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Facilitation promotes plant invasions and indirect negative interactions

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Numerous pressures influence the ecological capacity and health of drylands globally. Shrubs are often a critical component of these systems and can function positively as foundation species through facilitation of other species. Nonetheless, limited attention has been paid to the potential negative and indirect effects of shrubs. Here, we tested the hypothesis that plant facilitation can both accelerate the invasion process and amplify the negative effects of an invader on the native community. The invasive species *Bromus madritensis* ssp. *rubens* capitalized on facilitation by resident native shrub species. This in turn further degraded California mixed grasslands by negatively impacting other annual protégé plant species in these specific microhabitats. Indirect shrub-mediated interactions were thus a critical component of the ecological community assembly processes, and this suggests that we need to move beyond pairwise interactions to more rapidly advance grassland management and restoration theory.

Keywords: brome, *Bromus rubens*, California, drylands, *Ephedra californica*, facilitation, indirect interactions, invasion, management, positive interactions, San Joaquin Desert, shrubs

Introduction

Direct and indirect interactions are fundamental processes associated with plant community assembly. The characterization of the structure of these interactions is central to many components of ecological research including the relative importance of different complexes of species to ecosystem functioning (Simmons et al. 2019) and more broadly to coexistence theory (Levine et al. 2017). Unfortunately, invasion by non-native, exotic plants species can dramatically influence the structure of communities, and there are more examples of natives facilitating exotics than natives resisting exotics reported in the literature (Cavieres 2020). Indirect interactions can thus mediate some of these outcomes through neighborhood-level interactions (Waters et al. 2014). The success of some invasive plant species can be further explained by these indirect, and at times simpler, interaction complexes (Strauss 2014), and predicting the structure of these novel communities must thus include description of both direct and indirect interactions (Eklöf et al. 2013). Fortunately, new tools and perspectives such as the use of discrete spatial scales coupled to ecological context (Losapio et al. 2019) and use of foundation or common species to enable meaningful and representative snapshots of community complexity (Ellison 2019) can more rapidly advance tests of assembly theory that incorporate a range of interactions.

Drylands globally include grasslands, mixed-agriculture vegetation, scrublands and span semi-arid to arid climates and are often influenced by foundation plant species such as shrubs. A foundation species is typically defined as a species that positively controls the biodiversity of a system and provides fundamental processes that influence the functioning of an ecosystem (Soulé et al. 2005, Ellison 2019, O'Brien et al. 2020). Nonetheless, foundation species are frequently underexploited for conservation and management particularly when they are relatively common within an ecosystem (Crotty et al. 2019, Ellison 2019). We often manage for rare and threatened species, and this is absolutely legitimate, but depending on the species, commonness can control many key ecological processes supporting richness and diversity of species (White et al. 2012) and functions (Weigelt et al. 2008). Protégé species are typically defined as the species that associate with the foundation species and can comprise extensive biodiversity (Flores and Jurado 2003). Significant biotic and abiotic pressures influence capacity and function of drylands to support native plants, animals and human needs (Askarizadeh and Arzani 2018). Theory that informs better management of shrubs and other long-lived foundation plant species (Inman et al. 2013) with a focus on mitigating the impacts of invasive species at regional scales (Gaskin et al. 2020) can be pivotal in these ecosystems. This lever or ecological force multiplier, shrubs and indirect interactions, will inform applied restoration theory and implementation as we actively continue to manage for land use changes and extended droughts (Kogan and Guo 2015, Lortie et al. 2018a). Consequently, an examination of the direct and indirect interactions with native foundation species will illuminate the relative importance of some of the key biotic drivers of biodiversity in drylands.

Ephedra californica is an established foundation species in California that benefits plants and animals and can recover from damage (Lortie et al. 2018b, Ivey et al. 2020). *Bromus rubens* is both common and a significant source of interference and competition for other plant species in many introduced grasslands (Salo 2002, Salo et al. 2005, Abella et al. 2011). Structured vegetation sampling within the region that is anchored to these two species can thus examine some of the direct canopy effects of a native shrub species and the indirect effects of its canopy mediated by an invasive plant species. Previously, the direct facilitation of *Bromus rubens* by *Ephedra californica* was confirmed (Lucero et al. 2019), but here we expand the scope of this exploitation spatially and temporally and advance ecological interaction theory further by testing for indirect interactions. A contrast of plant community composition and structure at fine scales was used to examine the hypothesis that both foundation species facilitation and indirect effects mediated by a facilitated invasive species are key diversity drivers. Specifically, we predicted that the abundance of *Bromus rubens* (i.e. brome) was higher under the foundation species *Ephedra californica* and that its subsequent negative effect on other annual protégé species was an important indirect effect of the shrubs on net biodiversity patterns regionally.

