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The dark side of facilitation: native shrubs facilitate exotic annuals more strongly than native annuals

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Abstract

Positive interactions enhance biodiversity and ecosystem function, but can also exacerbate biological invasions. Facilitation of exotic invaders by exotic foundation species (invasional meltdown) has been studied extensively, but facilitation of exotic invaders by native foundation species has attracted less attention. Specifically, very few studies have examined the extent that native foundation species facilitate native and exotic competitors. Understanding the processes that mediate interactions between native and exotic species can help explain, predict, and improve management of biological invasions. Here, we examined the effects of native foundation shrubs on the relative abundance of the annual plant community – including native and exotic taxa – from 2015–2018 in a desert ecosystem at Carrizo Plain National Monument, California, USA (elevation: 723 m). Shrub effects varied by year and by the identity of annual species, but shrubs consistently enhanced the abundance of the annual plant community and facilitated both native (n=17 species) and exotic (n=4 species) taxa. However, at the provenance level, exotic annuals were facilitated 2.75 times stronger in abundance than native annuals, and exotic annuals were always more abundant than natives both near and away from shrubs. Our study reaffirms facilitation as an important process in the organisation of plant communities and confirms that both native and exotic species can form positive associations with native foundation species. However, facilitation by native foundation species can exacerbate biological invasions by increasing the local abundance of exotic invaders. Thus, the force of facilitation can have a dark side relevant to ecosystem function and management.

Keywords

Bromus rubens, deserts, exotic species, facilitation, invasional meltdown, native species, plant invasions, shrubs

Introduction

Positive interactions among species, or facilitation, can strongly influence the organisation of plant communities (Callaway 1995; Callaway 2007; Brooker et al. 2008), particularly in unproductive environments (Bertness and Callaway 1994; Maestre et al. 2009). Facilitation occurs when a foundation species ameliorates biotic or abiotic stresses that would otherwise inhibit the abundance, richness, fitness, and/or population growth of beneficiary species (Callaway 2007). For example, foundation shrubs in deserts can provide annual species with refuge from solar radiation and/or drought, resulting in increased richness and abundance of annual species inside shrub canopies relative to outside of canopies (Filazzola and Lortie 2014). Importantly, beneficiary species can experience facilitation from foundation species and interspecific competition from other beneficiary species simultaneously, which can influence the net outcome of biotic interactions (Poulos et al. 2014; Sheley and James 2014; Wright et al. 2014). Regardless, facilitation generally enhances biodiversity (Butterfield et al. 2013; McIntire and Fajardo 2014) and ecosystem function (Michalet 2006; Callaway 2007; Michalet and Pugnaire 2016).

However, facilitation can have a dark side when beneficiary species are exotic invaders. Invasive plant species pose a pervasive threat to ecosystem function worldwide (Simberloff et al. 2013), including strong effects on historic patterns of nutrient cycling (Liao et al. 2008), energy flow (Baxter et al. 2004; Pearson and Callaway 2008), and abiotic disturbance (D’Antonio and Vitousek 1992; Balch et al. 2013). These disruptions are often associated with sharp reductions in local biodiversity (Vila et al. 2011; Bellard et al. 2016). Interestingly, positive interactions have been shown to promote the success of invasive species in non-native communities (Simberloff 2006; Griffith 2010). Exotic invaders are commonly facilitated by exotic species (reviewed by Simberloff 2006), and such “invasional meltdown” (Simberloff and Von Holle 1999) is a leading hypothesis in invasion biology (Jeschke et al. 2012). Native foundation species can also facilitate exotic invaders, especially in harsh environments (Lenz and Facelli 2003; Cavieres et al. 2008; Altieri et al. 2010; Griffith 2010; Zarnetske et al. 2013; Badano et al. 2015; Hupp et al. 2017). However, native-invader facilitation has attracted less attention than the invasional meltdown hypothesis. Furthermore, very few studies have specifically addressed whether native foundation species in drylands benefit native and exotic beneficiary species to the same extent (but see Reisner et al. 2015; Ramírez et al. 2015). The biogeographic origins (i.e., provenance) of beneficiary species is an important consideration because exotic species displace native species in drylands globally (Balch et al. 2013; Bellard et al. 2016; Vitousek et al. 2017), and facilitation by native foundation species can influence the outcome of interactions between native and exotic taxa (Reisner et al. 2015). Strong facilitation of exotic species relative to native competitors could require conservationists to shift their focus from manipulating competitive interactions to facilitative ones in order to manage biological invasions (Funk et al. 2008).

