A seed–seedling conflict for *Atriplex polycarpa* shrubs competing with exotic grasses and their residual dry matter

MITCHELL L. COLEMAN,1,2,† C. ELLERY MAYENCE,2,3,4 MICHAEL D. WHITE,2,5 ANNA L. JACOBSEN,1 AND R. BRANDON PRATT1

1Department of Biology, California State University, Bakersfield, 9001 Stockdale Highway, Bakersfield, California 93311 USA
2Tejon Ranch Conservancy, 637 San Emidio Way, Frazier Park, California 93225 USA
3New Zealand Department of Conservation, Private Bag 4715, Christchurch 8140 New Zealand
4School of Biological Sciences, University of Western Australia, Perth, Western Australia 6005 Australia
5Department of Biological Sciences, San Diego State University, 5500 Campanile Drive, San Diego, California 92182 USA

Citation: Coleman, M. L., C. E. Mayence, M. D. White, A. L. Jacobsen, and R. B. Pratt. 2021. A seed–seedling conflict for *Atriplex polycarpa* shrubs competing with exotic grasses and their residual dry matter. Ecosphere 12(4):e03455. 10.1002/ecs2.3455

Abstract. Native saltbush, *Atriplex polycarpa*, shrub populations are widely diminished and fragmented in the southern San Joaquin Desert of California due to habitat conversion and invasion by exotic annual grasses of mostly Mediterranean origin. The role these grasses play in saltbush population demography is not well understood. We hypothesized that saltbush seedling recruitment and growth is limited by the competitive interactions with exotic grasses, preventing saltbush stands from maintaining their populations and expanding. We predicted that saltbush seedling recruitment would be reduced by (1) light and moisture competition with the grasses; and (2) the physical barrier of grass residual dry matter (RDM) formed during senescence. To test our predictions, we investigated saltbush seedling recruitment under field conditions across six saltbush populations. We examined how variations in edaphic structure and water availability by site may have affected saltbush seedling recruitment and longer-term population dynamics. In experimental plots where saltbush seeds were sowed, exotic grass RDM reduced saltbush seedling emergence compared to seeds sown in the absence of RDM; competition post-emergence was not significant. Saltbush seedlings transplanted into the field had lower mortality and less herbivory in invaded grassy habitats compared to seedlings planted in bare zones in between established, mature saltbush shrubs. Edaphic variation and water availability by site were likely key factors affecting the success of both grass invasion and saltbush recruitment. Our results suggest that there is a seed–seedling conflict: Sites favorable for saltbush seedling emergence (minimal grass cover among mature shrubs) are unfavorable for seedling survival due to high herbivory. Conversely, sites favorable for saltbush seedling survival (high grass coverage away from mature shrubs) are unfavorable for seedling emergence. The RDM produced by grasses represents an important stabilizing feedback favoring continued grass dominance.

Key words: *Atriplex polycarpa*; *Bromus*; Chenopodiaceae; competition; exotic annual grasses; recruitment; residual dry matter; San Joaquin Desert.

Received 10 August 2020; revised 10 November 2020; accepted 14 November 2020; final version received 25 January 2021. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† E-mail: mcoleman@tejonconservancy.org

INTRODUCTION

One of the chief threats to desert ecosystems is invasion by exotic species (Brooks et al. 2016). The San Joaquin Desert within the San Joaquin Valley in California, USA, has a Mediterranean-type rainfall pattern with cool moist winters and hot dry summers. The valley floor averages less...
than 250 mm of rainfall annually that is highly variable and unpredictable and has sparse native vegetation that primarily consists of species found in the Mojave Desert (Polis 1991, Pavlik 2008, Belnap et al. 2016). Due to the massive transformation of this region for agriculture, it is the most imperiled desert in North America (Germano et al. 2011). More than 60% of the native desert habitat on the valley floor, including *Atriplex polycarpa* (Torr.) S. Watson (saltbush; Chenopodiaceae) shrublands, has been converted to agriculture. Much of the remaining native habitat is highly invaded by exotic annual grasses.

Drought-adapted plants have evolved mechanisms to cope with unpredictable and low water availability (Osmond et al. 1987, MacKinnon et al. 2014). Despite adaptive mechanisms, seed germination and seedling recruitment are especially vulnerable to desert constraints. Limited seedling recruitment, both emergence and survival, is a characteristic of long-lived plants, and recruitment is often a population bottleneck (Harper et al. 1955). A single mature saltbush shrub in the San Joaquin Desert of California may produce tens of thousands of seeds every year, but in most years relatively few of these seeds germinate and successfully establish seedlings. Once seedlings emerge (January–March), they survive at very low rates, especially when co-occurring with abundant exotic annual grasses (Ciblis et al. 1998, Dodd and Donovan 1999, Germano et al. 2001, Coleman and Pratt 2019, Phillips et al. 2019).

Arid and semi-arid regions in the western United States and California have been invaded by numerous exotic annual grass species such as *Bromus madritensis* L., *Bromus diandrus* Roth, and *Avena sativa* L., that suppress native plant recruitment for a variety of reasons. In some cases, the grasses grow in such dense stands that they outcompete natives and decrease species richness (Corbin and D’Antonio 2004, Yelenik and Levine 2011). Grass seedlings generally emerge sooner than native grass and shrub seedlings and produce a dense, shallow root system (Wainwright et al. 2012). The grasses commonly share the same rhizosphere as co-occurring natives, which can limit native recruitment through competition for resources, especially water (Schultz et al. 1955, Yelenik and Levine 2011).

