**Cost of facilitation: invasive grasses limit recruitment of benefactor shrubs**

Alessandro Filazzola1\*, Michael Westphal2, and Christopher J. Lortie1

1. Department of Biology, York University, 4700 Keele St., Toronto, ON, M3J 1P3 Canada.

2. Bureau of Land Management, Central Coast Field Office, 940 2nd Avenue, Marina, CA, 93933, USA

\* Corresponding author. Tel.: 416-736-2100 ext 30533; fax: 416-736-5698.

E-mail address: fitz90@yorku.ca.

**Abstract**

The biodiversity of deserts is becoming increasingly threatened from global change including the introduction of invasive species. Desert shrubs are foundation species that can facilitate plant communities, but these ecological interactions can also benefit exotic species. The reciprocal costs of facilitation on the reproduction of benefactors has been examined through flowering and seed production? But not recruitment of the native benefactors with competing exotics? Is that what you mean>. We tested the hypothesis that the recruitment of benefactor shrubs is reduced by the presence of similar life-staged invasive grasses or something like – ie I think you need to be specific that is seed-seed interactions tested onwards - that they facilitate and this effect increases when resources are relatively more limited be more specific here too – that increasing water limitation shifts interactions to higher intensities of competition?. In the San Joaquin Desert of California, we measured the spatial association of the native shrub *Ephedra californica* with the non-native grass *Bromus madritensis – or flip? Did you measure brome with shrubs or baby shrubs with brome?*. We also collected seed, and we did greenhouse trials with *E. californica* and *B. madritnesis* at 5 densities and at 3 water levels or whatever etc.. In the field, *E. californica* facilitated *B. madritnesis* within their canopy, but the two species were negatively associated at the landscape-level at scales of ... In greenhouse trials, *E. californica* was negatively impacted by shade, but this species was tolerant of low water, disturbance, and variable soil substrates. Increasing densities of *B. madritensis* siginificantly? reduced the recruitment rate of *E. californica*, and other limitations did not mediate this effect. The hypothesis that the potential recruitment ofa benefactor species can be influenced by non-native protégé species was supported and this explains the association patterns at the landscape-level. Desert shrubs are relatively tolerant species of low-resource availability, but invasive grass cover can disrupt this tolerance and thus threaten the fundamental functioning of these systems.

**Keywords:** facilitation, positive interactions, trade-offs, costs, net interactions, exotic species, invasion, competition, recruitment, deserts, benefactor species

**Introduction**

Deserts are important ecological systems that are vulnerable to anthropogenic disturbance. In California, deserts support the highest levels of endemics relative to any other ecosystem regionally? (Baldwin et al. 2017). However, In the San Joaquin Desert of California, endemic species have seen significant declines in abundance because of habitat destruction, and the remaining undisturbed land is heavily invaded by Mediterranean grasses (Germano et al. 2011). Invasive grasses are a concern for these arid environments because they can cause the conversion of shrublands into annual grasslands (Bradley and Mustard 2005; Abatzoglou and Kolden 2011), increase fuel load for wildfires (Brooks et al. 2004), and threaten native animals (Filazzola et al. 2017). For instance, the grass genus *Bromus* *spp.* has been significantly dominant in North American Deserts including *B. tectorum* in the Great Basin Desert (Bradley and Mustard 2005), *B. madritensis rubens* in the Mojave/San Joaquin Deserts (Brooks 2003; Germano et al. 2012), and *B. diandrus* in the semi-arid areas of the western coast (Jackson 1985). These species have increased significantly in abundance and are projected to increase further with habitat disturbances (Hansen and Clevenger 2005; Monty et al. 2013) and climate change (Abatzoglou and Kolden 2011). The shrublands within the San Joaquin Desert represent some of the least impacted area by anthropogenic disturbance that support many endangered species (Germano et al. 2001; Haight et al. 2004; Bean et al. 2014; Filazzola et al. 2017), but continued invasion by non-native grasses threatens the endemic biodiversity. Examining shrub interactions with invasive species is critical for the development of restoration strategies to support desert biodiversity and conserve native species. Great intro. Wow!