Methods and results

Within the San Joaquin Desert, a cumulative total of 2838 independent 0.5 × 0.5 m plots were compiled comprising 114 852 unique observations within the region, and data with R code are fully open and published for reuse (Lortie et al. 2021). The sampling was explicitly structured to contrast shrub versus open-gap microhabitats in drylands by recording the density of all species under the shrub canopy of *Ephedra californica* and at adjacent microhabitats without a shrub canopy. Plant density was measured as the total number of individuals per species per plot. This sampling design simplifies drylands to two discrete microhabitat types (Pescador et al. 2014). Sampling was repeated at peak biomass each spring for consecutive years from 2015 to 2018, and it encompassed the entire length of the San Joaquin Desert from the northern most tip (38°53'56''N, 121°05'38''W) to the southern extent (35°04'20''N, 119°39'38''W). Relative differences in the frequency of brome was contrasted between the two microhabitats sampled regionally and longitudinally (i.e. through time), and the indirect effects of facilitation by shrubs on the plant community was examined directly under shrubs by exploring the relationship between brome and other exotics on the protégé native species.

Two statistical approaches were used to examine these effects – conventional generalized linear mixed models (Harrison et al. 2018) to test for facilitation of brome by shrubs and response surface methods that jointly model and visualize the interactions between multiple variables on a response (Phillips and Arnold 1989) to test for indirect effects (Inouye 2001, Meyers et al. 2009, Wu and Hamada 2009). Generalized linear mixed-effects models were used in the former instance treating year as a random effect and response data as negative binomial using the R packages lme4 (Bates et al. 2020) and MASS (Ripley et al. 2021) and two specific R packages supported the latter analyses and including rsm (Lenth 2020) and plot3D (Soetaert 2019). Residuals and coefficients of determination from the GLMMs were examined using the packages car (Fox et al. 2020) and MuMin (Barton 2020) whilst residuals and lack-of-fit were provided in the response surface methods analyses including the interaction term statistics. All statistical analyses were done in R ver. 4.0.4 (<www.r-project.org>), and code is publicly archived (Lortie et al. 2021).

Brome was present in 74% of all plots sampled regionally, and it was significantly more abundant under shrubs but not temporally consistent (Fig. 1, Table 1). This confirms that it is likely directly facilitated by the canopy of *Ephedra californica* and at least routinely capitalizes on this microhabitat by differential association throughout the region via any number of benefits that shrubs provide such as differences in competition, environmental amelioration or differences in consumer pressure (Alcántara et al. 2019). The indirect effects of shrubs through brome on other plant species were profound. First, native species were all but extirpated from shrub microhabitats throughout the region with increasing densities of brome and of other exotics (Table 1). Second, increasing brome significantly reduced the presence of other exotics in this microhabitat (Table 1). Characterization of the composition community with optimization of the natives as the key response and the influence of brome with other exotics in shrub microhabitats as factors highlighted the intensity of emergent indirect negative interactions between protégé species under shrub canopies (Fig. 2). Increasing densities of brome functionally zeroed out all other species from this microhabitat regionally (Table 1). The response surface clearly highlights the indirect negative effects of shrubs mediated by brome because more brome is less to no other plant species within these communities (Fig. 2). Consequently, the positive effects of a native foundation shrub species in providing a microhabitat within drylands for other species has become an invasive species hotspot best described by its indirect negative interactions – unfortunately for a number of years and widely throughout this region.

Implications

Invasive species are a challenge in many ecosystems including all naturally assembled grasslands. This has been framed as one of the most crucial contributors to global change in addition to direct climate drivers (Grainger et al. 2019), and numerous inter-related hypotheses describe this field of research (Enders et al. 2018). Consequently, we tested for benefits to an invasive species by a native foundation species and explored the indirect consequences of this facilitation on diversity. Similar to previous research, we confirmed that brome was facilitated (Lucero et al. 2019) and highly competitive (DeFalco et al. 2007). However, here we also confirmed two novel advances to ecological theory. Firstly, that this brome-mediated effect is regional not local, frequent in different annual growing seasons, and that the emergent property of this relatively stable direct community facilitation by shrubs can generate new indirect patterns and feedbacks in diversity (Strauss 2014) that are undesirable for conservation (Drake et al. 2016). Secondly, we show that analyzing indirect interactions through response surface modeling continues to be a powerful tool to not only infer interspecific competition (Inouye 2001) but to advance community ecology theory by incorporating indirect interactions into different contexts such as microhabitats. This structured snapshot approach can be more powerful in explaining ecological patterns than complex network or species-level indices, and there are many other contemporary tools to support this theory (Simmons et al. 2019). Furthermore, It is also likely that