The residual dry matter (RDM) formed from senesced shoots of the annual grasses is dense and fibrous and does not rapidly decompose after senescence in the arid climate (Chen et al. 2018). This differs from native forbs that typically produce less aboveground biomass and therefore less RDM, which is generally non-fibrous and fragments and decomposes more quickly—resulting in bare soil until the following growing season. Persistent and dense RDM modifies habitat by increasing shading of the soil surface and lowering light and temperature levels, thereby inhibiting seedling emergence and survival (Germano et al. 2001, Bartolome et al. 2007, Wolkovich et al. 2010, Coleman and Pratt 2019, Molinari and D’Antonio 2019). Light and temperature reduction from RDM may be especially detrimental for plants such as saltbush that exhibit the C4-photosynthetic pathway, which thrive in high light and temperature conditions, becoming competitively disadvantaged in shady habits compared to C3 plants (Ehleringer and Peary 1983). This is further exacerbated by the Mediterranean climate where available moisture is very limited outside of the approximately 4–5-month winter wet season (Germano et al. 2011). Resource competition and habitat modification by RDM from exotic grasses were previously found to negatively affect seeding recruitment of *A. polycarpa* in the San Joaquin Desert by both suppressing emergence and reducing survival (Coleman and Pratt 2019). This study was conducted at only a single field site under semi-controlled conditions; therefore, more rigorous, controlled testing in native habitat is warranted.

The present study was carried out under field conditions in native saltbush habitat in a range-land at the south end of the San Joaquin Desert, California (Appendix S1: Fig. S1). We sampled across sites representing a broad range of edaphic and hydrologic characteristics deemed important for saltbush population viability—hypothesizing that saltbush seedling recruitment is suppressed by the habitat-altering effects of exotic grasses. We predicted saltbush recruitment would be reduced by (1) structural modification of RDM during the dry season, and (2) competitive interactions with exotic grasses during the wet season. Furthermore, we predicted that distinct cohorts of shrubs would be identifiable by age due to past episodic recruitment during wet
years of abundant soil moisture availability and
mortality events during consecutive drought
years when grass populations were reduced.
Alternatively, if saltbush was recruiting success-
fully annually, sites would have a continuous age
structure. These predictions are consistent with
the highly variable interannual rainfall patterns
in the San Joaquin Desert (Germano et al. 2011)
and observations that seedling emergence in the
region is highly episodic (personal observations
of the authors), perhaps coinciding with intermittent
periods of drought when the grasses are dimin-
ished (Brome Crash Theory; Minnich 2008).
Lastly, we predicted that microsite differences,
particularly edaphic characteristics in our edaph-
ically diverse study area (Bartow and Dibblee
1981, Spiegel et al. 2016), and water resource
variation between the sites would affect saltbush
recruitment success.

METHODS

Study area

The study was conducted in the Comanche
Point region of Tejon Ranch at the southeast cor-
er of the San Joaquin Desert, California (Table 1;
Appendix S1: Fig. S1). This active rangeland has
a broad range of abiotic factors that could affect
saltbush recruitment, including topography (slope,
aspect), soil (texture and depth), fire, hydrology,
drought, and biotic factors (livestock grazing and
native animal herbivory).

Comanche Point consists of low hills underlain
by marine siltstone, sandstone, and conglomerate
formations (Dibblee and Minch 2008). The hills
are extensively dissected by seasonal drainage
channels and natural gullies (eroded badlands).
Major seasonal creeks (arroyos) include Tejon
Creek, Comanche Creek, and Little Sycamore
Creek. Dominant soil series include Chanac,
Pleito, and Badlands. The soil is relatively deep
(100+ cm), and the dominant soil texture is sandy
loam. Exotic annual grasses occur throughout the
area, the most dominant of which are B. madriten-
sis, B. diandrus, and A. sativa. We do not have data
on nitrogen deposition, but the site is located at the
southern terminus of the San Joaquin Desert and
we estimate that it receives 7–11 kg N ha⁻¹ yr⁻¹
(Bytnerowicz et al. 2016). Small, isolated, fast-
moving grass fires are common in the region,
with the last large fire encompassing the whole
study area occurring in the summer of 2011.

The region has a Mediterranean-type climate
with hot, dry summers and cool, moist winters
(Germano et al. 2001, 2011, CDFW 2003). It is
also classified as a desert in the context of the
amount of annual rainfall (average rainfall = 178 mm/yr; Germano et al. 2011). In a typical
year, rains begin in mid to late December and
persist until late March or early April. The dry
season typically spans from early May until
November. Within the study area, we assessed
saltbush recruitment at six sites differing in soil
characteristics and landscape position (Table 2).
We continually monitored air temperature and
precipitation with a weather station (Davis Van-
tage Pro1, Davis Instruments, Hayward, Califor-
ia, USA; Appendix S1: Fig. S1) positioned
central to the six sites.

Naturally emerged seedling survival

Approximately two-month-old saltbush seed-
lings were tagged at the juvenile (beyond cotyle-
don) stage and monitored over time to determine
survival (250 across five sites, Table 3). We mea-
sured survival once a month for 17 months (May
2016–October 2017) with a two-year re-measure-
ment conducted in June 2019. The seedlings were
tagged at their base within the plot used for
demographic analysis described below, approxi-
mately two months after initial emergence in
March 2016. The seedlings were chosen at ran-
dom. All tagged seedlings co-occurred with exo-
tic grasses, and grass cover was quantified (see
Exotic Grass Cover).

Table 1. Site characteristics of six saltbush (Atriplex
polycarpa) populations located in the Comanche
Point region of Tejon Ranch in the San Joaquin
Desert of California.

| Site number | Latitude (°) | Longitude (°) | Elevation (m) | Slope/aspect |
|-------------|--------------|---------------|---------------|--------------|
| 1           | 35.091943    | −118.810477   | 225           | 20°/West facing |
| 2           | 35.092488    | −118.819262   | 233           | Flat         |
| 3           | 35.135932    | −118.832060   | 203           | 35°/West facing |
| 4           | 35.136666    | −118.828924   | 207           | 30°/West facing |
| 5           | 35.131265    | −118.813313   | 185           | Flat         |
| 6           | 35.161564    | −118.796194   | 191           | 45°/Southwest facing |

Note: Geographic coordinates served as the central survey
te points for a demographic analysis of each site.
Survival of transplanted seedlings in native saltbush shrubland compared to exotic grassland

