

Shrubs as ecosystem engineers across an environmental gradient: effects on species richness and exotic plant invasion

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Abstract Ecosystem-engineering plants modify the physical environment and can increase species diversity and exotic species invasion. At the individual level, the effects of ecosystem engineers on other plants often become more positive in stressful environments. In this study, we investigated whether the community-level effects of ecosystem engineers also become stronger in more stressful environments. Using comparative and experimental approaches, we assessed the ability of a native shrub (*Ericameria ericoides*) to act as an ecosystem engineer across a stress gradient in a coastal dune in northern California, USA. We found increased coarse organic matter and lower wind speeds within shrub patches. Growth of a dominant invasive grass (*Bromus*

diandrus) was facilitated both by aboveground shrub biomass and by growing in soil taken from shrub patches. Experimental removal of shrubs negatively affected species most associated with shrubs and positively affected species most often found outside of shrubs. Counter to the stress-gradient hypothesis, the effects of shrubs on the physical environment and individual plant growth did not increase across the established stress gradient at this site. At the community level, shrub patches increased beta diversity, and contained greater rarified richness and exotic plant cover than shrub-free patches. Shrub effects on rarified richness increased with environmental stress, but effects on exotic cover and beta diversity did not. Our study provides evidence for the community-level effects of shrubs as ecosystem engineers in this system, but shows that these effects do not necessarily become stronger in more stressful environments.

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Introduction

Plants that strongly modify their local physical environment can be considered ecosystem engineers (Jones et al. 1994; Badano et al. 2006; Cuddington et al. 2007). An ecosystem engineer can have positive effects on neighboring plants through alteration of the physical or biotic environment. The mechanisms by which plants act as ecosystem engineers are various and can range from mitigating disturbances such as herbivory (Callaway et al. 2005; Cushman et al. 2011), intense sunlight (Valiente-Banuet and Ezcurra 1991) or wind (Carlsson and Callaghan 1991), to increasing the availability of soil resources (Schlesinger et al.

1990; Pugnaire et al. 1996; Shumway 2000; Cushman et al. 2010).

The stress-gradient hypothesis (SGH) is the prevailing model for predicting how plants acting as ecosystem engineers will affect neighboring plants (Bertness and Callaway 1994). It predicts that facilitation will be most common in environments that are physically or biologically stressful for plant growth. A mechanistic rationale for the SGH is that, as stress increases, the microenvironment produced by the engineering species stays relatively constant—thus the relative effect of the engineer is greater in an otherwise stressful environment (Bertness and Callaway 1994; Badano and Cavieres 2006; Maestre et al. 2009). Meanwhile, some competitive effects of an engineering species on co-occurring plants might decrease towards the stressful end of gradients (Pugnaire and Luque 2001). Because the net interaction is determined by the balance of positive (environment modification) and negative (competitive) effects, both of the above mechanisms could contribute to more positive effects at high stress (Brooker et al. 2005). Despite many field tests of the SGH, evaluating this mechanism is difficult because not all studies directly measure the physical effects of ecosystem engineers across gradients.

A recent meta-analysis of the SGH found strong support for its general predictions at the level of individual plant growth (He et al. 2013), but less research has addressed community-level effects (Hacker and Gaines 1997). Ecosystem engineering shrubs and cushion plants often have distinct understory species associated with them, representing a source of beta diversity (Valiente-Banuet and Verdu 2007; Cavieres and Badano 2009; Butterfield et al. 2013). This increase in beta diversity tends to be more pronounced in more stressful environments (Badano and Cavieres 2006; Cavieres and Badano 2009; Armas et al. 2011). At a smaller scale, the plant community within the ecosystem-engineered patch often contains more individual plants and a greater number of species (Badano et al. 2006; Cavieres and Badano 2009). Greater individual density within engineered patches likely occurs when the engineering species alleviates stresses that limit survival and establishment (Tewksbury and Lloyd 2001; Badano et al. 2006; Holzapfel et al. 2006; Forey et al. 2009). On the other hand, a few studies have also shown lower plant density and species density within ecosystem engineering plants (Gutiérrez et al. 1993; Maron and Connors 1996; De Villiers et al. 2001).

Ecosystem engineers are also likely to play a role in exotic plant invasion in stressful environments (Maron and Connors 1996; Badano et al. 2007; Griffith 2010; Cushman et al. 2011). We might expect exotic plants to benefit more than natives from habitat amelioration by ecosystem engineers if exotic plants have traits associated with greater competitive ability and lower stress tolerance than

native species (Holmgren and Scheffer 2010). This trade-off would give exotics an advantage in facilitated patches where growth and competition may be high and a disadvantage in stressful environments away from facilitators (Tielbörger and Kadmon 2000).

In this study, we investigate the ability of shrubs to act as ecosystem engineers and facilitate neighboring species across an abiotic stress gradient. We combine experimental and comparative approaches to evaluate the effects of shrubs on wind speed and soil conditions, and determine the consequences for individual plant growth and community composition. We test four hypotheses: (1) shrubs modify the physical environment in ways that facilitate the growth of individual plants; (2) communities in shrub patches have greater individual density, cover, and species richness; (3) shrub patches increase beta diversity and favor exotic species; and (4) the effects of shrubs in all these cases increase towards the stressful end of the gradient. By assessing the SGH at the community level, our study provides insight into the role of ecosystem-engineering plants in determining species diversity and exotic species invasion in stressful environments.

Study system

We conducted this study in a coastal hind-dune system located on Bodega Head in Sonoma County, CA, USA (38°19'N, 123°3'W). This area is characterized by a Mediterranean climate, strong northwest winds throughout the spring and summer, and fast-draining sandy soil low in nutrients and organic matter (Barbour 1973; McNeil and Cushman 2005; Cushman et al. 2010). As reported by Lortie and Cushman (2007), this site spans a roughly 250-m plant stress gradient driven by sand particle size and wind exposure (see Fig. S1 in the Electronic supplementary information, ESM). As one moves from the leeward end of the gradient to the NW, sand particle sizes increase and surface wind speeds increase. Moisture limitation is the likely mechanism of plant stress across this gradient because larger sand particles hold less water at field capacity and also because stronger surface winds increase evapotranspiration (Jury and Horton 2004). Indeed, Lortie and Cushman (2007) reported lower soil field capacity at the high stress end of the gradient and changes in the plant community consistent with a plant stress gradient: average plant size, perennial cover, native plant cover, and species richness all decreased to the NW or windward end of the gradient. Nutrient limitation may also play a role, as Lortie and Cushman (2007) also found lower nitrate pools at the more stressful end of the gradient. Importantly, the abundance of *Bromus diandrus* (Poaceae; hereafter referred to as *Bromus*), a dominant non-native grass at this site, appeared to

be sensitive to this stress gradient and was significantly lower at the more stressful NW end of this site.

Ericameria ericoides (Asteraceae; hereafter referred to as *Ericameria*) is a shrub endemic to coastal dunes in California, with an average of 20–30 % canopy cover at this site (Cushman et al. 2010). Many smaller plant species, including native and non-native annual forbs and grasses, often grow underneath the canopy of *Ericameria*. Previous research demonstrated that nitrogen pools, mineralization rates, and dry litter biomass were greater under *Ericameria* than in the open dune (Cushman et al. 2010). In addition, two plant species—the native forb *Claytonia perfoliata* and the invasive exotic grass *B. diandrus*—had greater cover and density underneath *Ericameria* canopies. In contrast, the biomass and richness of other species was greater in the open dune.

Methods

Effects of *Ericameria* on the physical environment

We designed this study on the a priori assumption that sites located further away from the SE end of the environmental gradient described above experience greater plant stress (Lortie and Cushman 2007). For the remainder of the paper, we refer to position on the gradient in meters away from the low-stress, leeward end of the gradient—e.g., a gradient position of 100 m is 100 m towards the more stressful windward end of the gradient than a position of 0 m. In order to measure the effects of shrubs across the gradient, we established 23 sampling transects 20 m long that ran perpendicular to the gradient and were spaced roughly every 10 m along the gradient (i.e., at positions 0–220 m along the gradient; Fig. S1 of the ESM). We randomly selected two *Ericameria* shrubs intercepted by each transect ($n = 46$) and measured their maximum canopy heights. We paired each selected shrub with an adjacent shrub-free patch at a randomly selected compass heading 1 m away from the edge of the shrub's canopy. If a shrub-free area we selected was within 1 m of an adjacent shrub canopy then the patch was relocated to the nearest shrub-free area.