Shrubs are important foundation species that facilitate the abundance and productivity of annual plants in desert ecosystems. Desert shrubs are tolerant of low-resource availability and once established can create microrefugia within their canopy by ameliorating climate extremes, inhibiting herbivory, and increasing soil moisture through hydraulic lift add a few more citations here so that it does not look like we just cite ourselves – toss in a michalet paper too? (Filazzola and Lortie 2014). Shrubs can thus facilitate annual species, typically through increases in plant densities, but not necessarily species richness (Gómez-Aparicio 2009; Pescador et al. 2014). Exotic species can sometimes take advantage of these shrub microhabitats by exploiting the increased resource availability or reduced abiotic stress (Holzapfel and Mahall 1999; Rodríguez-Buriticá and Miriti 2009). As a result, benefactor plants can facilitate the invasion of plant species into otherwise unsuitable habitat (Richardson et al. 2000; Mitchell et al. 2006). Increases in exotic abundance can in turn threaten the benefactor plants by reducing fitness, lowering productivity, and limiting recruitment (Holzapfel and Mahall 1999; McIntire 2014; Schöb et al. 2014a). In the deserts of North America, invasive grasses are common and continue to threaten the native shrubs species through competition and altered fire-frequencies (Link et al. 2006; Condon et al. 2011; Bradley et al. 2016). Examining the bidirectional interactions between benefactor and beneficiary species is an emerging and important field of research for understanding community assembly (Citations) – Schob, McIntire and Fajardo 2014 etc.. These interactions can inform management of some of the negative effects of invasive plant species.

The shrub *E. californica* is a dominant species that occurs frequently within the San Joaquin Desert and facilitates endemic species. At the Panoche Hills, *E. californica* dominated the landscape comprising greater than 80% of the perennial cover and at densities 3-5 times greater than other Ephedra species in the Mojave Desert (Webb et al. 1987). *E. californica* shares a narrow environmental niche that results in a relatively patchy distribution in the arid portions of California relative to more common species such as *Larrea tridentata*, *Artemisia tridentata*, and *Atriplex lentiformis* (Beatley 1975). However, in the San Joaquin Valley, *E. californica* often dominates the landscape, comprising greater than 80% of the perennial cover (Filazzola et al. 2017), at densities 3-5 times greater than other Ephedra species in the Mojave Desert (Webb et al. 1987). In systems where *E. californica* is dominant, the shrub acts as a foundation species supporting endemic species that are endangered (Filazzola et al. 2017) and facilitating the annual plant community (Lortie et al. 2018). *E. californica* has also been observed to facilitate exotic grass densities (Filazzola et al. 2018), but the effects of grasses on the shrub have never been tested. Testing limitations in *E. californica* recruitment is essential for the conservation of the remaining San Joaquin Desert because of the strong foundational role the shrub has in maintaining the endemic community. Ok but depends in journal – could move all this to Methods and out in a Study species subsection

The reciprocal effects of shrub facilitation on exotic species are necessary to explore because shrubs are often foundation species in deserts supporting community structure – now this connects better to the paragraph before the ephedra one. Here, we used the native shrub *E. californica* and the exotic grass *Bromus madritensis* because each are dominant species in the remnants of the San Joaquin Desert. We collected seed from the field and conducted greenhouse experiments using a density series of exotic grasses on the native shrub. We experimentally manipulated factors that can limit shrub recruitment including soil substrate, shade, soil moisture, and herbivory. We hypothesize that potential shrub recruitment is negatively impacted by increasing invasive grass densities and that these impacts are greater when the environment is relatively more limiting (sensu Grime – need to introduce somewhere above). We predict that 1) shrub emergence from seed and survival will be greatest without shade and in a sandy substrate (i.e. no light limitation and ideal substrate); 2) increasing densities of invasive grasses reduce the emergence and survival of shrub seedlings (competitive interference good or could just brome competitively interferes with ephedra?), and 3) limitations in resources or herbivory will further increase the negative impacts of invasive grasses on shrubs – hmm is this from the greenhouse trial?.