The saltbush populations surrounding Comanche Point are isolated from other saltbush populations and abruptly give way to grassland habitat dominated by exotic annual grasses immediately adjacent to native shrubs. To test the competitive inhibition of grasses on saltbush survival and related to edaphic factors, we out-planted 9-month-old saltbush seedlings into both grassland (treatment) and saltbush shrubland (control). There were a limited number of available seedlings for transplantation; thus, a subset of two from the main six sites were chosen to achieve sufficient treatment replication (Table 2). The two sites were chosen based on their dense saltbush habitat with sparse inter-shrub grass coverage, while also having immediately adjacent grasslands entirely devoid of saltbush. Seedlings and native soil were collected from the sites on 29 January 2016. Seeds were opportunistically collected from multiple individuals from each site based on phenology (not all shrubs were in fruit) and were kept in clear aerated glass containers until propagation, while the native soil was kept dry in shallow 40 x 20 cm greenhouse flats. Seeds did not require moisture/temperature stratification or physical scarification prior to propagation. In April 2016, the seeds were sown 1 cm deep in the native soil in a greenhouse on campus at California State University, Bakersfield, and irrigated once a day for 10 min. Once germinated, seedlings were planted in individual 20 cm tree tubes and moved outdoors, watering once weekly for the next six months, after which watering was reduced and they were hardened off for two months. The seedlings were twice fertilized at one-quarter the manufacturer’s recommended amount, once in July 2016 and once in November 2016 (Miracle-Gro All Purpose Plant Food, 100123; Scotts Miracle-Gro Company, Marysville, Ohio, USA). Seedlings were then out-planted at the two sites in early 2017 after adequate winter rainfall had occurred. At each site, seedlings were planted into both grassland (treatment) and saltbush shrubland (control) along a single randomly selected East/West oriented transect within each site (n = 38 seedlings per transect). Seedlings were spaced 1 m apart and watered at the time of planting with 500 mL of water each. We measured the survival and height of each seedling once per month for eight consecutive months through the dry season (February–October 2017), with a single recent round of data collected in June 2019. We also noted the cause of mortality when damage was visible.

Table 3. Survival and mortality of naturally occurring Atriplex polycarpa seedlings tagged across six sites.

| Site number | Number of seedlings tagged† | Number of survivors in 2017 | Mortality (%) in 2017‡ | Number of survivors in 2019 | Mortality (%) in 2019‡ | Grass coverage (%) in 2017‡ |
|-------------|-----------------------------|-----------------------------|------------------------|---------------------------|------------------------|---------------------------|
| 1           | 67                          | 15                          | 78\(^{A}\)             | 3                         | 96\(^{B}\)             | 60.4 (8.2)\(^{A}\)        |
| 2           | ...                         | ...                         | ...                    | ...                       | ...                   | 35.1 (4.6)\(^{B}\)        |
| 3           | 63                          | 29                          | 54\(^{B}\)             | 2                         | 97\(^{B}\)             | 18.4 (9.3)\(^{C}\)        |
| 4           | 40                          | 5                           | 88\(^{A}\)             | 0                         | 100\(^{A}\)            | 6.4 (1.9)\(^{D}\)         |
| 5           | 40                          | 25                          | 40\(^{B}\)             | 17                        | 58\(^{C}\)             | 71 (8.3)\(^{A}\)          |
| 6           | 40                          | 3                           | 92\(^{B}\)             | 1                         | 98\(^{B}\)             | 4.3 (0.76)\(^{D}\)        |
| Totals or mean | 250                        | 77                          | 70                      | 23                        | 92                    | 32.6                      |

Notes: Two hundred fifty seedlings were tagged in May 2016 and monitored every month for survival until October 2017. Coverage of exotic grasses represents mean grass levels measured at each site on 20 February 2017 (n = 30 measurements per site). Standard errors of the mean are shown in parentheses.

† Site 2 had no naturally occurring seedlings.

‡ Values with different letters vary significantly between sites (Tukey’s HSD, P < 0.05).
Size class analysis to estimate demography and historic recruitment events

Episodic seedling recruitment during high rainfall years and mature shrub mortality during severe drought years has been documented in California deserts (Casper 1996, Brown and Wu 2005, Miriti et al. 2007). Saltbush seedling recruitment is primarily episodic and associated with abundant soil moisture (personal observation of the authors). Similarly, mature shrub death is also episodic and linked primarily to drought (Sankary and Barbour 1972; personal observation of the authors). We observed an episodic seedling recruitment event in the winter and spring of 2016, which was at the end of a five-year drought phase (Minnich 2008). One reason why saltbush may recruit after successive years of intense drought could be that grasses are not as abundant, thus decreasing their competitive ability and the levels of remaining RDM. We predicted this might be an important factor for saltbush demographics. One way to determine if populations are expanding, stable, or contracting is to assess the age structure of a population. If a population contains a homogenous mix of ages, it indicates that recruitment is ongoing. If a population contains an even age of individuals or is composed of distinct even-aged cohorts, then it indicates that recruitment is episodic. We predicted that mature saltbush stands would contain distinctly aged cohorts due to past episodic recruitment events such as the one we observed in 2016.

A demographic analysis was conducted for each of the six sites to assess differences in age structure within and between sites. All measurements were taken between May and December 2016. The timeframe for measurements was due to the time-intensive approach for measuring each shrub. To account for changes to demographics with relatively fast-growing seedlings, we did not measure seedlings that germinated within the past growing season in the winter and spring of 2016. Saltbush produces anomalous secondary growth lacking clear growth rings, is multi-stemmed, and often experiences dieback of branches; therefore, there is no reliable way to non-destructively determine saltbush age in the field (Fahn and Zimmermann 1982). A common alternative approach is to use size as a proxy for age (Lefkovitch 1965); therefore, we measured size (canopy volume) to qualitatively estimate age. We assumed that smaller shrubs are younger and that larger shrubs are older.

Shrubs were selected for size measurements at each site by randomly staking a central survey point and measuring all shrubs within a 30-m radius of that point. We measured crown width (the shrub crown interval along the transect from the central point), cross width (the width perpendicular to crown width), and height of each shrub. We then used the crown width, cross width, and height to calculate the canopy volume in m³ of each shrub with the following formula from Thorne et al. (2002):

\[
\text{Canopy volume} = \frac{2}{3\pi} \times \frac{\text{height}}{\text{crown width}^2} \times (\text{cross width}/2).
\]

Exotic grass cover

We quantified grass abundance at each site on 20 February 2017 (climax of annual grass growth) by measuring the percentage of grass cover at random points at our six field sites (n = 30 plots). Measurements occurred within the 30-m radius of the demographic analysis at each site and near to the naturally emerged and tagged seedlings. We used a 20 × 50 cm plot to collect percent coverage data (Daubenmire 1959). We determined percent coverage by analyzing the total percentage of ground covered by exotic grasses within each plot, then assigning each species the appropriate percentage to the nearest integer in increments of five.