To characterize the effects of shrubs on the soil environment, we collected a 500-ml sample of surface soil including litter from each shrub and shrub-free patch. We dried samples at 60 °C for 48 h and then separated dried soil samples into seven distinct fractions: coarse organic matter (e.g., rabbit scat, twigs and leaves larger than 2 mm), very coarse sand (VCS; particles 2–1 mm), coarse sand (CS; 1–0.5 mm), medium sand (MS; 0.5–0.25 mm), fine sand (FS; 0.25–0.1 mm), very fine sand (VFS; 0.1–0.05 mm), and silt and clay (<0.05 mm). After first sieving out coarse organic matter, we transferred samples to a set of nested

sieves and shook each sample by hand for 2 min. We then weighed each soil fraction and calculated the amount of each as a proportion of the total sample weight. As an aggregate measure of sand texture, we calculated the geometric mean particle diameter for each sample, following Shirazi and Boersma (1984). For a subset of 11 paired shrub and open samples, one on every other transect, we also measured the organic carbon content in sand fractions (i.e., not including coarse organic matter) to the nearest 0.5 % with an organic carbon analyzer (Skalar Primacs, Salt Lake City, UT, USA) at Utah State University.

Above- and belowground effects of *Ericameria* on *Bromus*

We established a field experiment in January 2011 to separate the above- and belowground effects of shrubs on individual plant growth. We chose to use the annual grass *B. diandrus* as a phytometer because it is the most prevalent exotic annual species at this site and because its abundance changes across the gradient (Lortie and Cushman 2007). We selected 30 shrubs distributed along the length of the environmental gradient and paired each with an adjacent shrub-free area 50 cm away (we refer to each pair as a “block”). We filled four plastic pots (8.5 cm wide and 10 cm deep) with soil from underneath each shrub and shrub-free patch (8 pots total per block). We then rearranged the pots in each block so that two pots containing soil from under the shrub were placed in the shrub-free area and two pots with soil from the shrub-free area were placed under the shrub. This produced four treatment-level combinations between soil origin and shrub protection: shrub soil within shrub, shrub soil outside of shrub, shrub-free-soil within shrub, and shrub-free soil outside of shrub. We placed these pots in holes where soil had been collected so that soil levels in pots were flush with the natural soil level.

In January 2011, we transplanted a two-week-old bare root *Bromus* seedling into each of these 240 pots in the field (seedlings were grown from seed collected at the study site in the fall of 2010 and started in a greenhouse in store-bought potting soil). All other species germinating within these pots were removed. We harvested the above-ground biomass of these plants in late April 2011 when vegetative parts began senescing and the spikelets looked mature. We dried the biomass of each plant at 60 °C for 48 h and weighed it. As a measure of reproductive output, we also counted the number of spikelets on each plant upon harvesting.

Species association with *Ericameria* and shrub-free patches

We sampled vegetation in 20 × 30 cm quadrats placed at randomly selected positions within each shrub and

shrub-free patch described in “Effects of *Ericameria* on the physical environment” above. We used this small quadrat size so that we could fit sampling quadrats within shrub patches. Within quadrats, we counted individuals of each species, visually estimated the absolute percent cover, and then categorized it into one of the following classes: <1, 1–5, 6–15, 16–25, 26–50, 51–75, and 76–100 %.

Effects of *Ericameria* removal

In early March 2010, we haphazardly selected 70 *Ericameria* shrubs, ensuring that they were more or less evenly distributed along the environmental gradient. We selected shrubs that were not used in the studies above. Most selected shrubs were several meters away from each other (the nearest two shrubs were 2.8 m apart and only four shrubs were less than 4 m apart). Because the shrubs in this system are short and distances between shrubs are generally large, we believe proximity to neighboring shrubs had a minimal effect on the environment of shrub patches selected for this experiment. We marked the perimeter of each selected shrub canopy with pin flags and measured its position relative to the stressful end of the gradient. We assigned alternating removal and control treatment levels to each shrub along the gradient. For shrubs assigned to removal, we cut all *Ericameria* stems to ground level and removed them from the plot, taking care not to disturb other plants growing within the perimeter of the shrub.

At peak biomass of the first year (April 2010), we harvested the aboveground biomass of all species (excluding *Ericameria*) found in a single 20 × 30 cm quadrat placed at a random position within each shrub or shrub-removed patch. We sorted biomass to species, dried material for 48 h at 60 °C, and weighed it. In the second year of the experiment (April 2011), we followed the same procedure but sampled two 20 × 30 cm quadrats within each shrub that did not overlap with the previous year’s quadrats.

To quantify the effect of shrubs on wind, we measured wind speeds within experimental shrub patches (removals and controls) four different afternoons during the growing season between February 3rd and March 28th in 2011. We measured a 10-s average wind speed in m/s with a Kestrel® (Nielsen-Kellerman, Boothwyn, PA, USA) handheld anemometer placed 3 cm above the ground surface at the center of each shrub. We believed that wind speed at this height would have the most direct effect on the small plants we measured at this study site.

Statistical analyses

We used a simple linear regression to analyze how shrub height changed across the stress gradient. We analyzed how mean particle size, coarse organic matter, and organic

carbon in soil were affected by shrubs across the stress gradient using general linear models with position on the gradient, habitat (shrub patch and non-shrub patch), and their interaction as predictor terms. When a nonlinear effect of stress gradient position was evident, we assessed model fit with a quadratic effect of gradient position and tested whether this significantly improved model fit over a linear model. We compared models using *F* tests in the ‘Anova’ function in the statistical program R (R Core Team 2013).

Because the overall wind speed was different on each day measured, we scaled these measurements by subtracting each value from the day’s mean speed and then dividing by the standard deviation of measurements on that day. We then analyzed the average standardized wind speeds in response to position on the gradient, shrub treatment (shrub removed, shrub intact), and their interaction.

We log-transformed final aboveground biomass of *Bromus* in the transplant experiment and averaged this across the two focal plants within each of the four treatment combinations in each block. We analyzed average log biomass per plant in a model with fixed effects for position towards the stressful end of the gradient, shrub treatment, soil, and the two-way interactions between these factors. We assigned each block (i.e., each pair of open/shrub patches) as a random effect. Because the shrub treatment levels in each block were spatially clustered, we nested shrub treatment within block as a random effect in the model. We fitted linear mixed effects models with the ‘lme’ function from the nlme package in R (Pinheiro et al. 2013). We analyzed log-transformed spikelet production per plant using the same model structure as above. We assessed the significance of the main effects using *F* tests with the ‘Anova’ function in R.

To assess whether plant species composition as measured by absolute cover varied across the gradient and between shrub and shrub-free patches, we used non-metric multidimensional scaling analysis (NMDS) with the function ‘metaMDS’ in Vegan 2.0 (Oksanen et al. 2013). We used the ‘envfit’ function to test how position on the gradient and habitat type (shrub, shrub-free area) were associated with NMDS axes. We calculated Whittaker’s beta diversity between each pair of shrub and shrub-free patches as the cumulative richness within each pair of sampled patches divided by the average richness of these two individual patches (Anderson et al. 2011). As another measure of beta diversity, we calculated the Bray–Curtis distance between each pair of patches, $D_{jk} = \sum |x_{ij} - x_{ik}| / \sum (x_{ij} + x_{ik})$, where x_{ij} is the number of individuals of species i in shrub patch j and x_{ik} is the number of individuals of the same species in the paired shrub-free patch k (Oksanen et al. 2013). We regressed these measures of beta diversity across position on the stress gradient.