**Methods**

*Study Site and species*

The Panoche Hills Recreation Area (36°41.776′N, 120°47.886′W, at 650 m above sea level) located in the western portion of the San Joaquin Valley in California was used for field surveys and seed collection. It is a semi-arid climate with average precipitation of 25.5 cm and mean monthly temperatures of 8.9°C in January and 26.1° July as recorded at the Panoche Hills weather station Los Banos Weather Station (37°03.30’N, 120°51.00’W; U.S. Climate Data 2016). The site is a shrubland that is dominated by the invasive grass *Bromus madritensis* spp. *rubens* (hereafter *B. madritensis*). The dominant shrub is *Ephedra californica* (>80%), but there are other shrubs species including *Atriplex lentiformis* and *Ericameria linearifolia* (Hawbecker 1951). The native annual plant community is in relatively low abundance and includes *Phacelia tanacetifolia, Amsinckia grandiflora, Caulanthus lasiophyllus*, and *Lepidium nitidium.* The site is occasionally grazed by domestic sheep and has native herbivores including kangaroo rats (*Dipodomys spp.*), cotton-tailed rabbits (*Sylvilagus audubonii*), and black-tailed jackrabbit (*Lepus californicus*) (citation to animal presences).

*Ephedra californica* (Ephedraceae) is a native shrub to California that is distributed throughout the San Joaquin Desert and portions of the Mojave Desert (Germano et al. 2011; Ickert-Bond 2012). It is a member of the Gnetophyta division of plants with a hybrid form of reproduction that includes flowers and cones. *E. californica* has stems that range between 30 and 150 cm in length with small leaves between 2 and 6 mm (Ickert-Bond 2012). It is distinguished from other Ephedra species by having three leaves per node along its stem and membranous cones (Ickert-Bond 2012; Loera et al. 2012). *Bromus madritensis* (Poaceae) is a non-native grass species originating from the Mediterranean area of Europe (Saarela and Peterson 2012). It is widely distributed in arid and semi-arid areas of the western United States and threatens the persistent of perennial species where present in high densities (Salo 2005). *B. madritensis* is found more frequently and in higher biomass under *E. californica* canopies relative to open areas (Lortie et al. 2018; Filazzola et al. 2018). nice

*Field surveys*

In May of 2013, a total of 700 shrubs were surveyed, marked with metal tags, and georeferenced. The dimensions of the shrubs were measured including the longest diameter (D1), the diameter immediately perpendicular to D1 (D2) and the height of the shrub from soil surface to highest branch. The area of the shrub was calculated using the formula for the area of a circle, where r2 equaled half of D1 and D2 multiplied together (Eq 1). A visual estimate of shrub decadence, hereafter shrub canopy, on a Likert scale of 0–10 was also measured with 0 being no canopy or dead and 10 being a 100% of canopy green?. – did you use canopy decadence at all in paper?

Eq 1

Seed of *E. californica* was collected in May 2013 by collecting soil 5 cm below the surface under shrub canopies and sieving out sand or debris until only the seed remained with a 500 um sieve?. Seed of *E. californica* is relatively large (approximately 1 cm in diameter) allowing for rapid identification and collection of seeds. Seed of *B. madritensis* was collected from the seed heads of individual plants following senescence at the same site and near the shrubs. Any seed that was visible damaged, burst, or underdeveloped were removed from the collections. In September 2013, residual dry matter (RDM) was collected within a 20 x 20 cm quadrats placed at 1000 locations throughout the Panoche Hills in a grid-pattern and were spaced 10 m apart from each other. RDM is a measure used by land managers in California to estimate ecosystem productivity and 1 g per quadrat is estimated to be approximately 20 kg of biomass per acre (Bartolome et al. 2002). RDM is comprised of any remaining biomass at the end of the growing season (typically late summer) and in the San Joaquin Desert is primarily composed of senesced annual plants. We interpolated the RDM values at each shrub using ordinary krigging in ArcGIS (see method in Filazzola et al. 2017). Perfect.

Quick Qs – is this from another ms – I always try to ensure a bit different – just checking

How does canopy dec and rdm relate to the current study focus? I will wait and see but wondering if needed

Also – this section is called field survey so you mention the landscape association survey between ephedra and brome here in this section too right?