Water availability

Water availability may be a key factor affecting variation in saltbush population dynamics and grass invasion in the region (Spiegal et al. 2016). Saltbush tissue moisture was assessed by measuring branchlet water potential during the winter wet season and during the autumn end of dry season of 2017. Midday plant water potentials provide information on the moisture level the plants are accessing in the soil, how conductive the soil and plant is to water flow, and how high the transpiration rates are of the plants.

We measured midday branchlet water potentials (\(\Psi_w\)) from outer canopy (sun-exposed) and south-facing sides of the same three mature saltbush shrubs per site in the winter wet season (21 February 2017) and at the peak of the autumn dry season (4 October 2017). On both sampling dates, the weather was sunny. Three shrubs were
randomly selected per site. We clipped three branchlets from each shrub (subsamples), bagged them, and placed them in a cooler with ice packs (n = 3 samples and 3 subsamples per site per season). We then transported the samples back to a laboratory at CSU Bakersfield, and water potentials were measured with a pressure chamber within 3 h of harvest (Model 2000 Pressure Chamber Instrument; PMS Instruments, Corvallis, Oregon, USA).

Concurrent with branchlet water potential measurements in February and October 2017, we collected soil samples from various depths (surface, 10, 20, 50, and 100 cm) at each site and measured for soil water potential with a dew point potentiometer (WP4C; Meter Group, Pullman, Washington, USA) to assess soil moisture differences at different soil depths. One sample was taken from each sampling depth at each site.

Edaphic characteristics

We randomly collected three 10-cm soil cores at each site, within the demographic and percent percentage grass cover measurement areas. The three core samples from each site were then homogenized prior to analysis. Each sample was analyzed (Utah State University Analytical Laboratories, Logan, Utah, USA), using standard analytical techniques and procedures (Underwood and Guo 2013), for texture and a range of chemical properties (characteristics, i.e., pH, salinity, plant-available macronutrients including N, P, K, S, and the percent organic matter).

Grass competition and RDM effects on seedling emergence

We tested the effects of exotic grasses on saltbush emergence by manipulating competition and RDM across an in situ field experiment with treatments similar to those used in Coleman and Pratt (2019). This experiment was not conducted at the six sites as they were all actively grazed by cattle. We instead conducted the experiment at a site where cattle were excluded (Appendix S1: Fig. S1). The exclosure was located <1 km from the six main sites and in the same region. At the time of our experiment, the fenced exclosure was dominated by a dense cover of RDM, mostly *B. diandrus* and *B. madritensis*.

We randomly established sixty 20 × 50 cm plots to assess seed germination. We raked away the previous year’s RDM and weeded by hand where necessary. Seeds of saltbush were then sown in the plots (100 seeds per plot) and spread with a rake. Exotic grass competition and RDM were manipulated with the following treatments: (1) RDM (grass thatch) was either directly added to a specified amount onto the soil surface, or not added (±RDM); and (2) plots were either weeded or not to test competition (±weeded). We randomly assigned each plot to one of four treatments (n = 15 plots/treatment): (1) +RDM/−Weeded, (2) −RDM/−Weeded, (3) +RDM/+Weeded, (4) −RDM/+Weeded.

We standardized the amount of RDM added to +RDM plots by adding RDM until the light level (400–700 nm) at the soil surface underneath the RDM was approximately 300 µmols of quanta-m²-s⁻¹ measured on a clear sunny day at midday (ambient PPFD ~2000 µmols quanta-m⁻²-s⁻¹; Li 250A, Li-Cor Corporation, Lincoln, Nebraska, USA). This light level corresponded to the amount of shade produced from a moderately dense layer of RDM with a dry mass of about 0.015 kg/m², which was comparable to the RDM of moderately grass-invaded old-field areas throughout the San Joaquin Desert (Bartolome et al. 2007). The RDM added to the plots was collected in situ. When weeding, we avoided disturbing saltbush seeds and seedlings in the plots by frequently visiting the site when the annual grasses and forbs were just germinating (January–March) so they could be removed when small. We weeded plots as necessary at the same time as plot measurements were made.

To determine the effects of the treatments, we measured saltbush density (individuals/plot) from 20 February 2017 (immediately following emergence) to 26 April 2017. We used a 20 × 50 cm plot that was color-coded to aid assignment to different coverage classes (Daubenmire 1959). Measurements were made approximately every other week after initial emergence in the winter and spring of 2017 to capture the rapid emergence and mortality that occurred during that time (February–April).

Statistical analyses

Statistical analyses were conducted using JMP 13 (SAS Institute, Cary, North Carolina, USA), Minitab 18 (Minitab Inc., State College, Pennsylvania, USA), and (R Foundation for Statistical
Computing, v 3.6.2; \( \alpha = 0.05 \)). All data were checked for normality and constant variance and were log transformed, as necessary. In some cases, transformations failed, and non-parametric models were used. We conducted non-parametric analyses using the methods described in Barnard et al. (2007).

To assess variation in survival by site between tagged saltbush seedlings, we used a general linear model with binomial distribution (dead vs. alive) with Tukey’s HSD to test post hoc differences by site. We individually tested survival data from 4 October 2017 and June 2019. We assessed the total number of surviving seedling transplants as of 4 October 2017 by site (\( n = 2 \), sites 3 and 4) and by treatment (grassland vs. saltbush) with heterogeneity chi-square tests with the Yate’s correction (Barnard et al. 2007). Expected values of 19 (\( n = 38/2 \)) were used in accord with the null hypothesis that survival would not differ by treatment and would be 50%. A second null hypothesis was that survival would not vary by site. We chose 50% as a null hypothesis for mortality because 50% base mortality of seedlings from a previous study (Coleman and Pratt 2019). This was reasonable to account for both higher survival and higher mortality to the null relative to both the treatment (grassland transplants) and the control (saltbush shrubland transplants).