We used separate generalized linear models to test how position on the gradient, habitat type (shrub, shrub-free area), and their interaction affected five community-level measures: (1) total plant density (individuals per quadrat), (2) absolute total plant cover, (3) species density (richness per quadrat), (4) rarefied richness per quadrat, and (5) the ratio of exotic cover to native cover. For abundance and species density, we assessed the model fit with normal, Poisson, and negative binomial errors using either the ‘lm,’ ‘glm,’ or ‘glm.nb’ functions in R, and used the error structure that best fitted these data. We computed rarefied richness per quadrat at the level of 15 individuals. We log transformed the ratio of exotic to native cover for analysis so that it would not be bounded between zero and one; on this scale, positive values indicate exotic cover greater than native cover.

We analyzed the effect of the shrub-removal experiment on native and exotic biomass in 2010 and 2011. We included year (2010 or 2011), position on the gradient, shrub treatment (shrub removed or shrub intact) and the two-way interactions in these models. We used the ‘lme’ function from the nlme package for analysis and assigned shrubs as random effects to account for repeated sampling (Pinheiro et al. 2013). We removed interactions with year when they did not improve model fit assessed with likelihood ratio tests. We also tested the hypothesis that the response of each species to shrub removal would be inversely related to that species’ association with shrubs. To do this, we performed a Mann–Whitney test on the cover values of each species in shrub and shrub-free patches using the ‘wilcox’ function in R. We saved Z scores from each of these tests as a nonparametric measure of each species’ association with shrubs. We then calculated Z scores in the same way for the difference in each species’ harvested biomass between the removal and control treatments in 2010 and 2011 in the experimental dataset. We regressed each species’ response to shrub removal (i.e., the experimental Z score) against the strength of each species’ association with shrubs in the associational dataset (i.e., the cover Z score). We used a linear mixed model with the cover Z score, year, and their interaction as fixed effects, and set species as a random effect.

Results

Effects of *Ericameria* on the physical environment across the stress gradient

The height of *Ericameria* shrubs decreased significantly towards the more stressful end of the gradient ($F_{1,44} = 13.0$, $p < 0.001$, $R^2 = 0.21$; Fig. 1a). Proportions of each particle size class averaged across all samples were 6 % VCS,

47 % CS, 31 % MS, 15 % FS, 0.5 % VFS, and 0.1 % silt and clay. We excluded the silt and clay fraction from further particle size calculations because it made up a minimal fraction of the soil mass. Geometric mean particle diameter across all samples was 0.53 mm and varied from 0.29 to 0.90 mm. Particle size appeared to change nonlinearly across the gradient (Fig. 1b), and we found that a model with a quadratic effect of gradient position fitted the data significantly better than a model with no quadratic term ($F_{2,86} = 22.7$, $p < 0.001$). Overall, this model fitted the data well ($F_{5,86} = 43.1$, $p < 0.001$, $R^2 = 0.70$) and showed that particle size decreased slightly as distance from the least stressful end increased and then increased rapidly towards the stressful end of the gradient ($F_{2,86} = 88.4$, $p < 0.001$). Particle size was also significantly greater within shrub habitats ($F_{1,86} = 35.9$, $p < 0.001$). However, we did not find an interaction between habitat type and gradient position ($F_{2,86} = 1.4$, $p = 0.26$).

Coarse organic matter varied significantly with gradient position, shrub habitat, and their interaction ($F_{3,88} = 17.89$, $p < 0.001$, $R^2 = 0.36$; Fig. 1c). Coarse organic matter was 2–3 times greater in shrub habitats ($F_{1,88} = 39.1$, $p < 0.001$) and decreased towards the stressful end of the gradient but not outside of shrubs (gradient \times habitat interaction: $F_{1,88} = 6.5$, $p = 0.012$). Fine soil carbon appeared to peak in the middle of the gradient, and including a quadratic term for position on the gradient significantly improved the fit of the model over a linear model ($F_{2,16} = 4.4$, $p = 0.03$, Fig. S2 of the ESM). This model explained a significant proportion of the variation ($F_{5,16} = 3.0$, $p = 0.04$, $R^2 = 0.33$). After accounting for the quadratic effect of gradient position, there was a trend for soil carbon to be greater in shrub patches ($F_{1,16} = 4.1$, $p = 0.061$), but there was no interaction between the shrub effect and gradient position ($F_{2,16} = 0.2$, $p = 0.804$).

Shrub removal and position along the gradient significantly affected wind speeds ($F_{3,66} = 78.9$, $p < 0.001$, $R^2 = 0.77$; Fig. 1d). Wind speeds were one standard deviation greater (1.4 m/s on the windiest day sampled) in patches where shrubs were removed than in intact shrubs ($F_{1,66} = 169.1$, $p < 0.001$). Wind speed also increased linearly towards the stressful end of the gradient ($F_{1,66} = 66.2$, $p < 0.001$), but there was no interaction between gradient position and shrub removal ($F_{1,66} = 1.3$, $p = 0.25$).

Above- and belowground effects of *Ericameria* on *Bromus*

Survival of *Bromus* in the transplant experiment was high—230 out of 240 transplants survived to the end of the spring. Final aboveground biomass per plant was significantly greater when plants were grown in soil collected from under shrubs ($F_{1,57} = 7.0$, $p = 0.011$, Fig. 2). *Bromus* plants were also significantly larger when grown under

Fig. 1 Shrub height (a), mean sand particle size (b), soil coarse organic matter (c), and wind speed across the environmental stress gradient (d). In all panels, stress increases with position. In b and c, soil samples are from 46 shrub patches and 46 paired shrub-free patches. In d, wind speed was measured in 35 intact shrubs and 35 patches where shrubs were experimentally removed. Separate regression lines are shown for shrub (solid) and shrub-free (dashed) environments

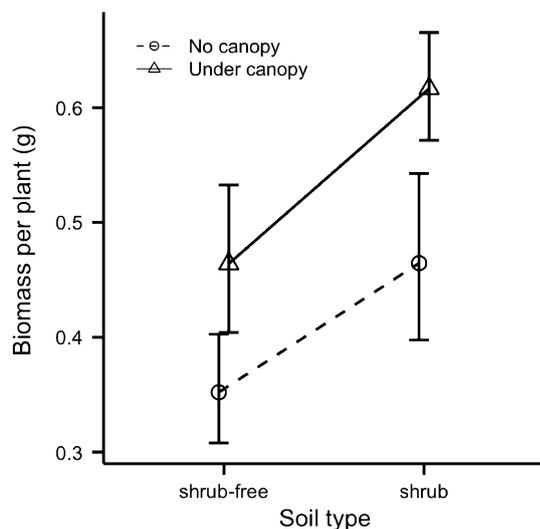
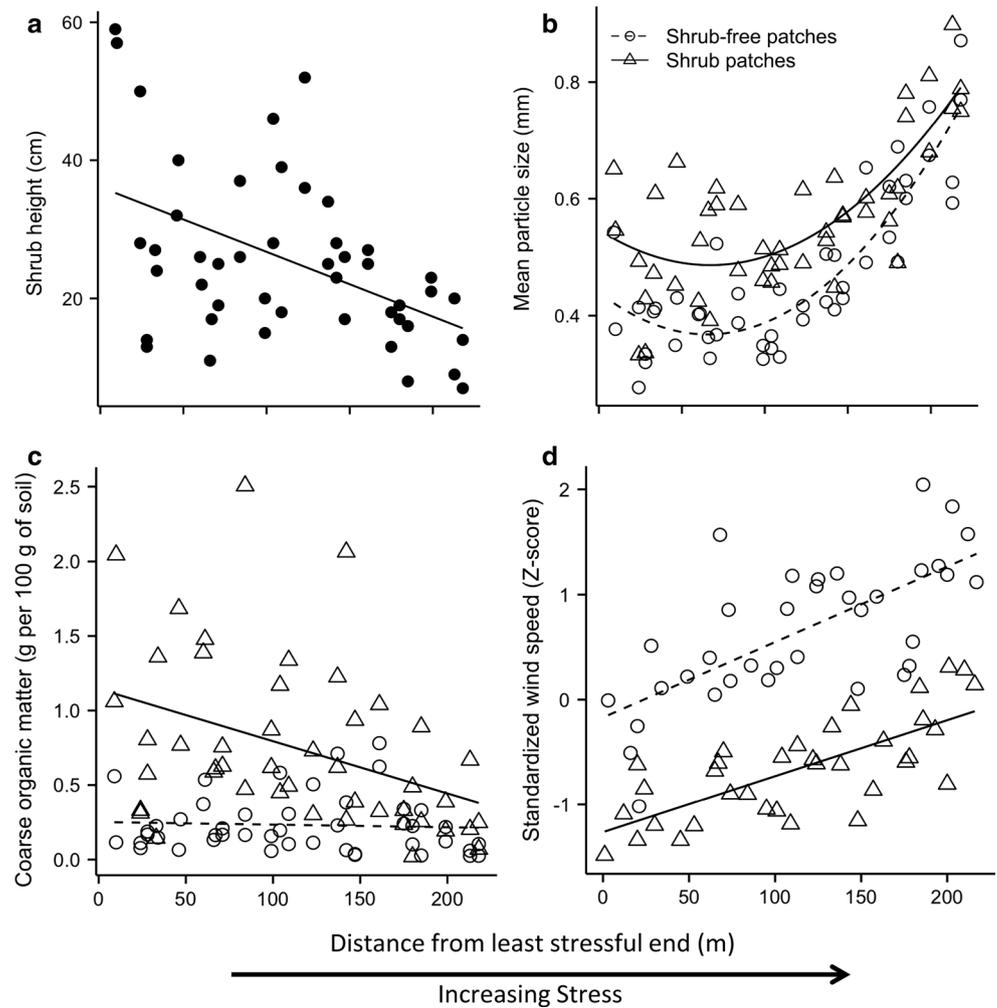