The objective of this study was to investigate the extent that native and exotic species of annual plants associate with (i.e., are facilitated by) native foundation shrubs in an arid ecosystem. This issue is timely because drylands worldwide are increasingly comprised of exotic species (Vitousek et al. 2017; Simpson and Eyler 2018), and facilitation by native foundation species has considerable potential to be used as a tool for restoring native biodiversity to drylands degraded by biological invasions and other anthropogenic disturbances (Padilla and Pugnaire 2006; Funk et al. 2008; Gomez-Aparicio 2009; Lortie et al. 2018c). Specifically, we examined the hypothesis that native and exotic annual species can associate differentially with native foundation shrubs. We tested the following predictions: (i) the net abundance of the annual plant community is greater near native foundation shrubs than away from shrubs; (ii) native and exotic annual species can both associate with native foundation shrubs to become beneficiary species; and (iii) the strength of facilitation depends upon the provenance of beneficiary species. To better understand community-level outcomes of biotic interactions, we also evaluated correlations between the abundance of native and exotic annual species near and away from native foundation shrubs.

Methods

Study site and species

We surveyed annual plant communities at Carrizo Plain National Monument in the San Joaquin Desert (Germano et al. 2011) of California (35.1N, 119.6W, elevation: 723 m) at peak flowering from March to April from 2015 to 2018 at a total of seven study sites (Suppl. material 1: Table A1). This area is characterised as an arid grassland (Buck-Diaz and Evens 2011), but the native shrubs *Ephedra californica*, *Gutierrezia californica*, and *Atriplex polycarpa* are also present (U.S. Department of the Interior 2011). Here, we explored the potential for *E. californica*, the most abundant shrub species at our sites (Buck-Diaz and Evens 2011; Noble et al. 2016), to act as a foundation species. *Ephedra californica* is a long-lived perennial associated with the creosote scrublands, chaparral, and arid grasslands of southwestern North America (Cutlar 1939) and can facilitate native annuals (Lortie et al. 2018a) and endangered vertebrates (Filazzola et al. 2017; Westphal et al. 2018). We sampled a total of 21 annual plant species throughout the study (Suppl. material 1: Table A2), including 17 native and 4 exotic species. Among the exotic species sampled was *Bromus madritensis* ssp. *rubens* (*B. rubens* hereafter), one of the most problematic exotic invaders in the region (Salo 2005). Annual precipitation, mean annual temperature, and mean winter temperature at the study sites ranged from 116.22–129.44 mm, 17.5–18.0 °C, and 10.19–12.14 °C, respectively (Suppl. material 1: Table A2).

Sampling

We sampled the abundance of the annual plant community using a paired shrub-open microsite contrast with 0.5 × 0.5 m quadrats (Pescador et al. 2014). Shrub microsites were defined as the area immediately beneath the canopy of *E. californica* shrubs, and open microsites were defined as interstitial spaces at least 1 m from any shrub canopy. We did not sample areas more than 5 m away from shrubs. A total of 1194 independent pairs of shrub and open microsites were sampled, and repeated-measures were avoided by randomly selecting sampling locations at each site for each year. The size of foundation plants can influence the direction and magnitude of their effects on neighbours (Tewksbury and Lloyd 2001; Miriti 2006; Brathen and Lortie 2015). To account for this, the height, width, and perpendicular width (m) of each foundation shrub were measured, and the volume for a sphere was used to summarise shrub sizes (m^3) as a covariate in subsequent analyses. Across all study sites, mean shrub width was 2.80 m ± 0.03 SE, mean shrub volume was 23.65 m^3 ± 0.26 SE, and mean shrub density was 44.43 shrubs/ha ± 8.98 SE. These measurements are well within ranges reported by other studies in similar systems (e.g., Lortie et al. 2018a). We recorded the total abundance of each annual species present in sampling quadrats, and the provenance of each annual species was retrieved from the CalFlora database (CalFlora 2018). Individuals were easy to distinguish because the annual species we sampled do not reproduce asexually. Data are publicly archived (Lortie et al. 2018b).