We compared a range of factors across all our field sites. Variation in canopy volume (as a proxy for demographic composition) was analyzed with Kruskal–Wallis tests. We used Mann–Whitney tests for differences in survival of naturally emerged seedlings. Histograms were fit with the default smoothing function in R software package ggplot2 to visualize the patterns in the distributions. To assess differences in the level of grass invasion between the six sites, we used a one-way ANOVA and Tukey’s HSD post hoc. Branchlet water potentials were compared by season and site with a two-way ANOVA and a Tukey’s HSD post hoc test. An interaction term between site and season was included in the model. Both site and season were fixed factors.

For the experiment examining the role of grass RDM and competition on saltbush seedling emergence, the maximum density of saltbush (count of individuals germinated/plot) was analyzed with a Kruskal–Wallis test. Maximum density represented the number of saltbush seedlings that germinated of the 100 seeds added to each plot, as a measure of apparent seed emergence. It is possible that this value would not represent emergence if some individuals died before the point of maximum density; however, this is unlikely as our plots were largely free from disturbance and when a seedling died it stayed in place and was easily observed. Moreover, mortality of seedlings did not begin until after the winter wet season and after the maximum densities were recoded. Thus, maximum density provided a reliable estimate of seedling emergence. We used contrasts to test for differences between individual factor levels (i.e., +RDM vs. –RDM and +weeded vs. –weeded). Variation between sites by canopy volume, branchlet and soil water potentials, seedling emergence, and edaphic characteristics was summarized with a principal components analysis (PCA) model. Two principal components were determined to be most informative from a SCREE plot. For the PCA, all the site loadings were divided by 8 so that they scaled in a similar range to the coefficients for the various factors to facilitate plotting on the same figure.

**RESULTS**

**Naturally emerged seedling survival**

Survival of naturally emerged seedlings to the juvenile growth stage varied among the six sites. Of 250 tagged seedlings in May 2016, 173 (70%) had perished by October 2017. As of June 2019, 227 (92%) of the individuals had perished (Table 3). Survival varied by site in 2017 (\( F_{1,4} = 12.75, P < 0.001 \)), with greater survival at Sites 3 and 5, and lower survival at Sites 1, 4, and 6 (Table 3). Site differences by 2019 were observed (\( F_{1,4} = 30.62, P < 0.001 \)), with the greatest survival at Site 5, lower survival at Sites 1, 3, and 6, and no survival at Site 4 (Table 3). The mean height of the surviving individuals surveyed in June 2019 was approximately 40 cm and these individuals appeared to be well established.

**Survival of transplanted seedlings in native saltbush shrubland vs. exotic grassland**

Eight months after out-planting, survival of saltbush seedlings transplanted into grassy habitat was twice as high compared to seedlings transplanted into established saltbush habitat (\( \chi^2 = 10.98, df = 1, P < 0.001 \)). The number of
surviving individuals was higher at Site 3 compared to Site 4 ($\chi^2 = 48.191$, df = 1, $P < 0.001$, Fig. 1A). Seedling mortality among the seedlings planted among shrubs appeared to be due to herbivory from kangaroo rats (Dipodomys heermanni), jackrabbits (Lepus californicus), and cottontail rabbits (Sylvilagus audubonii) between March and May 2017, as each seedling was repeatedly clipped at the base until mortality occurred. In contrast, herbivory-induced mortality was not observed for seedlings growing in the grassy habitat, and mortality in this treatment was caused by other unknown factors (e.g., drought stress) in the summer of 2017 (Fig. 1B). In June 2019, 47% of saltbush individuals transplanted into grassy habitat died (Fig. 1), whereas 100% of saltbush individuals transplanted amongst established saltbush shrubs had died.

**Exotic grass cover**

The level of exotic grass cover in the winter wet season (February 2017) varied significantly by site ($F_{1,5} = 80.36$, $P = 0.004$; Table 3). Sites 1 and 5 had a higher grass cover compared to the other sites (Table 3).

**Size class analysis to estimate demography and historic recruitment events**

Distinct size-structured cohorts were present both within and across sites. The six sites had a wide range of saltbush size distributions suggesting that sites differed in their population demographics, which was likely controlled by a range of site-specific factors ($H = 73.18$, df = 5, $P < 0.001$; Fig. 2, Table 4). There were only a few old shrubs (>1 m$^3$) at sites 3 and 4, suggesting that these sites were more recently established or that mortality of shrubs prevented them from attaining old age. Sites 3 and 4 had more shrubs per unit area. Sites 1, 2, 5, and 6 had many mature shrubs along with a range of smaller ones, suggesting ongoing recruitment combined with lower levels of mortality. Notably, size structure at all sites was at least bimodal (two more size cohorts), which may represent two (or more) past recruitment events.

**Water availability**

The study region is highly seasonal, with a hot dry summer and interannually variable precipitation occurring in the winter (Appendix S1: Fig. S2). Water resources were variable by site and season. Midday branchlet water potential varied predictably by season, being less negative in the winter wet season and more negative during the autumn dry season ($F_{1,1} = 2096.63$, $P < 0.001$). Saltbush water potentials also varied by site ($F_{1,5} = 58.10$, $P < 0.001$; Appendix S1: Fig. S3), and there was an interaction between season and site ($F_{1,5} = 63.65$, $P < 0.001$; Table 5), indicating that shrubs at the different sites responded differently to the changing seasons.
Soil moisture was limited during the dry season at all sites and soil depths (soil water potentials $<-4$ MPa; Appendix S1: Fig. S4). All sites had higher water potential in winter months than in the autumn indicating more available moisture at this time. All sites had the same water potential, except for Site 4 that did not reach as high a value of water potential suggesting less moisture at this site. This was likely driven by the fine texture (sandy clay loam) and 14x higher salinity of the soil at this site (Appendix S1: Table S1). Some of these factors were highly variable, yet we did not see any associations between these factors and the various response variables that we measured.

Grass competition and RDM effects on seedling emergence

Exotic grass RDM affected saltbush seedling emergence in our plots, whereas competition with the grasses had no noticeable effect. Peak saltbush emergence varied among the treatments ($H = 17.85$, $df = 3$, $P = 0.005$; Fig. 3). The presence of RDM reduced the emergence of seedlings when RDM was absent ($H = 16.98$, $df = 1$, $P < 0.001$). Competition for resources from the exotic grasses did not affect emergence ($H = 0.39$, $P = 0.533$). Seedling mortality was 100% for all treatments by April 2017.