Fig. 2 Interaction plot showing final aboveground biomass of *B. diandrus* plants grown in soil from shrub and open patches. Plants were grown either under shrub canopies or in shrub-free patches. Plant biomass was log-transformed for analysis, and back-transformed means \pm SE are shown

shrub canopies than when grown in the open ($F_{1,28} = 4.2$, $p = 0.049$). However, there was no interaction between soil and canopy treatments ($F_{1,57} = 0.001$, $p = 0.972$). Gradient position did not have a significant effect on final biomass ($F_{1,28} = 0.9$, $p = 0.353$) and did not interact with either soil ($F_{1,57} = 0.3$, $p = 0.586$) or canopy effects ($F_{1,28} = 0.4$, $p = 0.542$). Average spikelet production per plant showed the same pattern—a significant effect of soil type ($F_{1,57} = 5.8$, $p = 0.019$), a trend towards a shrub canopy effect ($F_{1,28} = 2.8$, $p = 0.105$), and no interaction between the two ($F_{1,57} = 0.02$, $p = 0.898$). Likewise, gradient position did not have an effect on spikelet production ($F_{1,28} = 0.6$, $p = 0.444$) and did not interact with soil ($F_{1,57} = 0.3$, $p = 0.574$) or canopy effects ($F_{1,28} = 0.1$, $p = 0.730$).

Species association with *Ericameria* and shrub-free patches

Nonmetric multidimensional scaling analysis of relative species cover reached a solution with a stress of 0.19.

Shrub and shrub-free patches formed distinct clusters in the NMDS plot and were separated by the first NMDS axis [confirmed with permutation analysis in the ‘envfit’ function: $R^2 = 0.21$, $p < 0.001$ (999 permutations); Fig. 3]. Species associated with shrub patches included the exotic grass *Bromus* and the native annual forbs *Pterostegia drymarioides* and *Claytonia perfoliata*, while species associated with shrub-free patches included the native annual forbs *Chorizanthe cuspidata* and *Cryptantha leiocarpa*. The second NMDS axis was significantly related to position on the gradient [‘envfit’ $R^2 = 0.35$, $p < 0.001$ (999 permutations)].

Plant density, total absolute cover, richness, and proportion of exotic cover varied substantially across the gradient and between habitat types. A negative binomial regression model best fitted the plant density data (proportion of deviance explained = 0.52). Plant density increased dramatically towards the stressful end of the gradient outside of shrubs, but increased only gradually within shrub patches (significant gradient position \times habitat type interaction term: Table 1a; Fig. 4a). Absolute cover increased towards the stressful end of the gradient underneath shrubs and in shrub-free patches ($R^2 = 0.13$; Table 1b; Fig. 4b). Species density was fitted with a negative binomial model (proportion of deviance explained = 0.16) and increased with stress in both habitats (Table 1c; Fig. 4c). In contrast, rarefied richness at the level of 15 individuals decreased towards the stressful end of the gradient in shrub-free patches more rapidly than under shrubs ($R^2 = 0.41$; Table 1d; Fig. 4d). Calculating rarefied richness at 10 or 20 individuals per quadrat did not qualitatively change the results. Most plots had a negative log ratio of exotic to native cover, indicating more native cover than exotic cover (Fig. 4e). Ten plots had no exotic cover and so the log ratio was undefined. We assigned these plots the smallest positive value for exotic cover observed. The ratio of exotic to native cover was significantly greater within shrub patches but did not change with stress ($R^2 = 0.10$; Table 1e). Whittaker’s beta diversity between shrub and shrub-free patches decreased towards the stressful side of the gradient, indicating that the species compositions in the habitats became more similar with stress ($F_{1,44} = 13.3$, $p < 0.001$, $R^2 = 0.21$; Fig. 5f). However, the Bray–Curtis distance between plot pairs calculated from the individual density of each species showed no significant relationship with position on the gradient ($F_{1,44} = 1.1$, $p = 0.30$, $R^2 = 0.002$; Fig. S3 of the ESM).

Effects of *Ericameria* removal

Shrub removals had 40 % less exotic biomass than controls (Table 2; Fig. 5a, b), and exotic biomass decreased towards the higher-stress end of the gradient in 2010 but not in 2011 (position \times year interaction: Table 2). We found no

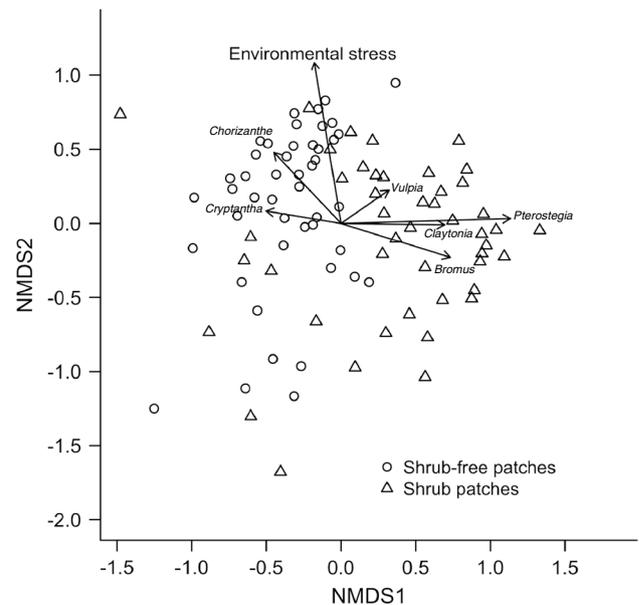


Fig. 3 Nonmetric multidimensional scaling analysis (NMDS) on absolute percent cover of species in 46 shrub and 46 shrub-free patches. Positions of six common plant species are shown with arrows and labeled with genera names. Each arrow points in the direction of increasing stress on the gradient

significant effect of shrub removal on overall native biomass (Fig. 5c, d). Native biomass decreased significantly towards the more stressful end of the gradient, and biomass was significantly lower overall in 2011 than in 2010 (year effect: Table 2).

Individual species’ responses to shrub removal were significantly predicted by the strength of each species’ association with shrubs in the comparative study ($F_{1,39} = 44.3$, $p < 0.001$; Fig. 6). Removal effects were also more strongly related to association strength in the second year (association strength \times year interaction; $F_{1,38} = 6.0$, $p = 0.019$).