Statistical analyses

Relative interaction indices ("RIIs" hereafter; Armas et al. 2004) were used to estimate the effects of *E. californica* shrubs on the relative abundance of annual species. We calculated RIIs as follows:

$$RII = \frac{A_s - A_c}{A_s + A_c}$$

where A_s is the abundance (i.e., no. individual plants) of an annual species in a shrub microsite and A_c is the abundance of the same annual species in the paired open microsite. RII values range from -1 to +1. Negative RII values indicate negative (competitive) effects of shrubs on annual species, positive values indicate positive (facilitative) effects, and a value of 0 indicates a neutral effect. Annuals are only considered to be beneficiary species of foundation shrubs when RII is positive.

To evaluate whether annual species were generally more abundant near *E. californica* shrubs than away from shrubs, we performed independent one-sample *t*-tests with mean RII (pooled per species per year) as the response variable for each year of the study. We used an additional one-sample *t*-test to summarise the net strength of shrub associations across all study years. We evaluated the net strength of species-specific shrub associations using a linear mixed-effects model with RII (pooled per species per year) as the response variable, species identity and shrub volume as fixed factors, and study year as a random factor. Treating year as a random factor accounted for stochastic sources of inter-annual variation, such as climate (Suppl. material 1: Table A2).

To test whether native and exotic annual species associated differentially with *E. californica* at the provenance level, we employed independent generalised linear models for each year of the study with RII (pooled per species) as the response variable and species provenance as a fixed factor. We contrasted the net strength of native vs. exotic associations with shrubs across all study years using a linear mixed-effects model with RII (pooled per species per year) as the response variable, species provenance and shrub volume as fixed factors, and study year as a random factor.

We inferred the outcome of biotic interactions between native and exotic annuals at the provenance level using *t*-tests and linear models. For shrub and open microsites and for each year of the study, we contrasted the net abundance of native vs. exotic annuals using independent one-sample *t*-tests with abundance (i.e., not RIIs) as the response variable. We then regressed net native abundance against net exotic abundance using linear models. These regressions addressed the effects of exotic annual species on the abundance of native annual species. Negative line slopes suggested competitive effects; positive line slopes suggested facilitative effects (Pearson et al. 2016).

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 et al. 2018). *T*-tests, generalised linear models, and linear models used the t.test, glm, and lm functions, respectively (R Development Core Team 2018). We used the emmeans function of the emmeans package (Lenth et al. 2018) for post-hoc contrasts of factors from generalised and mixed-effects linear models. R code is publicly archived at Zenodo (Lortie 2018).

Results

Annual plant species were generally more abundant near native foundation shrubs than away from shrubs. Across all species and years, annual plants were 1.35 (± 0.68 SE) times more abundant under shrubs than in the open (df = 2381, *t*-value = 12.97, $P < 0.01$). Accordingly, net RII summarised across all species and years was greater than zero (RII = 0.22 ± 0.05 SE, df = 30.00, *t*-value = 4.98, $P << 0.01$) (Table 1). In addition, RII values summarised across all annual species were greater than zero for each year of the study except 2017 and were never less than zero (Table 1).

In each year of the study, native and exotic annual species positively associated with *E. californica* to become beneficiary species (Fig. 1). Many shrub-annual plant associations were neutral, but none were negative (Fig. 1, Suppl. material 1: Table A3). Interestingly, the only annual species that formed a positive association with *E. californica* across all study years was the exotic invader *B. rubens* (RII = 0.55 ± 0.16 SE, df = 4.09, *t*-value = 2.72, $P = 0.05$) (Suppl. material 1: Table A3). Shrub size did not affect association patterns at the species level (Suppl. material 1: Table A4).

Interestingly, native and exotic annuals associated differentially with native foundation shrubs at the provenance level. At the provenance level, net RII summarised

Table 1. Mean effects (RII ± SE) of shrubs on annual species at the community level. RII values are summarised across all annual species for each year of the study (2015–2018) and for all study years combined (Net). $P \leq 0.05$ indicates that RII values differ significantly from zero, according to independent *t*-tests.