*Greenhouse experiments*

Two greenhouse experiments were conducted. The first? tested the optimal substrate and light for *E. californica* without neighbours, and the second? tested the impacts of *B. madritensis* densities on *E. californica* recruitment including these abiotic factors?. Each experiment used plant pots that were 10 cm in diameter and 10 cm in height. In the first experiment, we used 160 pots with five different soil substrates based on percentage of sand content: 0%, 25%, 50%, 75%, and 100%. The sand that was used was Quikrete ® Play Sand (https://www.quikrete.com/) and the soil that used was collected from the Panoche Hills in May 2013 by sieving the ground samples using a 0.125 mm sieve. All mixtures included a 5% perlite component. Half of the total pots were also placed in a shade treatment generated via 100%? shade cloth (they come in different permeabilities so list what you used here). On November 20th of 2014, three seeds of *E. californica* were placed in each pot and water immediately. Surveys were conducted every week and watered every other day until February 25th 2015. Surveys measured the number of emerged plants and their survival from the previous survey – hmm and from number of seeds added? Ie 3?. After 14 weeks, all above-ground biomass was harvested, oven-dried at 85°C for 3 days, and weighed to the nearest milligram.

In the second experiment, we used 700 plant pots with five different densities of *B. madritensis* seeds: 0, 2, 5, 10, & 20. We also tested abiotic factors that may limit the growth of *E. californica* by using modifications on the control conditions tested in the first greenhouse trial. The optimal and thus control conditions (i.e. no limitations) were full light, moderate water (10 mL / day), unclipped, and soil substrate that is 50% sand, 45% topsoil, and 5% perlite. The six different treatments that were low water (5 mL / day), high water (20 mL / day), partial shade, full shade, *E. californica* clipped once, and clipped twice orthogonally?. Each *B. madritensis* density level had 20 replicates and thus there were 100 pots used in each treatment. Tiny bit unclear if all levels crossed by others – maybe state directly The location of each pot was randomized within each treatment, and a single *E. californica* seed was added to each pot. The experiment began on August 19th, 2015 and was surveyed every two-weeks for 10 weeks. Surveys measured for each species the number of emerged plants and their survival from the previous survey. All above-ground biomass was harvested, separated by species, oven-dried at 85°C for 3 days, and weighed to the nearest...

*Statistical analysis*

We correlated? the density of *E. californica established shrubs* in the field to the biomass of *B. madritensis under its canopies?*. We binned the area of *E. californica* and calculated the average shrub density and RDM weight for each size-category hmm? So RDM is the measure of brome biomass?. We then fitted a linear model with shrub density as the predictor and log-transformed RDM as the response – buy why? I thought it was brome effects on shrub not the other way around?. To test for optimal conditions for the growth of *E. californica,* we examined the rates of recruitment and survival in the greenhouse experiments. We fitted a GLMM? model with percentage of sand in soil as the predictor and the total number of *E. californica* germinants as the response. This model was fitted to a second-order polynomial why?. We calculated rates of survival using a Cox proportional hazards regression model using Breslow approximation (Andersen et al. 1982). These models were fit with sand and shade-level as the predictors and the survival between census periods as the response variable. Ok – bit confusing

We tested the effects of *B. madritensis* on *E. californica* by fitting a linear model with number of total number of emerged *B. madritensis* individuals as the predictor variable in the greenhouse density trial . The average value of *E. californica* for each *B. madritensis* level was calculated and fitted as the response variable including number of emerged individuals, final number of surviving individuals, above-ground biomass, and below-ground biomass – why though? I thought the point was exotic effects on native benefactor ie the cost of facilitation – I think you need to flip and explain the stats making it clear you are testing CoF not the other way around…. We also tested the effects of the different treatments and the initial density of *B. madritnesis* on *E. californica* for the total biomass and final number – should be propoportion I think not number of individuals (i.e. recruitment) so this the key not the other way to put this first - . We fitted generalized linear regression (GLMs) with a binomial distribution for recruitment and a Gamma distribution for total biomass of values above zero (Citation). We chose this two-part model structure to estimate both the probability of the plant emerging (presence/absence) and the biomass values of plants that emerged (Foster and Bravington 2013). Models were run separately for each treatment type (i.e. water, shade, and clipping). We ran each model separately because the treatments were not fully crossed – ahah so not orthogonal?, and this method allowed for comparisons among levels within each treatment. All stats were done in R… etc and list and cite packages above for each test.