Discussion

Generally ecosystem engineers are expected to have positive effects on species diversity and invasion in stressful environments (Hacker and Gaines 1997; Bruno et al. 2003). While many studies of plant communities confirm that positive effects on individual plants increase with environmental stress (He et al. 2013), only a handful of studies have tested how community-level effects change with environmental stress (Cavieres and Badano 2009; Armas et al. 2011). We used a comparative study and a paired removal experiment to test if ecosystem-engineering shrubs increase beta diversity, abundance, species density, and exotic species invasion more in stressful conditions than in less stressful conditions. While we found strong evidence of the

Table 1 Significance of main effects of gradient position, habitat, and their interaction on individual density, cover, richness, rarefied richness (at the level of 15 individuals), and proportion of exotic cover in 92 shrub and open patches

(a) Density per quadrat	<i>df</i>	Deviation	<i>df</i> _{Resid}	Residual deviation	$P(>X^2)$
Position	1	84.8	90	129	<0.001
Habitat	1	11.7	89	118	<0.001
Position × habitat	1	14.6	88	103	<0.001
Null			91	214	
(b) Cover per quadrat	<i>df</i>	SS	SSM	<i>F</i>	$P(>F)$
Position	1	7,970	7,970	9.9	0.002
Habitat	1	3,105	3,015	3.8	0.053
Position × habitat	1	2,086	2,086	2.6	0.112
Residual	88	71,171	809		
(c) Richness per quadrat	<i>df</i>	Dev	<i>df</i> _{Resid}	Resid Dev	$P(>X^2)$
Position	1	16.5	90	106	<0.001
Habitat	1	1.6	89	104	0.212
Position × habitat	1	1.2	88	103	0.271
Null			91	122	
(d) Rarefied richness	<i>df</i>	SS	SSM	<i>F</i>	Pr(>F)
Position	1	31.6	31.6	25.3	<0.001
Habitat	1	20.7	20.7	16.5	<0.001
Position × habitat	1	8.6	8.6	6.8	0.011
Residual	63	78.7			
(e) Proportion exotic	<i>df</i>	SS	SSM	<i>F</i>	Pr(>F)
Position	1	2.9	2.9	2.5	0.118
Habitat	1	10.3	10.3	8.9	0.004
Position × habitat	1	2.1	2.1	1.8	0.180
Residual	88	102.5	1.2		

Negative binomial models were fitted for density and species richness per quadrat, and generalized linear models with normal errors were fitted for cover, rarefied richness, and proportion of exotic cover. *P* values are from chi-square tests of the change in residual deviance for negative binomial models and *F* tests for GLMs

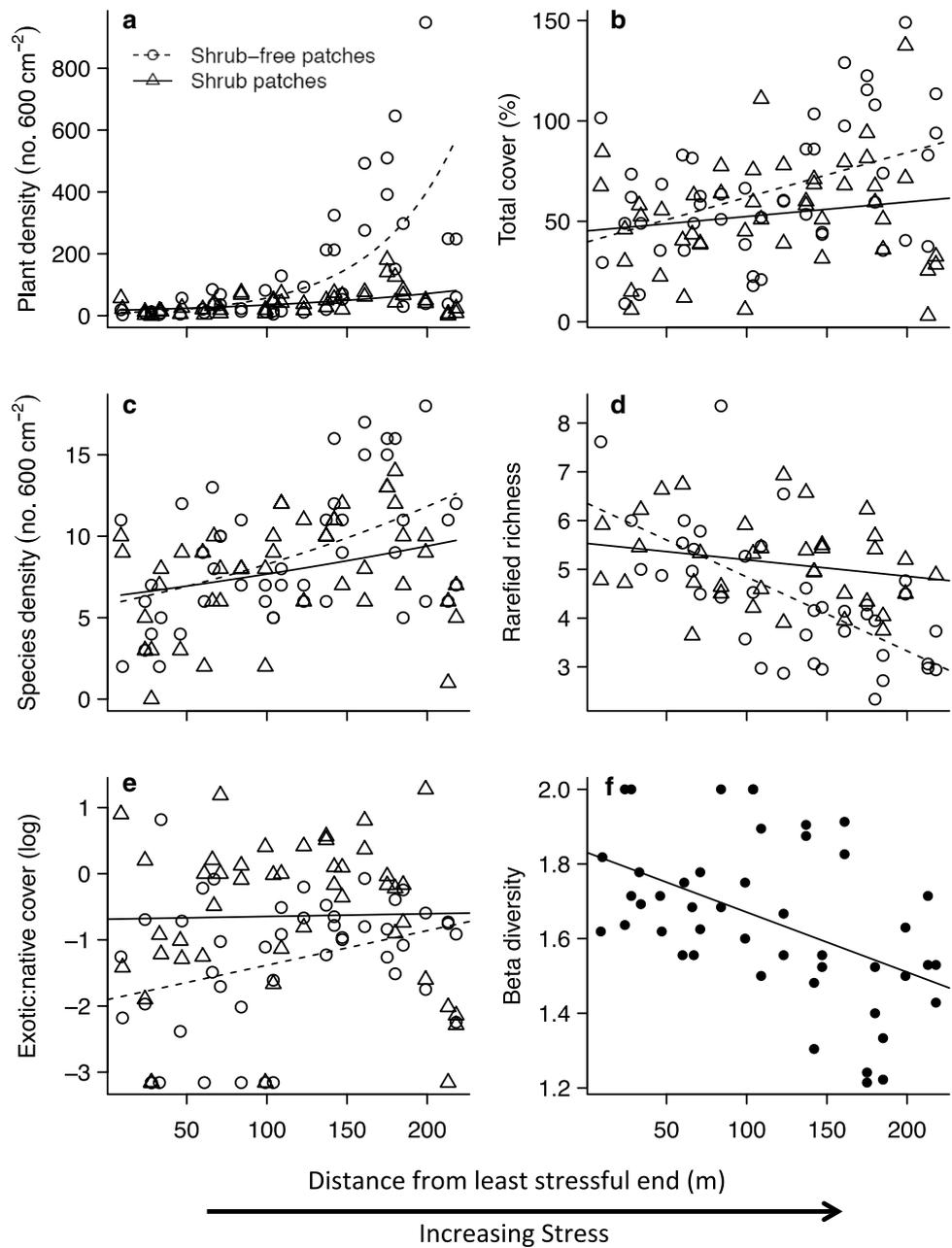
importance of ecosystem engineering on this plant community, the effects did not always increase towards the more stressful end of the environmental gradient in this coastal dune system.

Shrubs in this coastal dune engineer the local ecosystem by changing particle size distribution, increasing soil organic matter, and reducing local wind speeds (Figs. 1 and S2 of the ESM). The strong effects of shrubs on wind and organic matter support our first hypothesis and are largely consistent with other research showing the importance of shrubs in creating spatial heterogeneity in soil (Schlesinger et al. 1990; Alpert and Mooney 1996; Pugnaire et al. 1996; Shumway 2000). We expected that soils under shrubs would have greater proportions of wind-blown fine sand and silt (Gutiérrez et al. 1993; Zhao et al. 2007), but instead found significantly higher coarse sand fractions underneath shrubs than in shrub-free patches (Fig. 1b). Larger grained sands do not hold as much moisture or nutrients as

fine sand (Lortie and Cushman 2007), so this could have a negative effect on plants in shrub patches. While this effect was unexpected, greater particle size under shrubs has been reported in at least one other study (Sankey et al. 2012).