Year	RII	df	*t*-value	*P*-value
2015	0.18 (0.07)	11.00	2.86	0.01
2016	0.10 (0.05)	8.00	2.21	0.05
2017	0.39 (0.31)	3.00	2.06	0.13
2018	0.38 (0.14)	5.00	3.62	0.01
Net	0.22 (0.05)	30.0	4.98	<<0.01

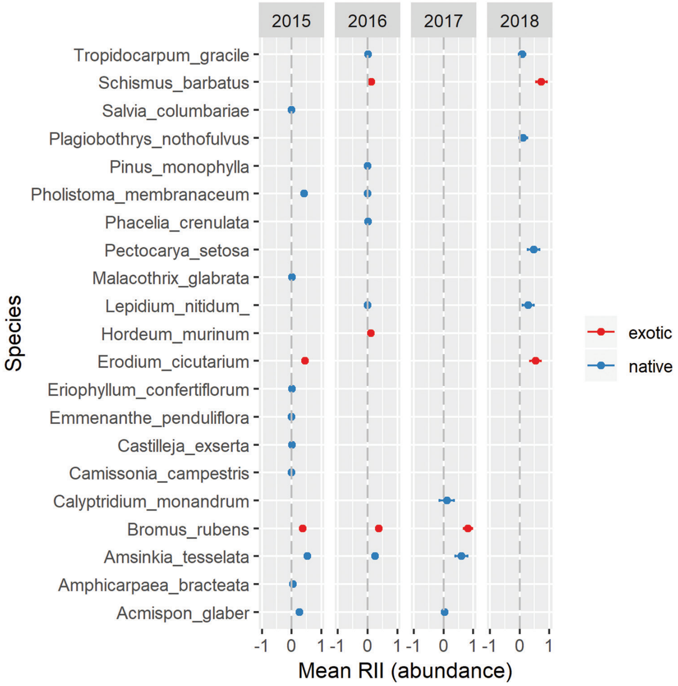

Figure 1. Year-by-year effects (RII ± 95% CI) of native foundation shrubs on the abundance of annual species. Net effects across all years are summarised in Suppl. material 1: Table A3.

Table 2. Mean effects (RII ± SE) of shrubs on annual species at the provenance level. RII values are summarised across native (RII_{native}) and exotic (RII_{exotic}) annual species for each year of the study (2015–2018) and for all study years combined (Net). $P \leq 0.05$ indicates that RII values differ at the provenance level, according to independent generalized linear models (2015–2018) and a linear mixed-effects model (Net).

Year	RII_{native}	RII_{exotic}	df	Z-ratio	*P*-value
2015	0.13 (0.06)	0.41 (0.14)	11.00	1.90	0.05
2016	0.05 (0.05)	0.21 (0.07)	8.00	1.91	0.05
2017	0.25 (0.18)	0.82 (0.30)	3.00	1.61	0.10
2018	0.24 (0.09)	0.64 (0.12)	5.00	2.66	<0.01
Net	0.16 (0.13)	0.44 (0.15)	21.01	*9.28	<0.01

*F-value; see Suppl. material 1: Table A5 for complete statistics across all years was 2.75 ± 0.14 SE times greater for exotic annuals than for native annuals (df = 21.01, *Z*-ratio = 3.05, $P < 0.01$), and this general trend (i.e., greater RII values for exotic annuals than native annuals at the provenance level) was apparent in each year of the study except 2017 (Table 2). At the provenance level, RII values for native annuals were never greater than RII values for exotic annuals (Table 2). Shrub size did not affect association patterns at the provenance level (Suppl. material 1: Table A5).

Regardless of year and microsite, exotic annual species were always more abundant than native annual species. Summarised across all years, the net abundance of exotic annuals was 4.97 ± 0.78 SE and 3.05 ± 0.78 SE times greater than the net abundance of native annuals in shrub and open microsites, respectively (df ≥ 1863.40, *t*-value ≥ |28.89|, $P < 0.01$) (Suppl. material 1: Table A6). This trend (i.e., greater net abundance of exotic annuals than native annuals) was apparent in shrub and open microsites for each year of the study (Suppl. material 1: Table A6).

At the provenance level, the relationship between the abundance of native and exotic annuals varied considerably by year (Fig. 2). In 2015 and in both shrub and open microsites, native and exotic abundance were negatively related (line slope ≤ -0.25 ± 0.03 SE, df ≥ 838, *t*-value ≥ |8.83|, $P < 0.01$) (Suppl. material 1: Table A7). In 2016–2017, we detected no relationships between native and exotic abundance (df ≥ 28.00, *t*-value ≤ |1.01|, $P \geq 0.31$) (Suppl. material 1: Table A7). In 2018, native and exotic abundance were unrelated in shrub microsites (line slope = 0.04 ± 0.02 SE, df = 22.00, *t*-value = 1.62, $P = 0.12$) but positively related in open microsites (line slope = 0.35 ± 0.04 SE, df = 22.00, *t*-value = 7.88, $P < 0.01$) (Suppl. material 1: Table A7).

