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ARTICLE

Unfriendly neighbors: When facilitation does not contribute to restoration success in tidal marsh

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Abstract

Large-scale restoration projects are an exciting and often untapped opportunity to use an experimental approach to inform ecosystem management and test ecological theory. In our \$10M tidal marsh restoration project, we installed over 17,000 high marsh plants to increase cover and diversity, using these plantings in a large-scale experiment to test the benefits of clustering and soil amendments across a stress gradient. Clustered plantings have the potential to outperform widely spaced ones if plants alter conditions in ways that decrease stress for close neighbors. Here, we test whether intraspecific facilitation improves restoration outcomes using a suite of seven high marsh species native to central California salt marshes. We also applied a biochar treatment to test whether soil amendment boosts restoration success. We compared the performance of clustered and uniform plantings across the high marsh elevation gradient for 3 years. There was a strong effect of elevation on plant performance and clear signs of plant stress related to soil conditions. Clustering slightly improved the survival of one species out of seven, although clustering did not benefit that species in a follow-up experiment under more stressful conditions. By contrast, clustering had strong negative effects on the growth and/or cover of all species tested. The stressors in this system—likely related to compaction and soil salinity—were not mitigated by neighbors or biochar. The prevailing negative effect on seven species from distinct evolutionary lineages lends strong generality to our findings. We therefore conclude that for this and similar high marsh systems, intraspecific facilitation confers no benefits and practitioners should space plants widely to minimize competition. To take full advantage of the learning opportunities provided by large-scale restoration projects, we recommend including experimental treatments and monitoring the response of multiple species across years to refine best practices and inform adaptive management.

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KEYWORDS

competition, estuary, facilitation, intraspecific interactions, restoration, salt marsh, stress gradient

INTRODUCTION

Restoration can greatly improve biodiversity and the provision of ecosystem services in degraded habitats (Liu et al., 2024; Rey Benayas et al., 2009), but outcomes are strongly influenced by choices made during project design (Ehrenfeld, 2000; Shimamoto et al., 2018). Once harmful sources of disturbance have been removed, resource managers must determine whether desired species can be relied upon to colonize restored habitat naturally, or whether more active efforts will be required to meet project aims (Baur, 2014; Chazdon et al., 2021; Holl & Aide, 2011; Meli et al., 2013). Practitioners often focus on dominant foundation species as a linchpin to restore critical ecosystem function and stimulate further recovery of biotic communities (Bangert et al., 2013; Liu et al., 2024; Yando et al., 2019), and such species may recruit easily at restored sites when propagules are plentiful and disperse readily (Armitage et al., 2006; Lindig-Cisneros & Zedler, 2002). Yet, evidence that biodiversity can enhance ecosystem functions and services continues to accumulate (Cardinale et al., 2012; Rey Benayas et al., 2009), suggesting that practitioners should broaden the scope of restoration projects beyond the establishment of foundation species alone (Hughes et al., 2018).

To restore diversity and function in compromised ecosystems, land managers need proven strategies that support the establishment of multiple species under real-world project conditions. Stress is a strong driver of restoration outcomes (Bayraktarov et al., 2016), and even “benign” habitat may become stressful after site preparation activities. For example, large-scale grading to restore hydrological regimes or remove resident communities creates bare habitat where erosion, soil temperatures, and evaporation rates are elevated. Because exposure stress increases with the size of a bare patch, plot-scale experiments may not identify practices that are effective at mitigating stress on a landscape scale (Bertness, 1991; Zedler & Kercher, 2005). Yet, large-scale restoration projects are rarely designed as experiments to shed light on underlying drivers of plant performance, or to compare the effect of different restoration treatments on stress.

Biotic interactions influence stress and restoration success, and restoration practices have tended to focus on limiting competition among transplants—perhaps a legacy of ecology’s early preoccupation with competition as the dominant driver of community structure (Goldberg &

Barton, 1992; Hairston et al., 1960; Schoener, 1983). More recently, facilitation has been recognized as an important driver of community structure (Fowler, 1986; Stachowicz, 2001), with stress mediating the balance of positive and negative interactions in the Stress Gradient Hypothesis (SGH) framework (Bertness & Callaway, 1994). The SGH proposes that facilitation will be most important where stress is greatest, and this framework underlies much of the work demonstrating facilitation in natural communities to date (He et al., 2013). Based on this evidence, practitioners have been encouraged to incorporate facilitation into restoration designs for stressful systems (Halpern et al., 2007; Padilla & Pugnaire, 2006). Planting seedlings in the shelter of established “nurse plants” or clustering groups of transplants together has reduced stress and improved plant performance in some restoration projects (Duggan-Edwards et al., 2020; Gómez-Aparicio et al., 2004; Silliman et al., 2015). However, the proportion of studies that have tested whether positive interactions improve restoration outcomes is very low (Zhang et al., 2018).