In general we found support for our use of position towards the NW on the gradient as a measure of stress, as wind speed and sand particle size were generally greater as distance to the NW side of the gradient increased (Fig. 1). However, soil properties did not change linearly across the gradient: particle size did not increase across the less stressful half of the gradient (0–100 m) and then increased dramatically across the more stressful half (100–220 m; Fig. 1b). Moreover, fine soil carbon actually peaked near the middle of the gradient (Fig. S1 of the ESM). This indicates that, at the low stress end of the site, position on the gradient may not have been as useful an indicator of soil stress. However, in general, we note that the wind speeds and particle size distributions are consistent with the NW

Fig. 4 Plant density (a), absolute percent cover (b), species density (c), rarefied species richness (d), and log ratio exotic:native species cover (e) in 46 pairs of shrub and shrub-free patches across the stress gradient. Beta-diversity between pairs of shrub and shrub-free patches (f). Regression lines are shown when either habitat or gradient position was a significant predictor of the response variable. Individual density and species density data were fitted with negative binomial models. In b, values for total cover can exceed 100 % because of overlapping plant canopies. In e, the ratio of exotic to native cover is log-transformed so that positive numbers show patches where exotic cover was greater than native cover



end of the gradient being more stressful for plant growth, so we believe that our use of this site as a linear stress gradient is still valid.

Counter to our hypothesis that the effects of shrubs on the physical environment would be greater at the more stressful end of the gradient, the effects of shrubs on sand particle size and wind did not increase towards the more stressful end of the environmental gradient (Fig. 1a–c). In fact, the positive effect of shrubs on coarse organic matter became weaker at the more stressful end of the gradient. One possible explanation for this result is that shrubs become shorter towards the more stressful end of the

gradient (Fig. 1a), which could reduce their effects on the physical environment. Further research could examine whether this supports the hypothesis that facilitating plants will have diminishing effects in the most stressful environments as their growth becomes limited (Holmgren and Scheffer 2010).

We found support for our hypothesis that the physical effects of shrubs would facilitate the growth of other species: *Bromus* plants grew larger and produced more flowers when transplanted under shrub canopies or when planted in soil collected from under shrubs (Fig. 3). Surprisingly, *Bromus* grown in shrub-free patches showed only small

Fig. 5 Aboveground biomass for exotic (a, b) and native (c, d) species in sampling quadrats from within 35 shrub removal patches and 35 control shrub patches across the environmental stress gradient. Biomass was collected from separate quadrats in each patch in spring of 2010 (a, c) and spring of 2011 (b, d). Regression lines are shown to assist in visualizing the shrub removal effect, and do not necessarily indicate significance of the gradient effect (see text for details). Note the log scale on the y axis

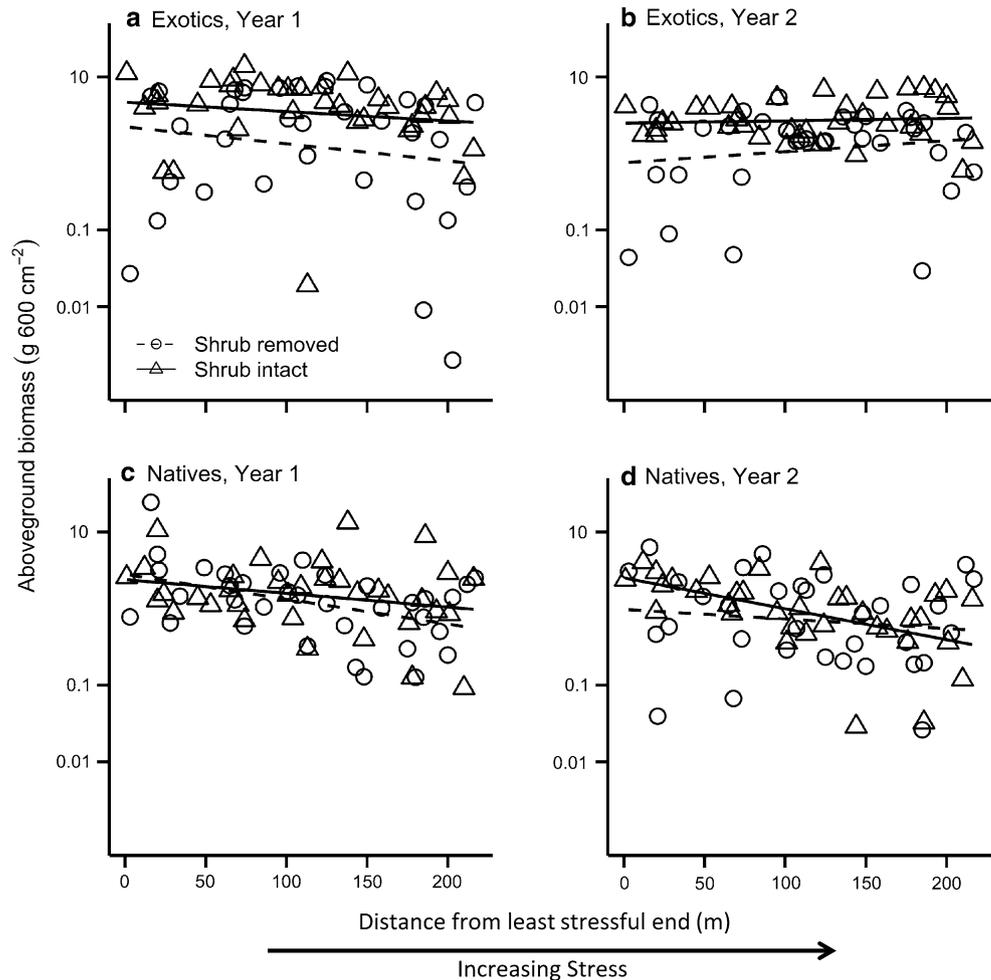


Table 2 Significance of main effects of gradient position, shrub removal treatment, year, and gradient by shrub removal interaction are shown for native and exotic aboveground biomass (log-transformed grams per quadrat) harvested from shrub removal and control plots

	<i>df</i>	<i>F</i>	<i>P(>F)</i>
(a) Native species			
Position	1.66	12.5	0.001
Treatment	1.66	0.9	0.356
Year	1.69	11.1	0.001
Position × treatment	1.66	0.0	0.889
(b) Exotic species			
Position	1.66	0.6	0.439
Treatment	1.66	14.7	0.003
Year	1.68	10.5	0.002
Position × treatment	1.66	0.0	0.942
Position × year	1.68	4.1	0.046

Separate linear mixed models were fitted for native and exotic species. We only report interactions between year and position or year and treatment that significantly improved model fit based on likelihood ratio tests

decreases in growth towards the stressful end of the gradient, and—counter to the stress-gradient hypothesis—we did not find a habitat × gradient interaction effect on *Bromus* facilitation. The strong effect of soil on *Bromus* growth was likely due to increased soil organic matter, which can increase water-holding capacity and nutrient availability in dune soils (Kutiel and Danin 1987; Alpert and Mooney 1996; Bonanomi et al. 2008). Positive aboveground effects of shrubs on *Bromus* could be due to shelter from direct solar radiation (Valiente-Banuet and Ezcurra 1991) and a decrease in wind speeds (Carlsson and Callaghan 1991; Lortie and Cushman 2007).

We found strong evidence that facilitative effects of shrubs extended beyond *Bromus* to many other species: the species most associated with shrub patches were also those that were most reduced by shrub removal (Fig. 6). We also found that overall exotic biomass was greater in intact shrub patches than in removed shrubs (Fig. 5c, d). Interestingly, we also saw a year effect in our removal experiment: about twice as much biomass per plot was harvested in the first year of the experiment (2010) as in the next