**Results**

The 700 shrubs measured in the field were on average 1.33 ± 0.015 m tall, 3.45 ± 0.051 m along the longest diameter, 9.32 ± 0.27 m2 in area, and a density of 43.2 ± 6.27 shrubs per hectare. *B. madritensis* was the dominant grass species comprising greater than 60% of the annual plant community (Filazzola et al. 2018). The average RDM value was 7.04 ± 0.21 g per quadrat or 348 ± 10.4 kg of biomass per hectare. Shrub density was negatively correlated to the interpolated RDM values with larger and less dense shrubs being more frequent in areas of high RDM (F18 = 13.9, p = 0.0015, r2 = 0.41; Figure 1). So is the assumption here that RDM is all or mostly exotic?? Some referee will challenge this so best make a clear statement in methods about this… do you also have brome densities? I think you do right? If not, I have those data from another dataset for you – should add I think? Be cool to test. Do you still have the RDM in bags? I think I saw it in the storage room in lumbers? What proportion of RDM is brome?

The proportion established of ephedra? in the abiotic factor greenhouse trial was significantly greater in pots with full-sun (χ2 = -10.7, p = 0.0011) and at intermediate levels of sand within the soil (F2 = 20.6, p = 0.046, r2 = 0.91; Figure 3). However, the rate of survival for *E. californica* was significantly lower in full-sun microsites (χ2 = -12.8, p < 0.001; Figure 2a) and with increasing sand in soil (χ2 = -23.3, p < 0.001; Figure 2b). ok – I would call the first trial abiotic factor trial and the second one density competition trial or something like that to make it clear.

The average rate of germination in all greenhouse trials for *E. californica* was 9.86% and for *B.* *madritensis* was 51.4% when grown in monocultures? Or across all treatments?. The abundance of *B. madritensis* per pot had no effect on *E. californica* proportionate emergence … ie you only added 3 seeds right so really unlikely there would be so use proportion? (F14= 1.23, p = 0.28) or final number of individuals (F14 = 0.26, p = 0.62), but significantly reduced above-ground (F14= 6.32, p = 0.025; Figure 4a) and below-ground biomass of ephedra? (F14= 12.8, p < 0.001; Figure 4b). There was no effect of the initial seed density of *B. madritensis* on *E. californica* total biomass or final proportion of individuals established (Table 1) – this is all pretty confusing and not sure a referee will buy it. Need to make much more clear and link what you are doing statistically to the purpose of paper. Clipping and shade treatments significantly reduced the total biomass of *E. californica*, but there was no effect of what?? between the different water levels (Table 1). confusing

**Discussion**

Foundation shrub species support desert ecosystems through positive interactions, but exotic species can also capitalize on this facilitation and in turn impact the benefactors. This reciprocity hypothesis between benefactor and exotic beneficiary species can be negative was supported in the San Joaquin Desert suggesting that there can be a cost of facilitation to native foundation plant species in arid systems. There was an inverse relationship between shrub densities at the landscape scale and invasive grass cover (RDM) in the field. Both above and below-ground biomass for *E. californica* decreased with non-native grass densities in greenhouse trials. However, there was no evidence that environmental constraints such as light, clipping, or water availability increased the extent of suppressed recruitment of *E. californica* by a common invasive grass species. Conserving desert biodiversity can be challenging given the sensitivity of these systems to disturbance and relatively slow ability to recover (Lovich and Bainbridge 1999). These findings suggest that bidirectional interactions between foundational plant species and common exotic grasses are a critical factor in native recruitment and potential long-term resilience and longevity in a region. GOOD.

*Reciprocal cost of facilitation – so there is cost of facilitation NOT reciprocal cost because reciprocal means both pay but brome is not facilitating…. Be careful with use of terms. There are reciprocal interactions and a cost of facilitation. I think….confused so ensure you sort out these terms however you us them early in the paper*