Variation across sites

Relationships between the numerous response variables that we measured were summarized with a PCA analysis (Fig. 4). The first component (PC1) explained 45% of the variation. Sites 2 and 4 loaded most strongly with PC1 with Site 1 to a lesser degree. The positive end of this PC reflects lower summer moisture availability and large plants with a diverse range of canopy sizes, which tracked closely with Site 2. The negative end of PC1 reflects high seedling emergence, density, mature shrub density, and soil salinity, which tracked closely with Site 4. Sites 3 and 4 loaded strongly with the second component.
(PC2), which explained 24% of the variation. The positive end of PC2 reflects low winter water availability, elevated N and P, and soil salinity, which tracks closely with Site 4. The negative end of PC2 reflects high grass coverage and seedling emergence, which best describes Site 1. All sites fall in their own unique regions of the loading plot indicating that each site has its own unique set of defining factors.

**DISCUSSION**

**Exotic grasses and seedling recruitment: A seed/seedling conflict in saltbush populations**

We predicted that exotic grass competition and RDM would be key factors affecting saltbush recruitment (Coleman and Pratt 2019, Phillips et al. 2019). We found that RDM significantly diminished saltbush emergence, whereas competition with exotic annual grasses did not. This suggests that habitat modification by exotic grass RDM may be the primary factor limiting saltbush populations and is supported by a recent experiment (Coleman and Pratt 2019). The effect of the RDM is likely due to the decreased soil light and temperature levels under thick layers of RDM, which may be especially detrimental to the C4-photosynthetic pathway of *Atriplex* species (Ehleringer and Pearcy 1983). The presence of dense RDM is likely a significant impediment to saltbush recruitment and represents a stabilizing feedback that favors persistent grass dominance in arid communities (Park and Jenerette 2019).

The lack of a competitive effect between annual grasses and saltbush seedlings may be due to largely spatially separated use of soil resources between their two different root system growth forms. Grass roots are fibrous and shallowly rooted, whereas saltbushes produce woody taproots that penetrate far deeper into the soil profile, even at the seedling stage (Chen et al. 2018, Phillips et al. 2019). The spatial separation of the root systems of annual grasses and saltbushes in the soil profile suggests that they largely avoid below-ground competition (Cleland et al. 2016).

The role of exotic species in affecting seedling recruitment has been documented in numerous other studies (Schultz et al. 1955, Hamilton et al. 1999, Corbin and D’Antonio 2004, Liu and Stiling 2006). Seedlings are a sensitive stage in the life cycle of many plants, especially long-lived woody shrubs like saltbushes. Saltbushes emerge during the wet season, which is during the winter months when days are at their shortest. The combination of short daylengths and shading from RDM may be too much for the C4-photosynthetic saltbushes to overcome because of their low quantum efficiency compared to C3 species (Ehleringer and Pearcy 1983).

Transplanted saltbush seedlings survived differently in grassland vs. saltbush-dominated

| Site number | Number of shrubs measured | Density (individuals/m²) | Min canopy volume (m³) | Median canopy volume (m³) | Max canopy volume (m³) | Interquartile range of canopy volume (m³) |
|-------------|----------------------------|--------------------------|------------------------|--------------------------|------------------------|------------------------------------------|
| 1           | 235                        | 0.083                    | 2.1 × 10⁻⁴            | 0.014                    | 26                     | 0.076                                    |
| 2           | 145                        | 0.051                    | 8 × 10⁻⁵              | 0.814                    | 27.3                   | 1.986                                    |
| 3           | 418                        | 0.148                    | 0.005                 | 0.045                    | 12.4                   | 0.4127                                   |
| 4           | 337                        | 0.119                    | 4.7 × 10⁻⁵            | 0.175                    | 3.16                   | 0.2471                                   |
| 5           | 144                        | 0.051                    | 0.0008                | 0.407                    | 26.4                   | 2.223                                    |
| 6           | 160                        | 0.057                    | 0.001                 | 0.441                    | 3.13                   | 1.0505                                   |
| Mean        | 230                        | 0.081                    | 0.001                 | 0.315                    | 17                     | 1.00                                     |

*Note*: All shrubs were measured within a 30-m radius at each site.

| Source of variation | df | SS    | MS    | F     | P     |
|---------------------|----|-------|-------|-------|-------|
| Site                | 5  | 60.20 | 12.040| 58.10 | 0.000 |
| Season              | 1  | 434.52| 434.524| 2096.63| 0.000 |
| Site × season       | 5  | 65.96 | 13.191| 63.65 | 0.000 |
| Error               | 96 | 19.90 | 0.207 |       |       |
| Total               | 107| 580.58|       |       |       |

*Note*: Measurements were taken on clear, sunny days in the winter (February 21; wet season) and autumn (October 4; end of dry season) of 2017. df, degrees of freedom; MS, Mean Square Within Groups; SS, Sum of Squares.
habitats. We predicted that seedlings transplanted into relatively bare zones areas among mature saltbush shrubs would have greater survival than those planted in grass-dominated areas. This was not the case. Higher saltbush mortality occurred in the shrublands, which appeared to be primarily due to herbivory by small mammals using the mature saltbushes as

Fig. 3. Seed sowing experiment showing mean density of saltbush (*Atriplex polycarpa*) seedlings by treatment between February and April 2017. Plots were variably weeded or unweeded of exotic annual grasses and treated or untreated with a standard amount of residual dry matter (RDM) to assess the grass-related effects on saltbush emergence and rate of mortality. Symbols means and errors bars are 95% confidence intervals.

Fig. 4. Principal components analysis matrix assessing variation between six saltbush (*Atriplex polycarpa*) sites. The model used a SCREE plot to select two principal components. Abbreviations are IQR, interquartile range; \(\Psi_w\), water potential (values shown are absolute and not negative); seedling emergence, number of seedlings which germinated and were tagged for survival in January 2017; seedling density, number of seedlings counted within the demographic analysis at each site.
cover from predators. Seedling predation as a limiting factor of recruitment is a well-known phenomenon (Bartholomew 1970, Maron and Simms 1997, Cushman et al. 2011, Busch et al. 2012). Small desert mammals are also known to prefer native plant taxa in some habitats, thus providing a competitive advantage to exotics (Callaway et al. 1999, Pearson et al. 2011).