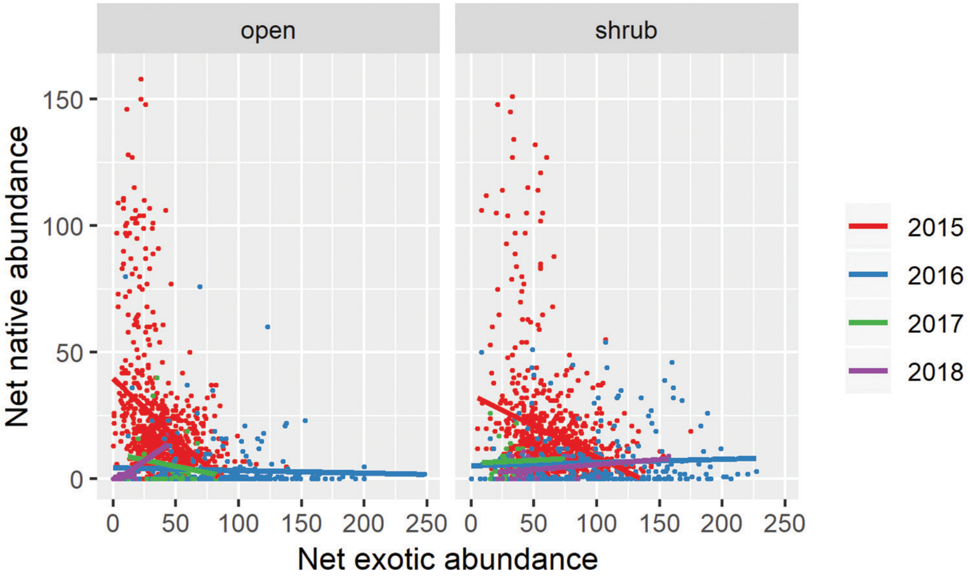

Figure 2. Net abundance of native annuals plotted against net abundance of exotic annuals for each year of the study (2015–2018). Statistics are shown in Suppl. material 1: Table A7.

Discussion

Facilitation is an important process in the assembly of plant communities in drylands and other extreme environments globally (Callaway 2007), but few studies have contrasted the effects of native foundation species on native vs. exotic beneficiary species (but see Reisner et al. 2015; Ramírez et al. 2015; Hupp et al. 2017; Llambi et al. 2018). Understanding how ecological processes affect native and exotic taxa has important implications for the conservation of ecosystems affected by biological invasions (Simberloff et al. 2013, Pearson et al. 2018). In an arid grassland, we found that native and exotic annual species consistently formed positive associations with the native shrub *E. californica*. However, the strength of these associations depended upon the provenance of beneficiary species – at the provenance level, exotic annuals consistently associated more strongly with *E. californica* shrubs than native annuals, and in terms of relative abundance, exotic species always dominated annual plant communities. Thus, the force of facilitation had a dark side at Carrizo Plain.

Our study coincides with a broad literature suggesting that ecological processes can have markedly different effects on native and exotic taxa in the same communities (reviewed by Levine et al. 2003; Mitchell et al. 2006; Catford et al. 2009; Pearson et al. 2018). Most studies have focused on the effects of negative interactions like competition (Seabloom et al. 2003; Vila and Weiner 2004; Callaway et al. 2011) and predation (Maron et al. 2012; Lucero 2018; Lucero and Callaway 2018), but our study is unique in contrasting the effects of positive interactions on native and exotic taxa at the provenance level. The extent that community-level processes have divergent effects on native and exotic neighbours has been hotly debated (Davis et al. 2011; Simberloff 2011) but is an important consideration for explaining, predicting, and managing biological invasions (Pearson et al. 2018).