Topic sentence about costs first. Shrubs facilitate the annual plant community and this can negatively impact shrub recruitment rate. Other foundational species have been observed to facilitate neighbouring species resulting in a decrease in their own fitness (Schöb et al. 2014a; Schöb et al. 2014b) or decreases in productivity (Holzapfel and Mahall 1999; Armas and Pugnaire 2005). High densities of beneficiary plants under shrub canopies can reduce the water availability for the benefactor plants (Holzapfel and Mahall 1999; Armas and Pugnaire 2005). In these cases, the benefactor species will shift its allocation of resources and display different traits in response to the competitive feedbacks experienced by greater annual associations (Schöb et al. 2014b). We did not record trait set within this study, but did observe a significant effect of invasive grass cover on shrub recruitment that can limit the establishment of new shrub individuals within the population. A similar study conducted in the Mojave Desert also described that a non-native grass had higher densities within canopies of the shrub *Ambrosia Dumosa* and negatively impacted the seedling establishment of this perennial (Rodríguez-Buriticá and Miriti 2009). The current population of *E. californica* at Panoche Hills could thus represent “living relicts” that will inevitably be lost and replaced by the invasive grass species (Young et al. 2005). Additionally, *Bromus* species are fire-adapted that further increases the vulnerability of the system because of significantly greater fuel loads and more frequent burn-scenarios (Salo 2005; Monty et al. 2013). These findings are consistent with a trend that is occurring in the Mojave and Great Basin Deserts that includes the conversion of native shrubland to invasive annual grasses (Salo 2005; Condon et al. 2011; Abella et al. 2011; Abatzoglou and Kolden 2011). However, it has also been suggested that evolution can occur and that the reciprocal effects of beneficiaries on benefactors will result in populations of foundational shrub species that can co-exist with the non-natives (Bronstein 2009; Schöb et al. 2014a). Continued exploration of bi-directional interactions is important to ecological theory because it can improve our ability to predict changes to community structure from species invasion.

*Recruitment strategies for desert shrubs*

Desert shrubs often require specific habitat requirements for successful recruitment. California supports multiple Ephedra species that radiated because of increasing aridity in North America approximately 4 million years ago (Loera et al. 2012). Certain species of the Ephedra genus, such as *E. californica,* thus have characteristics that are desert adapted, such as tolerance to low water availability or preference for well-drained soil (Lunt et al. 1973). We observed these traits in *E. californica* with the highest recruitment rates in relatively sandy soil and did not find a correlation with water treatments to biomass productivity. Interestingly, survival rates of *E. californica* decreased with sand in substrate, but propose this was because of the increased desiccation rate of the small pots that likely would not occur in natural soils (citation to a Gibson paper about greenhouse experiment limitations or his book). *E. californica* also had a preference for full-sun treatments, and in the field, it displayed growth pattern of increasing height towards the north-west (Appendix A) similar to other desert shrub species, e.g. *Larrea tridentata* (Neufeld et al. 1988). Our clipping treatment reduced above-ground biomass, but this did not significantly influence the survival of *E. californica* suggesting the species is resilient to some herbivory during establishment. These findings support a field clipping study of adult individuals that showed that *E. californica* can recover quickly after full canopy removal within two years (Lortie et al. 2018). *E. californica* is relatively tolerant to most arid communities and thus factors limiting the species occurrence are likely due to evolutionary history (Loera et al. 2012) and habitat destruction for agriculture (Germano et al. 2011; Soulard and Wilson 2015). Concluding sentence…

Topic sentence – Recruitment is important in disturbed and high stress environments. The recruitment rates of Ephedra species are relatively robust??. For instance, in a four year study in the Mojave Desert surveying shrub recruitment of 201 individuals, *E. nevadensis* was the only species to recruit among 11 common shrub species with a survival rate of 4.7% (Ackerman 1979). Similarly in the Sonoran Desert, the frequency of emerged seedlings for *E. trivurica* is low at less than ten individuals in seven years, but individuals have been observed to reach greater than 50 years of age (Goldberg and Turner 1986). We observed a significantly greater survival rate (i.e. 9.86%) but this was recorded in a shorter time-frame. When considering the rate of survival for *E. nevadensis* within a year, the values are more similar, 7.4% (Ackerman 1979). *E. californica* has a low frequency of recruitment and a high rate of survival relative to other shrub species, which makes it susceptible to factors that inhibit the rate of seedling establishment.  *This paragraph needs work or could be cut.*

*Management Implications*

*E. californica* is a foundational species with known facilitation effects that could be easily propagated for land managers intending to restore desert habitat that is degraded. The San Joaquin Desert has seen significant declines in area leaving only remnant habitat that supports the remaining endangered species (Germano et al. 2011). Initiatives in California, such as the retirement of agricultural land for endemic species (Lortie et al. 2018b), intend on restoring significant portions of the San Joaquin desert and planting shrubs could be a viable strategy. There is a need to consider multi-trophic approaches in community ecology, especially in the context of restoration (Siebold et al. 2018). Identifying the basic ecological interactions associated with *E. californica* can inform restoration strategies by using a “bottom-up” approach of planting shrubs to facilitate the neighbouring plant and animal species. *E. californica* is a good candidate species for restoration using this approach because the seeds have high rates of viability and we observed significant emergence rates relative to other desert shrub species. Although the recruitment of *E. californica* can be limited by *Bromus* species, we found that reducing resources or herbivory did not increase this effect suggesting invasion alone is limiting the shrub species. This suggests that if the exotic grasses are properly managed, successful recruitment of *E. californica* is possible and thus the potential restoration of remnant San Joaquin habitat. – might instead conclude that you cannot ignore the exotic annuals and that a potential issue of restoring for benefactors is competition with exotics and that a restoration strategy must manage for exotics at the same time as adding in native benefactors.