Our results indicate that low RDM levels between established shrubs create an environment favorable for seedling emergence, but unfavorable for seedling survival, whereas grassy areas are unfavorable for seedling emergence, but favorable for seedling survival. Overall, saltbush suffers from a lack of favorable site conditions for recruitment to occur. Such seed–seedling conflicts have been previously described (Lamont et al. 1993, Schupp 1995).

Variation across sites
The presence of a diversity of sizes of mature shrubs at some Sites (1, 5, and 6) suggests episodic recruitment and that factors causing mortality of established shrubs were such that plants were able to attain a mature age. Other Sites (2, 3, and 4) had a less diverse size range suggesting that recruitment may be less common. The factors controlling demography in long-lived plants that produce secondary anomalous growth, and therefore a lack of discrete annual growth rings, are difficult to ascertain. Since saltbush stands are not expanding throughout the San Joaquin Desert; then mortality must be equal to or greater than recruitment. The balance between annual grasses and saltbush has largely reached some level of equilibrium. It is likely that before exotic annual grasses invaded, saltbushes occupied a much greater extent of the landscape. Annual grasses and mature saltbush shrubs do not directly compete—but annual grasses and saltbush seedlings do. Every loss of ground by saltbush (mature shrub mortality) has likely largely resulted in gains of ground by exotic grasses.

Mature shrub water status, seedling survival, demography, and edaphic characteristics all varied by site. The PCA summary showed that grass cover and seedling emergence were associated with greater winter soil moisture and lower soil salinity. This makes sense as these winter germinating annual plants would need adequate soil moisture to germinate and establish as seedlings. Another pattern was that denser stands of shrubs were associated with drier winter soil moisture conditions. This could mean that dense stands of shrubs are using more water or that hydrology differs, such as canopy interception losses or soil infiltration rates, that is not allowing rainfall to penetrate the soil. It could also mean that the soil is simply better drained due to coarser soil texture, sandier soil. Dense RDM significantly affects these processes as well (Bartolome et al. 2007).

Synthesis
Exotic grass RDM is the primary biotic factor impeding saltbush from recruiting. There appears to be a seed–seedling conflict wherein saltbush seedlings emerge more successfully in the absence of RDM, but then have higher rates of mortality due to increased exposure to native herbivorous mammals. This leads to a stabilizing feedback that promotes grass persistence and prevents saltbush population growth. Somewhere in the balance of these two adverse conditions (RDM suppression vs. herbivory suppression), there is positive recruitment. These findings have implications for management and restoration of saltbush communities in the San Joaquin Desert. A simple management tactic of clearing away RDM and seeding with saltbush seeds could be effective if combined with enclosures designed to reduce herbivory. Another solution could be to conduct intense intermittent livestock grazing as a management tool for high RDM, followed by seeding with saltbush. If herbivory is controlled, transplanting out-grown saltbush seedlings may be a more effective method of restoration compared to the generally used method of direct seed casting.

ACKNOWLEDGMENTS
We thank Dr. David Germano of California State University, Bakersfield (CSUB), for his comments and advice which greatly improved the quality of the manuscript. We also thank the Educational Partnership Impacting Colleges and Careers (EPIC) between CSU Bakersfield, Mrs. Gayle Batey, and the Tejon Ranch Conservancy for providing funding and logistical support, which enabled us to carry out this research at Tejon Ranch. We thank the Tejon Ranch Company for access to their property. We acknowledge support from the National Science Foundation (NSF CREST HRD-1547784 and NSF CAREER IOS-1252232). We also...
thank Dr. Adam Guo, Dr. David Miller, and Morgan Kayser of the CSUB Geology Department for helping us to analyze the soil samples. Lastly, we thank Alex Baer, Eva Arrieta, Logan Salazar, Brenda Aguilar, Waleed Alnatour, Eneas Torres-Andrade, and Lindsey Coleman for assisting with data collection and entry. We declare no conflict of interest for this work.

LITERATURE CITED

Barnard, C., G. Francis, and P. McGregor. 2007. Asking questions in biology. Pearson Education Limited, Essex, UK.

Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. Science 170:1210–1212.

Bartolome, J. W., R. D. Jackson, A. D. K. Betts, J. M. Connor, G. A. Nader, and K. W. Tate. 2007. Effects of residual dry matter on net primary production and plant functional groups in California annual grasslands. Grass and Forage Science 62:445–452.

Bartow, J. A., and T. W. Dibblee. 1981. Geology of the Tejon Hills area—Arvin and Tejon Hills. Report 81–297. United States Geological Survey, Bakersfield, California, USA.

Belnap, J., R. H. Webb, T. C. Esque, M. L. Brooks, L. A. Defalco, and J. A. MacMahon. 2016. Deserts. Pages 635–662 in H. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

Brooks, M. L., C. S. Brown, J. C. Chambers, C. M. D’Antonio, J. E. Keeley, and J. Belnap. 2016. Exotic annual Bromus invasions: comparisons among species and ecoregions in the western United States. Pages 11–60 in M. J. Germino, J. C. Chambers, and C. S. Brown, editors. Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, Berlin, Germany.

Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern Ponderosa pine landscape. Ecology 86:3030–3038.

Busch, M., C. Knight, C. M. Mazia, K. Hodara, E. Muschetto, and E. Chaneton. 2012. Rodent seed predation on tree invader species in grassland habitats of the inland Pampa. Ecological Research 27:369–376.

Bytnorowicz, A., M. Fenn, E. B. Allen, and R. Cisneros. 2016. Atmospheric chemistry. In H. A. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

California Department of Fish and Wildlife (CDFW). 2003. Atlas of the biodiversity of California. California Department of Fish and Wildlife, Sacramento, California, USA.

Callaway, R. M., T. H. Deluca, and W. M. Belliveau. 1999. Biological control herbivores may increase competitive ability of the noxious weed Centaurea maculosa. Ecology 80:1196–1201.