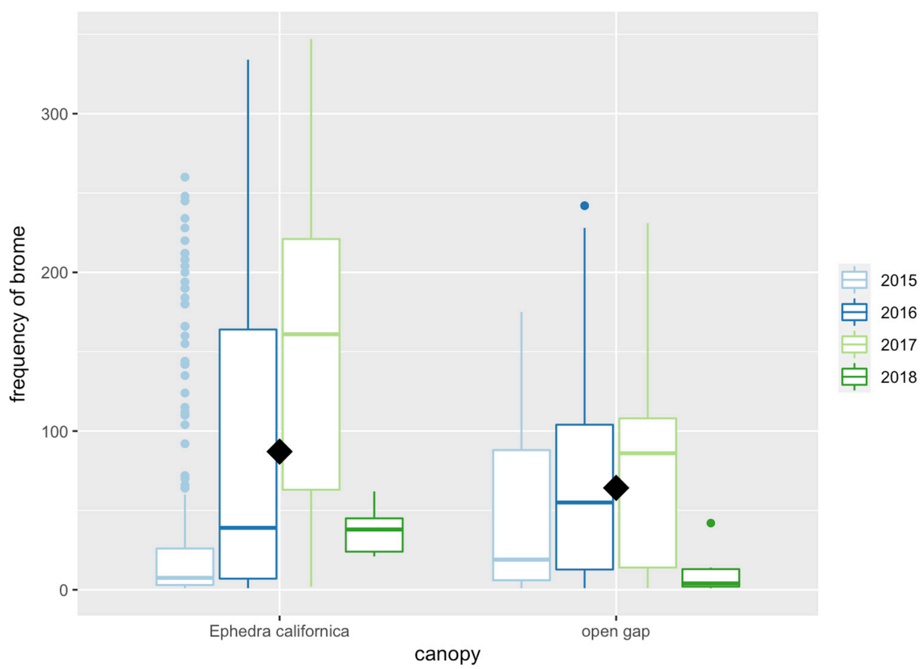

Figure 1. The relative frequencies of *Bromus rubens* (i.e. brome) within the San Joaquin Desert, California. Two microhabitats were censused for four years. *Ephedra californica* is a native shrub species, and plots were censused under its canopy. Open-gap microsites did not have a canopy of a woody or dominant plant species. The comparative boxplots show three quartlies including the median, and the black diamonds show the grand mean for each microhabitat summed across all years.

Table 1. The effects of shrub facilitation on the relative frequencies of *Bromus rubens* (i.e. brome) within the San Joaquin Desert, California and its subsequent effects on the plant community. Generalized linear mixed models (GLMMs) included year as a random effect fit to a negative binomial distribution. A response surface method (RSM) were also used to examine indirect effects of shrubs on natives mediated brome and other exotic plant species. Model describes GLMM or RSM, coefficient describes the mean effect of model or slope plus standard error, test statistic for GLMMs is a χ^2 statistic and a t-statistic for the RSM if slope is significantly different from 0, p-value is value for each specific factor listed, and R^2 is the percent variation explained by model.

Model	Factor	Coefficient ± SE	Test statistic	p-value	R^2
GLMM	Brome facilitation				
	Shrub effect	0.29 ± 0.05	5.36	< 0.0001	0.25
GLMM	Native abundance				
	Brome	−0.29 ± 0.05	−5.82	< 0.0001	0.17
	Exotics	0.088 ± 0.05	1.61	0.11	
	Brome:Exotics	0.50 ± 0.06	7.73	< 0.0001	
GLMM	Native richness				
	Brome	−0.34 ± 0.03	−11.1	< 0.0001	0.30
	Exotics	0.15 ± 0.03	5.76	< 0.0001	
	Brome:Exotics	0.29 ± 0.03	9.39	< 0.0001	
RSM	Native abundance				
	Brome	−0.05 ± 0.005	−9.79	< 0.0001	0.07
	Exotics	−0.029 ± 0.01	−2.63	0.009	

brome and many other exotic plants can capitalize on native shrubs in other grasslands and negatively impact other taxa such as native invertebrates (Poniatowski et al. 2018).