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**Table 1:** Generalized linear models (GLMs) that tested the response of *E. californica* abundance and total biomass in greenhouse trials with treatments of different water levels, shading, and clipping. Seeds of *E. californica* were also grown in a density series with *B. madritensis*. Significant was denoted at α = 0.05 and shown in bold with sign of effect.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Water | | | Shade | | | Clipping | | |
|  | sign | *χ2* | *p-value* | sign | *χ2* | *p-value* | sign | *χ2* | *p-value* |
| Abundance |  |  |  |  |  |  |  |  |  |
| density | 0 | 2.78 | 0.095 | 0 | 0.73 | 0.39 | **-** | **4.21** | **0.04** |
| treatment | 0 | 0.20 | 0.90 | **-** | **11.5** | **0.003** | 0 | 0.55 | 0.76 |
| density \* treatment | 0 | 0.087 | 0.96 | 0 | 1.43 | 0.49 | 0 | 0.82 | 0.66 |
| Biomass |  |  |  |  |  |  |  |  |  |
| density | 0 | 0.11 | 0.54 | 0 | 0.40 | 0.23 | 0 | 0.62 | 0.18 |
| treatment | 0 | 0.10 | 0.84 | **-** | **2.02** | **0.027** | **-** | **9.29** | **< 0.001** |
| density \* treatment | 0 | 0.53 | 0.40 | 0 | 0.029 | 0.95 | 0 | 0.99 | 0.23 |