Casper, B. B. 1996. Demographic consequences of drought in the herbaceous perennial Cymoptanthe flava: effects of density, associations with shrubs, and plant size. Oecologia 106:144–152.

Chen, B. W., C. M. D’Antonio, N. Molinari, and S. L. Peng. 2018. Mechanisms of influence in grass litter on germination and growth of coexisting species in California. Biological Invasions 20:1881–1897.

Ciblis, A. F., D. M. Swift, and E. D. McArthur. 1998. Plant-herbivore interactions of Atriplex: current state of knowledge. General Technical Report RMRS-GTR-14. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Cleland, E. E., J. L. Funk, and E. B. Allen. 2016. Coastal sage scrub. Pages 429–444 in H. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

Coleman, M. L., and R. B. Pratt. 2019. The effects of exotic grass on seedling recruitment of native Atriplex polycarpa (Torr.) S. Watson (Chenopodiaceae) shrubs in the San Joaquin Valley of California. Biological Invasions 21:1871–1876.

Corbin, J. D., and C. M. D’Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283.

Cushman, J. H., C. J. Lortie, and C. E. Christian. 2011. Native herbivores and plant facilitation mediate the performance of an exotic grass. Ecology 99:524–531.

Daubenmire, R. F. 1959. Plants and environment: a textbook of plant autecology. John Wiley and Sons Inc., New York, New York, USA.

Dibblee, T. W., and J. A. Minch. 2008. Geologic map of the Arvin [south half] & Tejon Hills. United States Geological Survey, Bakersfield, California, USA.

Dodd, G. L., and L. A. Donovan. 1999. Water potential and ionic effects on germination and seedling growth of two cold desert shrubs. American Journal of Botany 86:1146–1153.

Ehleringer, J., and R. W. Peary. 1983. Variation in quantum yield for CO2 uptake among C3 and C4 plants. Plant Physiology 73:555–559.

Fahn, A., and M. H. Zimmermann. 1982. Development of the successive cambia in Atriplex halimus (Chenopodiaceae). Botanical Gazette 143:353–357.

Germano, D. J., G. B. Rathburn, and L. R. Saslaw. 2001. Managing exotic grasses and conserving declining species. Wildlife Society Bulletin 29:551–559.
Germano, D. J., G. B. Rathburn, L. R. Saslaw, B. L. Cypher, E. A. Cypher, and L. M. Vrendenburgh. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31:138–147.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between native perennial and non-native grasses in California. Oecologia 121:518–526.

Harper, J. L., P. A. Landragin, and J. W. Ludwig. 1955. The influence of environment on seed and seedling mortality. New Phytologist 54:107–118.

Lamont, B. B., E. T. Witowski, and N. J. Enright. 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. Ecology 74:501–521.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1–18.

Liu, H., and P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. Biological Invasions 8:1535–1545.

MacKinnon, E. D., R. B. Pratt, and A. L. Jacobsen. 2014. Functional trait differences between weedy and non-weedy plants in southern California. Madroño 61:328–338.

Maron, J. L., and E. L. Simms. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (Lupinus arboreus). Oecologia 111:76–83.

Minnich, R. A. 2008. California’s fading wildflowers: lost legacy and biological invasions. University of California Press, Berkeley, California, USA.

Miriti, M. N., S. Burtica-Rodriguez, S. J. Wright, and H. F. Howe. 2007. Episodic death across species of desert shrubs. Ecology 88:32–36.

Molinari, N. A., and C. M. D’Antonio. 2019. Where have all the wildflowers gone? Biological Invasions 22:957–968.

Osmond, C. B., M. P. Austin, J. A. Berry, W. D. Billings, J. S. Boyer, J. W. Dacey, P. S. Nobel, S. D. Smith, and W. E. Winner. 1987. Stress physiology and the distribution of plants. BioScience 37:38–48.

Park, I. W., and G. D. Jenerette. 2019. Causes and feedbacks to widespread grass invasion into chaparral shrub dominated landscapes. Ecological Society 34:459–471.

Pavlik, B. M. 2008. The California deserts: an ecological discovery. University of California Press, Berkeley, California, USA.

Pearson, D. E., R. M. Callaway, and J. L. Maron. 2011. Biotic resistance via granivory: establishment by exotic, naturalized, and native asters reflects generalist preference. Ecology 92:1748–1757.

Phillips, M. L., B. E. McNellis, M. F. Allen, and E. B. Allen. 2019. Differences in root phenology and water depletion by an exotic grass explains persistence in a Mediterranean ecosystem. American Journal of Botany 106:1210–1218.

Polis, G. A. 1991. The ecology of desert communities. The University of Arizona Press, Tucson, Arizona, USA.

Sankary, M. N., and M. G. Barbour. 1972. Autecology of Atriplex polycarpa from California. Ecology 53:1155–1162.

Schultz, A. M., J. L. Launchbaugh, and H. H. Biswell. 1955. Relationship between grass density and brush seedling survival. Ecology 36:226–238.

Schupp, E. W. 1995. Seed-seeding conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 10:399–409.

Spiegel, S., J. W. Bartolome, and M. D. White. 2016. Applying ecological site concepts to adaptive conservation management on an iconic Californian landscape. Rangelands 38:365–370.

Thorne, M. S., Q. D. Skinner, M. A. Smith, J. D. Rodgers, W. A. Laycock, and S. A. Cerekci. 2002. Evaluation of a technique for measuring canopy volume of shrubs. Journal of Rangeland Management 55:235–241.

Underwood, M. B., and J. Guo. 2013. Data report: clay mineral assemblages in the Shikoku Basin, Nankai Trough sediment inputs, IODP sites c0011 and C0012. Pages 2–34 in Proceedings of the Integrated Ocean Drilling Program 322. Integrated Ocean Drilling Program.

Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology 49:234–241.

Wolkovich, E. M., D. A. Lipson, R. A. Virginia, K. L. Cottingham, and D. T. Bolger. 2010. Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. Global Change Biology 16:1351–1365.

Yelenik, S. G., and J. M. Levine. 2011. The role of plant-soil feedbacks in driving native-species recovery. Ecology 92:66–74.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3455/full