The indirect negative effects of shrubs through brome strongly suggest that this exotic species cannot be ignored in drylands and that its presence in a facilitation context likely obliterates any potential direct positive biodiversity benefits of shrubs for native species. Indirect interactions can comprise different mechanistic pathways ecologically and cannot be neglected in conservation theory and practice (Sotomayor and

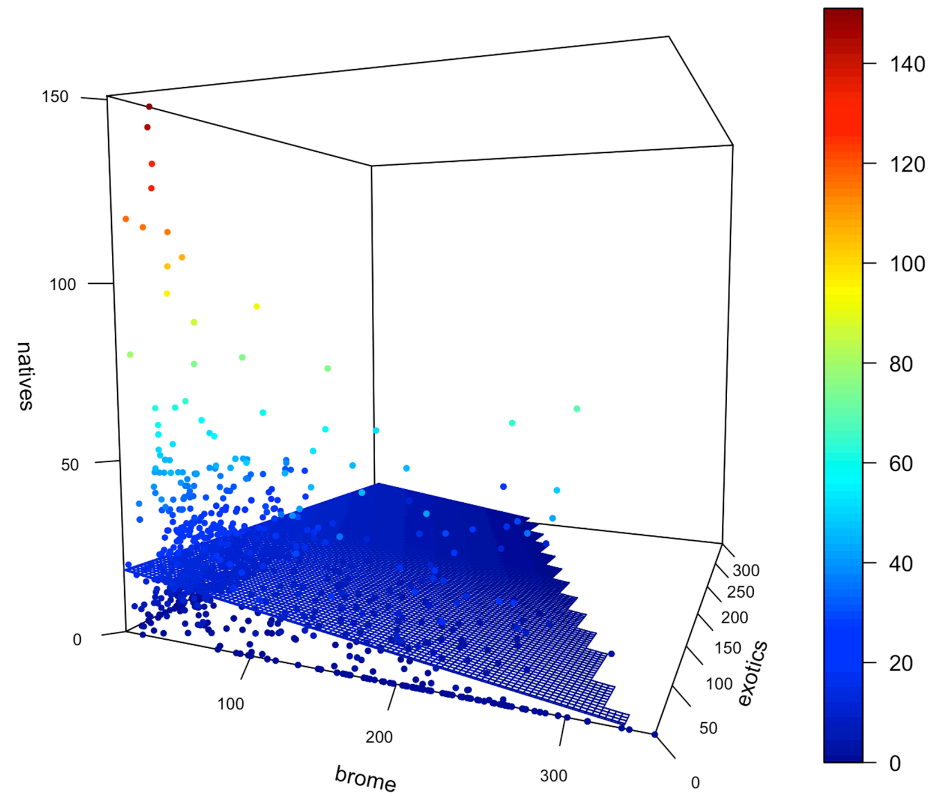

Figure 2. A multi-dimensional plot of the relative abundances of plant species in the San Joaquin Desert in California. The abundance data were sampled under the canopy of the shrub species *Ephedra californica* regionally. Brome is *Bromus rubens*, and exotics describes all other non-native species to California. Natives are the remaining species with provenance listed as California (source Calflora). Response surface methodology was applied to these data to examine optimal responses of natives by brome and exotic indirect interactions within this micro-habitat (see text for details).

Lortie 2015). Brome specifically can negatively impact foundation shrub species (Filazzola et al. 2020). Reciprocal negative effects can have significant long-term effects on community dynamics if benefactors cannot recruit (McIntire 2014). This community assembly framework for fundamental ecological theory has been proposed for exotics (Pearson et al. 2018), but we propose that it now must be considered for restoration and management. Consequently, the form and function of drylands provided by shrubs must leverage the ecological theory of indirect interactions to tackle restoration through selective grazing, native seeding of specific microhabitats, and the active examination of interactions with native foundation species.

Data availability statement

All data and R code are publicly available at the Knowledge Network for Biocomplexity <https://knb.ecoinformatics.org/view/doi:10.5063/RF5SF0>.

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Author contributions

Christopher J. Lortie: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead). **Alessandro Filazzola**: Conceptualization (equal); Data curation (equal); Formal analysis (equal). **Charlotte Brown**: Conceptualization (equal). **Jacob Lucero**: Conceptualization (equal). **Mario Zuliani**: Investigation (equal). **Stephanie Haas**: Investigation (equal). **Malory Owen**: Investigation (equal). **H. Scott Butterfield**: Funding acquisition (lead). **Emmeleia Nix**: Investigation (equal). **Michael Westphal**: Funding acquisition (equal); Investigation (equal).

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