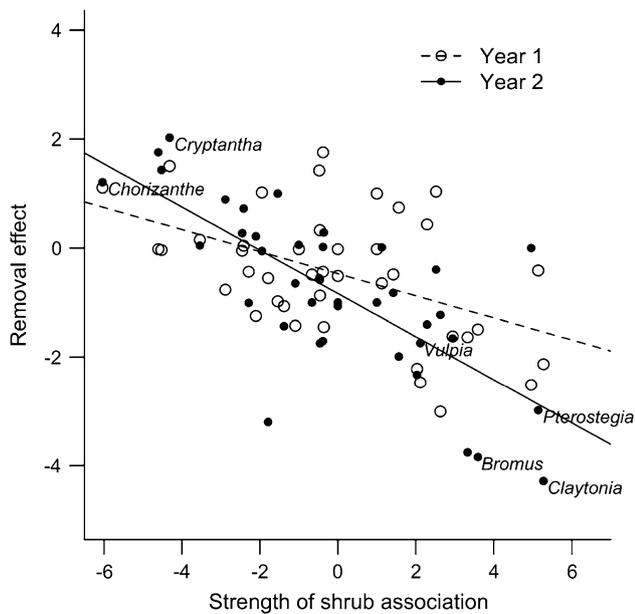


Fig. 6 Effect of shrub removal on aboveground biomass of species in years one and two regressed over the strength of each species' spatial association with shrubs across the gradient. Negative scores on the y axis represent a negative response to shrub removal, whereas positive scores on the x axis represent a positive spatial association with shrubs. Points for six common species are labeled with genera names

year (Fig. 5). Records from a weather station 1 km away showed that this site received nearly 50 % more rainfall between January and April (the active growing season) in the first year of the study than in the second. While there was no year \times treatment effect, we believe that this supports the idea that moisture deficit is an important source of stress in this environment. The finding that many species' abundances were reduced following the removal of only the aboveground shrub parts demonstrates that soil effects alone are not entirely responsible for facilitation. While much work on shrubs as ecosystem engineers has focused on soil effects (Schlesinger et al. 1990; Alpert and Mooney 1996; Bonanomi et al. 2008), our work adds to the evidence that aboveground effects of shrub canopies can be important as well (Holzapfel and Mahall 1999).

At the patch scale, we found that plant density was actually lower underneath shrubs than in shrub-free patches (Fig. 4a), but total absolute cover was more or less equal (Fig. 4b). This finding was somewhat unexpected and goes against our second hypothesis. Most other studies of ecosystem-engineering plants report greater density within engineers (Facelli and Temby 2002; Badano et al. 2006; Holzapfel et al. 2006). Only a few studies have shown lower plant density and species density within engineers (Gutiérrez et al. 1993; De Villiers et al. 2001; Cushman et al. 2010). Lower density within shrubs could result if facilitation increases growth but also increases competition

within shrub patches (Tielbörger and Kadmon 2000). In this model, plants within shrubs are larger, so fewer individuals can survive in the same amount of space. Plants outside of shrubs are smaller, and because of this many more of them occupy the same amount of space. This pattern makes sense considering the stress involved at this site: outside of shrubs, wind may reduce the ability of plants to grow tall and shade out their neighbors. In contrast, we predict that in environments where facilitation acts mainly to increase plant establishment and survival, we should see greater density within engineering plants—for instance, higher plant density is observed in cushion plants in the high Andes because cushion plants facilitate recruitment and survival (Badano et al. 2007).

Species density was also greater outside of shrubs, and this increased towards the stressful end of the gradient (Fig. 4c)—again the opposite of what has been reported by most other studies, and counter to our second hypothesis (Tewksbury and Lloyd 2001; Badano et al. 2006; Holzapfel et al. 2006; Forey et al. 2009). However, effects of shrubs on species density appear to have been driven by the changes in individual density discussed above (Gotelli and Colwell 2001). Rarified richness showed the opposite pattern and actually did support our second hypothesis (Fig. 5d). It is possible that richness is greater within shrub patches because both stress-tolerant and stress-intolerant species can coexist within shrub patches, whereas only stress-tolerant species can persist in shrub-free areas. Most species found in shrub-free patches at our site were occasionally sampled underneath shrubs, whereas some species found underneath shrubs were never found in shrub-free patches. We suspect that spatial heterogeneity in light, wind, and soil conditions could be greater within shrub patches and that this could have promoted higher species diversity within shrubs (Pugnaire et al. 1996).

Although the effects of shrubs were positive for many species and for rarified richness, a number of species were more abundant outside of shrubs and increased in abundance following shrub removal (Fig. 6). These species may be excluded from shrub patches by reduced light (Alpert and Mooney 1996), or by competition among the species within shrub patches (Tielbörger and Kadmon 2000). Supporting this, we note that the species negatively associated with shrubs were often smaller annual forbs, while taller forbs and grasses often benefited from shrubs. This supports the notion that functional traits underlie patterns of species response to facilitation or ecosystem engineering by plants (Schöb et al. 2012).

Species-specific facilitation by shrubs resulted in shrub patches harboring a distinct species assemblage from shrub-free patches (Fig. 3), supporting in part our hypothesis that ecosystem engineers would increase beta diversity. Not only did patterns of species abundances in shrub

patches differ from those in shrub-free patches, but synthetic community analysis also showed that shrub patches increased native species richness across the entire site (see Supporting Information A1 and Fig. S4 in the ESM), a result similar to those seen in other recent studies of ecosystem-engineering plants (Valiente-Banuet and Verdu 2007; Cavieres and Badano 2009; Butterfield et al. 2013).

While shrubs did have significant effects on beta diversity, we did not find strong support for our hypothesis that shrub effects would increase beta diversity more towards the more stressful end of the gradient. Whittaker's beta diversity, the proportion of species unique to either shrub or shrub-free patches, decreased towards the stressful end of the gradient, indicating that shrub and shrub-free patches were actually more similar at the more stressful end of the gradient (Fig. 4f). We hypothesize that this pattern results from two mechanisms. First, shrub patches themselves become smaller towards the high-stress end of the gradient and may therefore have a weaker effect on community composition. Second, this pattern could be driven by the increase in species and individual density towards the stressful end of the gradient (Fig. 4c). The high density within quadrats at the stressful end of the gradient could make it increasingly probable that sample quadrats would share the same species, thereby lowering beta diversity (Anderson et al. 2011). Indeed, when we considered the Bray–Curtis distance—which includes information on species abundance—as a measure of beta diversity, we saw no significant decrease in beta diversity across the gradient (Fig. S3 of the ESM).

We found partial support for another component of our third hypothesis (that facilitation would benefit exotic species more than natives). Exotic cover as a proportion of total cover was significantly greater within shrubs (Fig. 4e), and shrub removal had a negative effect on patch-scale exotic biomass and little effect on native biomass (Fig. 5a, b). Shrubs also reduced the biomass of the dominant exotic annual grasses *Bromus* and *Vulpia* (Fig. 6). However, we did not find that shrub patches contributed to overall exotic richness at this site (see Online Resource A1 and Fig. S4b of the ESM). Also, while shrubs facilitated exotic species, the effect did not increase across the stress gradient (Fig. 4e). Even at the high-stress end of the gradient, many exotic species were able to persist outside of shrubs. Overall, our study adds to evidence that shrubs and other ecosystem engineers can be hotspots for exotic species invasion (Maron and Connors 1996; Badano et al. 2007; Griffith 2010; Cushman et al. 2011), but not that this effect is necessarily stronger in more stressful environments.

Despite the support for the SGH at the individual level (He et al. 2013), the implications of positive interactions for overall community characteristics such as species richness and invasion by exotic species remain complex (Bruno

et al. 2003; Badano et al. 2006). Our study shows that, while ecosystem engineers do indeed have large community-level effects, the directions of many of these effects were different from those observed in other plant communities. We found striking species-specific responses of understory plants to shrubs—many species were either directly or indirectly inhibited rather than facilitated by shrubs. Our field experiment assessing the effects of shrub removal for almost every plant species in the community adds rigor to this conclusion. Lastly, we found strong support for the hypothesis that a native ecosystem engineer has important facilitative effects on dominant exotic species. This contributes to growing evidence that native species do not always suppress exotic invasion and can in fact facilitate exotic plant invasion in many environments.