Our study underscores the potential for facilitation by native foundation species to exacerbate biological invasions. Native foundation species can increase the ecophysiological performance (Cavieres et al. 2008), abundance (Lenz and Facelli 2003; Reisner et al. 2015; Hupp et al. 2017), population growth (Griffith 2010), and spatial distribution (Altieri et al. 2010) of exotic invaders. In addition, facilitation by native foundation species may help explain the initial colonisation of some exotic species in non-native communities (Stohlgren et al. 2006; Fridley et al. 2007). In this context, the initial colonisation of exotic species like *B. rubens*, *Schismus barbatus*, and *Erodium cicutarium* at Carrizo Plain may have been facilitated by native foundation shrubs. However, this interpretation should be viewed with some caution because exotic annuals in this system can clearly colonise open microsites without the aid of shrubs (Suppl. material 1: Table A6). Because exotic annuals were relatively more abundant than native annuals in both shrub and open microsites (Suppl. material 1: Table A6), we argue that shrub facilitation probably reinforced but did not entirely drive the dominance (in terms of relative abundance) of exotic annuals in this system. Our study emphasises the importance of interpreting the effects of ecological processes within the context of net outcomes at the community level (Brooker et al. 2005; Soliveres et al. 2015).

There was considerable inter-annual variation in the effects of *E. californica* on annual species. The strength of positive interactions is known to increase with environmental severity (Bertness and Callaway 1994; Maestre et al. 2009; He et al. 2013; Gao et al. 2018), and environmental severity (i.e., drought and heat stress) can fluctuate widely from year to year in deserts (Venable 2007). In this context, native shrubs facilitated the abundance of the greatest number of species in 2015 (Fig. 1), the study's driest year (Suppl. material 1: Table A2). Drought intensity is predicted to increase in deserts across southwestern North America in the 21st century (Cook et al. 2015). If so, the number of species that associate with shrubs and the strength of these associations may also increase (He et al. 2013; Gao et al. 2018), along with any negative net outcomes of facilitation.

We observed no effects of shrub size on association patterns at either the species or provenance levels (Suppl. material 1: Tables A4, 5). This accords with a recent study by Lortie et al. (2018a) showing that the positive effects of *E. californica* on annual species are independent of canopy size. Our study extends these results by considering the provenance of annuals. In other severe environments, shrub size has strongly influenced the direction and magnitude of association patterns (Tewksbury and Lloyd 2001; Miriti 2006; Brathen and Lortie 2015) and may be an important consideration for other foundation species at Carrizo Plain.

Our study hints that facilitation by *E. californica* shrubs can alter the outcome of interspecific interactions among native and exotic neighbours. In 2018, the abundance of native and exotic annuals was positively related in open microsites (where *E. californica* was absent) but unrelated in shrub microsites (where *E. californica* was present). These relationships suggest facilitation between native and exotic annuals in open but not shrub microsites. Thus, it is possible that *E. californica* attenuated positive interactions between native and exotic annuals in that year. Facilitation of native species by exotic neighbours – including invasive species – is not necessarily unusual in deserts. For instance, in the Great Basin Desert, Lucero et al. (2015) found evidence that the native perennial grass *Elymus elymoides* was more abundant and produced a significantly greater seed rain in areas invaded by exotic *Bromus tectorum* than in adjacent non-invaded areas. Thus, invasive species do not always impose negative effects on native neighbours. Importantly, a positive relationship between native and exotic abundance does not necessarily indicate facilitation; native and exotic plants could both respond favourably to particularly good microsites.

Our study highlights the potential for beneficiary species to experience facilitation from foundation species and interspecific competition from other beneficiary species simultaneously. In 2015, competition and facilitation appeared to operate in tandem to influence biodiversity patterns under shrubs (Fig. 2, Tables 1, 2). This coincides with a number of recent studies (Maestre et al. 2004, Poulos et al. 2014; Sheley and James 2014; Wright et al. 2014; Reisner et al. 2015; Llambi et al. 2018). The relative importance (*sensu* Brooker et al. 2005) of these biotic interactions likely depends upon abiotic conditions and the ontological development of interacting species (Callaway et al. 1996; Fagundes et al. 2018; Gao et al. 2018; Pierce et al. 2018).