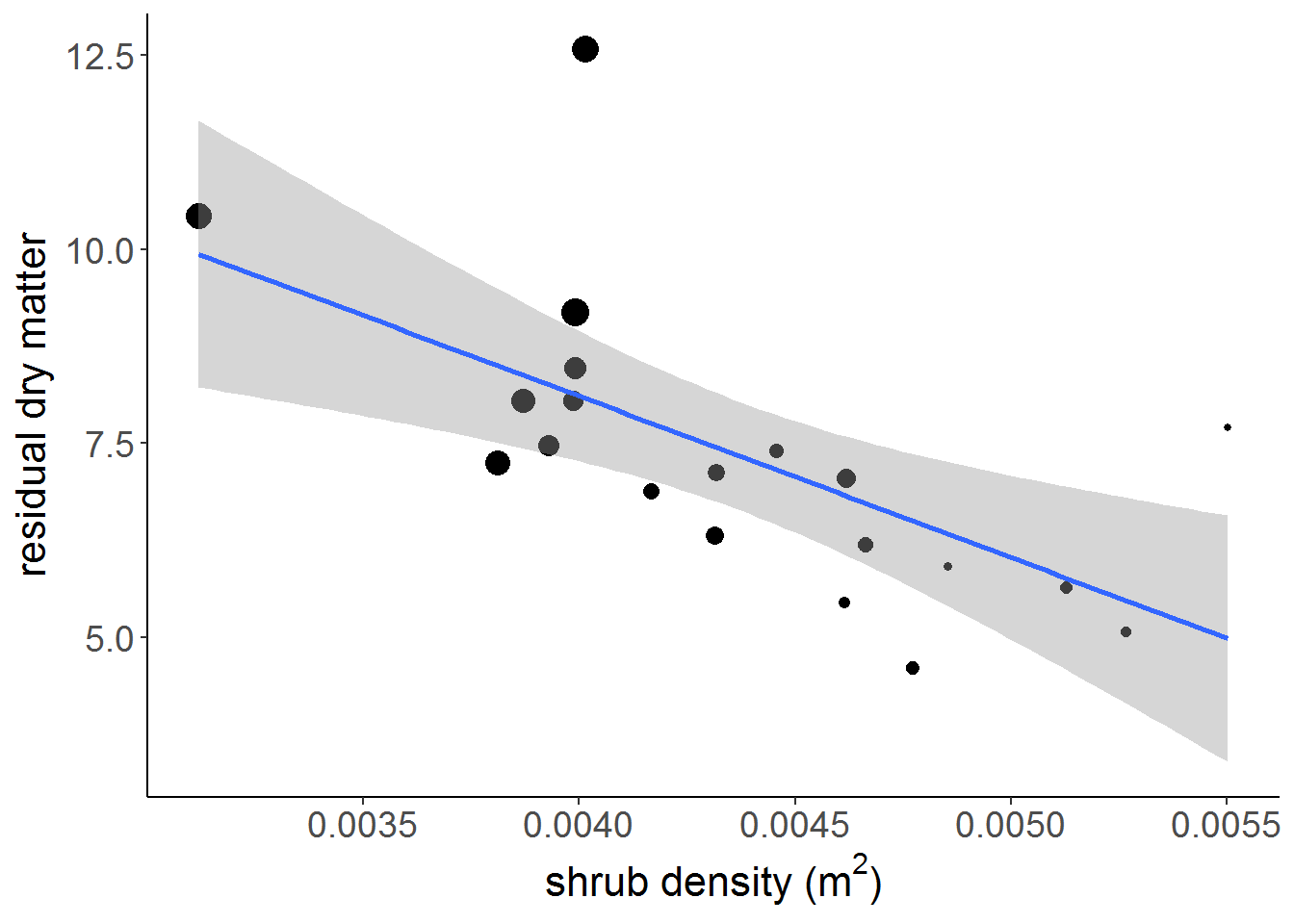
**Figures**

**Figure 1:** The relationship of *E. californica* density and log-transformed residual dry matter at Panoche Hills. The size of the points represents the 20 different size classes for *E. californica*. Error bar represents 95% confidence interval (r2 = 0.41).

**Figure 2:** The rate of survival for *californica* with different soil substrates (gradient of sand quantities) and different microsites (full-sun, shaded). Line represents mean model fit and dashed lines are 95% confidence intervals calculated from Breslow approximation.

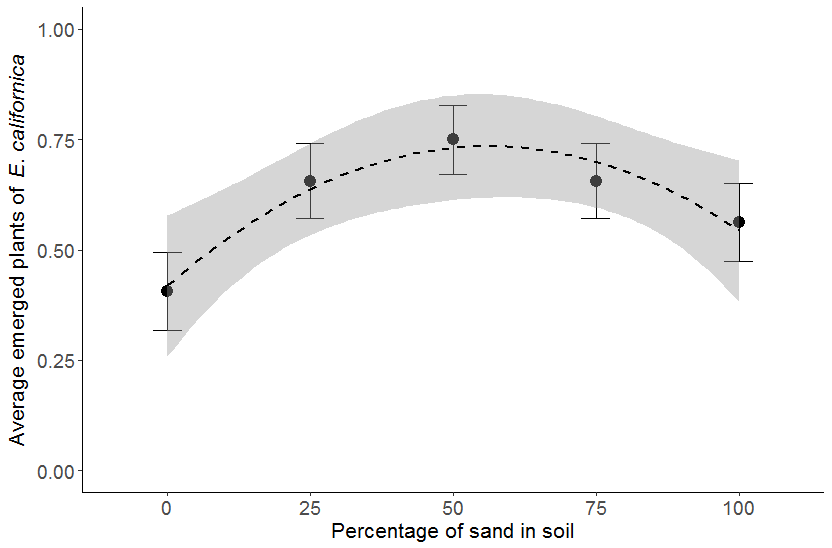
**Figure 3:** The total number of surviving individuals of *E. californica* with different soil substrates (gradient of sand quantities) and different microsites (full-sun, shaded). Each value represents mean number of emerging individuals in each treatment and error bars are 95% confidence intervals.

**Figure 4:** The relationship of final above-ground (a) and below-ground (b) biomass of *E. californica* with number of *B. madritensis* individuals. Line represents mean model fitted for above-ground (R2 = 0.26) and below-ground (R2 = 0.61) biomass with 95% confidence interval shown in shaded area.



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Make lines thicker, font size on axes bigger and relabel the y-axis



better font sizes

relabel average to mean

what about proportion established and nor emerged – you mean to the end of experiment right?

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