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References

- Alpert P, Mooney HA (1996) Resource heterogeneity generated by shrubs and topography on coastal sand dunes. *Vegetation* 122:83–93. doi:10.1007/BF00052818
- Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14:19–28. doi:10.1111/j.1461-0248.2010.01552.x
- Armas C, Rodríguez-Echeverría S, Pugnaire FI (2011) A field test of the stress-gradient hypothesis along an aridity gradient. *J Veg Sci* 22:818–827. doi:10.1111/j.1654-1103.2011.01301.x
- Badano EI, Cavieres LA (2006) Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *J Biogeogr* 33:304–313. doi:10.1111/j.1365-2699.2005.01384.x
- Badano EI, Jones C, Cavieres L, Wright J (2006) Assessing impacts of ecosystem engineers on community organization: a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* 115:369–385. doi:10.1111/j.2006.0030-1299.15132.x
- Badano EI, Villarreal E, Bustamante RO, Marquet PA, Cavieres LA (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *J Ecol* 95:682–688. doi:10.1111/j.1365-2745.2007.01262.x
- Barbour MG, Craig RB, Drysdale FR, Ghiselin MT (1973) Coastal ecology: Bodega Head. University of California Press, Berkeley
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends Ecol Evol* 9:191–193. doi:10.1016/0169-5347(94)90088-4

- Bonanomi G, Rietkerk M, Dekker SC, Mazzoleni S (2008) Islands of fertility induce co-occurring negative and positive plant–soil feedbacks promoting coexistence. *Plant Ecol* 197:207–218. doi:10.1007/s11258-007-9371-0
- Brooker R, Kikvidze Z, Pugnaire FI et al (2005) The importance of importance. *Oikos* 109:63–70. doi:10.1111/j.0030-1299.2005.13557.x
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125. doi:10.1016/S0169-5347(02)00045-9
- Butterfield BJ, Cavieres LA, Callaway RM, Cook BJ, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Schöb C, Xiao S, Zaitchek B, Anthelme F, Björk RG, Dickinson K, Gavi-lán R, Kanka R, Maalouf JP, Noroozi J, Parajuli R, Phoenix GK, Reid A, Ridenour W, Rixen C, Wipf S, Zhao L, Brooker RW (2013) Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecol Lett* 16:478–486. doi:10.1111/ele.12070
- Callaway RM, Kikodze D, Chiboshvili M, Khetsuriani L (2005) Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* 86:1856–1862. doi:10.1890/04-0784
- Carlsson BA, Callaghan TV (1991) Positive plant interactions in tundra vegetation and the importance of shelter. *J Ecol* 79:973–983. doi:10.2307/2261092
- Cavieres LA, Badano EI (2009) Do facilitative interactions increase species richness at the entire community level? *J Ecol* 97:1181–1191. doi:10.1111/j.1365-2745.2009.01579.x
- Cuddington K, Byers JE, Wilson WG, Hastings A (2007) Ecosystem engineers: plants to protists. Academic, New York
- Cushman JH, Waller JC, Hoak DR (2010) Shrubs as ecosystem engineers in a coastal dune: influences on plant populations, communities and ecosystems. *J Veg Sci* 21:821–831. doi:10.1111/j.1654-1103.2010.01196.x
- Cushman JH, Lortie CJ, Christian CE (2011) Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *J Ecol* 99:524–531. doi:10.1111/j.1365-2745.2010.01776.x
- De Villiers AJ, Van Rooyen MW, Theron GK (2001) The role of facilitation in seedling recruitment and survival patterns, in the Strandveld Succulent Karoo, South Africa. *J Arid Environ* 49:809–821. doi:10.1006/jare.2001.0823
- Facelli JM, Temby AM (2002) Multiple effects of shrubs on annual plant communities in arid lands of South Australia. *Austral Ecol* 27:422–432. doi:10.1046/j.1442-9993.2002.01196.x
- Forey E, Lortie CJ, Michalet R (2009) Spatial patterns of association at local and regional scales in coastal sand dune communities. *J Veg Sci* 20:916–925. doi:10.1111/j.1654-1103.2009.01095.x
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391. doi:10.1046/j.1461-0248.2001.00230.x
- Griffith AB (2010) Positive effects of native shrubs on *Bromus tectorum* demography. *Ecology* 91:141–154. doi:10.1890/08-1446.1
- Gutiérrez JR, Meserve PL, Contreras LC, Vásquez H, Jaksic FM (1993) Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia* 95:347–352. doi:10.1007/BF00320987
- Hacker SD, Gaines SD (1997) Some implications of direct positive interactions for community species diversity. *Ecology* 78:1990–2003. doi:10.2307/2265939
- He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett* 16:695–706. doi:10.1111/ele.12080
- Holmgren M, Scheffer M (2010) Strong facilitation in mild environments: the stress gradient hypothesis revisited. *J Ecol* 98:1269–1275. doi:10.1111/j.1365-2745.2010.01709.x
- Holzapfel C, Mahall BE (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80:1747–1761. doi:10.1890/0012-9658(1999)080[1747:BFAIBS]2.0.CO;2
- Holzapfel C, Tielborger K, Parag HA, Kigel J, Sternberg M (2006) Annual plant–shrub interactions along an aridity gradient. *Basic Appl Ecol* 7:268–279. doi:10.1016/j.baae.2005.08.003
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386. doi:10.2307/3545850
- Jury W, Horton R (2004) Soil physics, 6th edn. Wiley, Hoboken
- Kutiel P, Danin A (1987) Annual-species diversity and aboveground phytomass in relation to some soil properties in the sand dunes of the northern Sharon Plains, Israel. *Vegetation* 70:45–49
- Lortie CJ, Cushman JH (2007) Effects of a directional abiotic gradient on plant community dynamics and invasion in a coastal dune system. *J Ecol* 95:468–481. doi:10.1111/j.1365-2745.2007.01231.x
- Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol* 97:199–205. doi:10.1111/j.1365-2745.2008.01476.x
- Maron JL, Connors PG (1996) A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302–312. doi:10.1007/BF00328732
- McNeil SG, Cushman JH (2005) Indirect effects of deer herbivory on local nitrogen availability in a coastal dune ecosystem. *Oikos* 110:124–132. doi:10.1111/j.0030-1299.2005.13686.x
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) vegan: Community Ecology Package. R package version 2.0-9. <http://CRAN.R-project.org/package=vegan>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2013) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-111. <http://CRAN.R-project.org/package=nlme>
- Pugnaire FI, Luque MT (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos* 93:42–49. doi:10.1034/j.1600-0706.2001.930104.x
- Pugnaire FI, Haase P, Puigdefábregas J, Cueto M, Clark SC, Incoll LD (1996) Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos* 76:455–464. doi:10.2307/3546339
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Sankey JB, Germino MJ, Sankey TT, Hoover AN (2012) Fire effects on the spatial patterning of soil properties in sagebrush steppe, USA: a meta-analysis. *Int J Wildland Fire* 21:545. doi:10.1071/WF11092
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247:1043–1048. doi:10.1126/science.247.4946.1043
- Schöb C, Butterfield BJ, Pugnaire FI (2012) Foundation species influence trait-based community assembly. *New Phytol* 196:824–834. doi:10.1111/j.1469-8137.2012.04306.x
- Shirazi MA, Boersma L (1984) A unifying quantitative analysis of soil texture. *Soil Sci Soc Am J* 48:142. doi:10.2136/sssaj1984.03615995004800010026x
- Shumway SW (2000) Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. *Oecologia* 124:138–148. doi:10.1111/j.1469-8137.2012.04306.x
- Tewksbury JJ, Lloyd JD (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127:425–434. doi:10.1007/s004420000614

- Tielbörger K, Kadmon R (2000) Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies? *Plant Ecol* 150:53–63. doi:[10.1023/A:1026541428547](https://doi.org/10.1023/A:1026541428547)
- Valiente-Banuet A, Ezcurra E (1991) Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. *J Ecol* 79:961–971
- Valiente-Banuet A, Verdu M (2007) Facilitation can increase the phylogenetic diversity of plant communities. *Ecol Lett* 10:1029–1036. doi:[10.1111/j.1461-0248.2007.01100.x](https://doi.org/10.1111/j.1461-0248.2007.01100.x)
- Zhao HL, Zhou RL, Su YZ, Zhang H, Zhao LY, Drake S (2007) Shrub facilitation of desert land restoration in the Horqin sand land of Inner Mongolia. *Ecol Eng* 31:1–8. doi:[10.1016/j.ecoleng.2007.04.010](https://doi.org/10.1016/j.ecoleng.2007.04.010)