We hypothesised that any competitive effects of exotic annuals on native annuals in 2015 may have been driven by *B. rubens*, as this exotic species was facilitated more strongly and consistently than any other (Fig. 1, Suppl. material 1: Table A3). To test this, we regressed the abundance of native annuals (all species combined) against the abundance of *B. rubens* for each year of the study. We found no negative relationship between the net abundance of native annual species and *B. rubens* in 2015 or any other year (Suppl. material 1: Fig. A1), suggesting that any competitive effects of exotics on natives were not driven by *B. rubens* alone. However, it is important to note that *B. rubens* has strongly reduced the abundance of native competitors in arid environments similar to our study system (Brooks 2000; Salo 2005). The source of such context-dependence is unclear, but the presence of competitive interactions between native and invasive species at fine spatial scales is consistent with an extensive literature (reviewed by Levine et al. 2003; Vila and Weiner 2004; Mitchell et al. 2006; Liao et al. 2008; Vila et al. 2011).

Our data do not speak to the mechanisms by which facilitation occurred. Non-mutually exclusive mechanisms of facilitation include seed trapping, amelioration of abiotic stress, modification of soil biogeochemical processes, increasing pollinator visitation, and/or providing herbivore protection (reviewed by Filazzola and Lortie 2014). Importantly, we do not know whether native and exotic species were facilitated via the same mechanisms. If native and exotic species generally capitalise on different mechanisms of facilitation, conservationists could potentially manage biological invasions by disrupting the mechanistic pathways specific to exotics.

Our findings have practical implications. Because *E. californica* canopies were hotspots for the abundance of native and exotic annual species, conservationists may consider targeting their efforts to control invasive species under shrub canopies. For example, herbicide applications to reduce the density of invasive species and subsequent reseeding efforts to increase the density of native species (Huddleston and Young 2005; Rowe 2010; Clements et al. 2017) might yield the greatest dividends if focused under shrub canopies. In addition, reducing the density of *B. rubens* and *S. barbatus* under shrub canopies could help decrease wildfire risk by reducing fine fuel loads (Brooks 1999; Brooks et al. 2004). Positive feedbacks between wildfire and the abundance of exotic invaders are well documented (reviewed by D'Antonio and Vitousek 1992; Brooks et al. 2004), and wildfire-invasion feedbacks may cause rapid state changes in dryland vegetation (Balch et al. 2013; Horn and St. Clair 2017).

Furthermore, our study suggests caution in using facilitation by native shrubs as a tool for restoring native biodiversity to degraded environments. Drylands in California and globally are being retired from intensive agricultural use due to drought, poor soils, and changing climate (Webb et al. 2017), presenting critical opportunities for restoring native biodiversity (Kelsey et al. 2018; Lortie et al. 2018c). In this context, facilitation by native shrubs has attracted considerable interest as a restoration tool (Padilla and Pugnaire 2006; Funk et al. 2008; Gomez-Aparicio 2009; Lortie et al. 2018c). However, strong facilitation of exotic and invasive species by *E. californica* could undermine restoration efforts in our study area. For instance, the San Joaquin kit fox (*Vulpes macrotis* ssp. *mutica*) is an endangered species endemic to the San Joaquin Desert (Williams et al. 1998) that has been identified as a potential target for restoration (Lortie et al. 2018c). Importantly, kit foxes avoid areas with high densities of exotic grass species like *B. rubens*, *S. barbatus*, and *Hordeum murinum* (Smith et al. 2005). Accordingly, facilitation of these exotic grass species by *E. californica* (Fig. 1) could be counterproductive to the restoration of kit foxes and many other wildlife species that avoid areas with high densities of exotic grasses (Ostoja and Schupp 2009; Freeman et al. 2014; Filazzola et al. 2017). Our study highlights the need for ecological restoration based on facilitation to be tailored to the species and environments in question (Noumi et al. 2015).

Conclusions

Our study reaffirms facilitation as an important force in the organisation of plant communities and confirms that both native and exotic beneficiary species can positively associate with native foundation shrubs. However, we found that the magnitude of facilitation depended upon the biogeographic origins of beneficiary species – at the provenance level, exotic species were facilitated in abundance much stronger than native species. Importantly and regardless of inter-annual variation in climate, the net outcome of biotic interactions that included facilitation was an annual plant community dominated (in terms of relative abundance) by exotic species. Our study stresses that the effects of ecological processes like facilitation must not be decoupled from net outcomes relevant to conservation and restoration. In systems like ours where facilitation increases the abundance of invasive species, managing positive interactions may be a useful conservation strategy.

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Supplementary material 1

Supplementary materials

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Data type: multimedia

Explanation note: Supplementary materials for this article are included in Appendix A1, which consists of one supplementary figure (Fig. A1) and seven supplementary tables (Tables A1–A7).

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