | 0.022  | 19  | 6.476   | <.001   |
|            | RII   | Exotic richness    | −0.069| 0.131  | 19  | −1.034  | .314    |
|            | RII   | Native abundance   | −0.139| 0.074  | 19  | −3.701  | <.001   |
|            | RII   | Native cover       | −0.162| 0.081  | 19  | −3.937  | <.001   |
|            | RII   | Native richness    | −0.230| 0.107  | 19  | −4.222  | <.001   |
|            | RII   | Total richness     | −0.120| 0.078  | 19  | −3.027  | .007    |
| Mojave     | 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    |
|            | RII   | B. rubens abundance| 0.305 | 0.054  | 19  | 11.094  | <.001   |
|            | RII   | B. rubens biomass  | 0.028 | 0.009  | 19  | 5.802   | <.001   |
|            | RII   | B. rubens cover    | 0.468 | 0.021  | 19  | 42.924  | <.001   |
|            | RII   | B. rubens spikelets| 0.070 | 0.022  | 19  | 6.149   | <.001   |
|            | RII   | Exotic richness    | −0.271| 0.285  | 19  | −1.869  | .078    |
|            | RII   | Native abundance   | −0.019| 0.033  | 19  | −0.976  | .346    |
|            | RII   | Native cover       | −0.024| 0.047  | 19  | −0.883  | .392    |
|            | RII   | Native richness    | −0.126| 0.062  | 19  | −3.597  | .003    |
|            | RII   | Total richness     | −0.077| 0.060  | 19  | −2.517  | .021    |
|            | 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    | −0.333| 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)
| Site       | Index | Vegetation measure     | Mean  | 95% CI | df  | t-value | p-Value |
|------------|-------|------------------------|-------|--------|------|---------|---------|
| RII        | Total richness | -0.084 | 0.074 | 19    | -2.232 | .038    |
| l_{imp}    | B. rubens abundance | 0.133 | 0.034 | 19    | 7.647  | <.001   |
| l_{imp}    | B. rubens biomass   | 0.047 | 0.018 | 19    | 5.193  | <.001   |
| l_{imp}    | B. rubens cover     | 0.254 | 0.054 | 19    | 9.147  | <.001   |
| l_{imp}    | B. rubens spikelets | 0.104 | 0.021 | 19    | 9.819  | <.001   |
| l_{imp}    | Exotic richness    | -0.077 | 0.081 | 19    | -1.862 | .078    |
| l_{imp}    | Native abundance    | -0.036 | 0.028 | 19    | -2.546 | .0197   |
| l_{imp}    | Native cover       | -0.044 | 0.037 | 19    | -2.340 | .030    |
| l_{imp}    | Native richness    | -0.050 | 0.088 | 19    | -1.123 | .275    |
| l_{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   |
| l_{imp}   | B. rubens abundance | 0.161 | 0.026 | 19 | 12.181 | <.001 |
| l_{imp}   | B. rubens biomass   | 0.064 | 0.035 | 19 | 4.851  | <.001 |
| l_{imp}   | B. rubens cover     | 0.333 | 0.042 | 19 | 9.422  | <.001 |
| l_{imp}   | B. rubens spikelets | 0.130 | 0.052 | 19 | 15.475 | <.001 |
| l_{imp}   | Exotic richness    | -0.005 | 0.085 | 19 | -0.113 | .911   |
| l_{imp}   | Native abundance    | -0.145 | 0.106 | 19 | -2.676 | .015   |
| l_{imp}   | Native cover       | -0.175 | 0.113 | 19 | -3.0338 | .007 |
| l_{imp}   | Native richness    | -0.281 | 0.131 | 19 | -4.199 | <.001 |
| l_{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   |
| l_{imp}   | B. rubens abundance | 0.260 | 0.053 | 19 | 9.422  | <.001 |
| l_{imp}   | B. rubens biomass   | 0.021 | 0.009 | 19 | 18.967 | <.001 |
| l_{imp}   | B. rubens cover     | 0.422 | 0.043 | 19 | 18.967 | <.001 |
| l_{imp}   | B. rubens spikelets | 0.066 | 0.018 | 19 | 7.072  | <.001 |
| l_{imp}   | Exotic richness    | -0.033 | 0.076 | 19 | -0.8337 | .415 |
| l_{imp}   | Native abundance    | -0.030 | 0.052 | 19 | -1.111 | .281   |
| l_{imp}   | Native cover       | -0.087 | 0.100 | 19 | -1.653 | .116   |
| l_{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 |
|------|-------|--------------------|------|--------|----|----------|---------|
| All  | $l_{imp}$ | Total richness | −0.020 | 0.051 | 19 | −0.736 | .471 |
| RII  | $l_{imp}$ | B. rubens abundance | 0.833 | 0.095 | 5 | 17.230 | <.001 |
| RII  | $l_{imp}$ | B. rubens biomass | 0.634 | 0.052 | 5 | 24.094 | <.001 |
| RII  | $l_{imp}$ | B. rubens cover | 0.801 | 0.121 | 5 | 12.939 | <.001 |
| RII  | $l_{imp}$ | B. rubens spikelets | 0.490 | 0.040 | 5 | 23.775 | <.001 |
| RII  | $l_{imp}$ | Exotic richness | −0.010 | 0.025 | 5 | −0.754 | .485 |
| RII  | $l_{imp}$ | Native abundance | −0.387 | 0.181 | 5 | −4.187 | .009 |
| RII  | $l_{imp}$ | Native cover | −0.402 | 0.163 | 5 | −4.843 | .005 |
| RII  | $l_{imp}$ | Native richness | −0.324 | 0.150 | 5 | −4.223 | .008 |
| RII  | $l_{imp}$ | Total richness | −0.102 | 0.040 | 5 | −5.017 | .004 |
| $l_{imp}$ | B. rubens abundance | 0.216 | 0.005 | 5 | 6.904 | <.001 |
| $l_{imp}$ | B. rubens biomass | 0.043 | 0.007 | 5 | 6.665 | <.001 |
| $l_{imp}$ | B. rubens cover | 0.374 | 0.004 | 5 | 10.533 | <.001 |
| $l_{imp}$ | B. rubens spikelets | 0.087 | 0.006 | 5 | 8.500 | <.001 |
| $l_{imp}$ | Exotic richness | −0.093 | 0.033 | 5 | −2.443 | .058 |
| $l_{imp}$ | Native abundance | −0.059 | 0.014 | 5 | −2.200 | .079 |
| $l_{imp}$ | Native cover | −0.080 | 0.016 | 5 | −2.589 | .049 |
| $l_{imp}$ | Native richness | −0.132 | 0.015 | 5 | −3.038 | .029 |
| $l_{imp}$ | Total richness | −0.076 | 0.005 | 5 | −5.120 | .004 |