Salt marshes have strong gradients in abiotic conditions across elevation and support a limited flora, making them excellent systems to test restoration designs intended to mitigate stress for a suite of species. Studies documenting positive interactions between plants in natural marsh systems (Bertness & Hacker, 1994; Bertness & Leonard, 1997) suggest the potential value of facilitation as a marsh restoration tool. Drastic loss of salt marsh habitat also makes these systems high-priority targets for restoration that will benefit from experiments to establish best practices (Barbier et al., 2011; Gedan et al., 2009). Several restoration projects have demonstrated that close neighbors can relieve exposure stress in intertidal habitat (Clausing et al., 2023), and anoxia or erosion stress in subtidal and low marsh habitat (Bos & Van Katwijk, 2007; Silliman et al., 2015). These stressors weaken at higher elevation where inundation periods and wave action are reduced, so restoration designs that incorporate facilitation may not be beneficial in the high marsh (Bertness & Ellison, 1987; Bertness & Hacker, 1994; Silliman et al., 2015). However, stress related to desiccation and evaporative salt concentration can increase at higher elevations—particularly in dry climates. Climate has a strong effect on plant interaction patterns and restoration outcomes, and neighbor interactions in the high marsh may play out differently in Mediterranean or arid

climates compared with mesic systems (Bertness & Ewanchuk, 2002; Silliman et al., 2015). In Mediterranean high marsh, desiccation and hypersaline conditions during dry summers (Callaway et al., 1990; Mahall & Park, 1976) may be more important stressors than the tidally-driven anoxia that is prevalent at lower elevations. In addition, most studies testing facilitation in marsh restoration design have focused on single species that are strong dominants at lower marsh elevations (e.g., *Spartina* or *Salicornia*). Plant communities in the high marsh are more diverse (Peinado et al., 1995; Wasson & Woolfolk, 2011), and there is a need to identify restoration strategies that support the establishment of a suite of species in restored habitat. On the central California coast, several high marsh species tend to occur as patches in a *Salicornia pacifica* matrix, suggesting that intraspecific facilitation may help these species establish and spread. Earlier work in this system did not find that clustering improved the survival or growth of two high marsh specialists (Tanner et al., 2022). However, this study was carried out in a particularly mesic year, and in small-scale plots where topsoil was retained. Outcomes may differ on a vast expanse of bare, low organic soil in a constructed marsh, especially if rainfall is limited.

Soil amendments may also play an important role in the success of marsh restoration plantings. Restoration of wetlands that have been degraded by fill or by subsidence usually requires the addition or removal of sediment, which can result in substrates that differ from native marsh soils (Langis et al., 1991; Mendelssohn & Kuhn, 2003; Stagg & Mendelssohn, 2010). For example, soils on constructed marsh habitat can have more sand and less organic content than reference marsh, slowing the recovery of plant and invertebrate communities (McAtee et al., 2020). In dry climates like southern California, restored marsh soils may also become hypersaline, contributing to the failure of restoration plantings (Zedler et al., 2003). Soil amendments have the potential to mitigate plant stress on restored habitat, and biochar is viewed as a particularly promising soil amendment for the marsh because it has improved plant performance in other systems where drought or salinity are prominent stressors (Agegnehu et al., 2017; Ali et al., 2017; Luo et al., 2017). A stable form of carbon-rich charcoal, biochar can increase the water-holding capacity of soil and competitively bind Na⁺ ions, leading to lower salt concentrations in plant tissues and improving plant performance (Ali et al., 2017; Hammer et al., 2015). To date, research on biochar effects in coastal salt marsh restoration projects remains limited.

In this work, we tested different restoration treatments in a landscape-scale high marsh restoration project situated in Monterey Bay, California (USA), which has a

Mediterranean climate. Growing conditions at this site may be particularly stressful due to the large bare site footprint, its high position in the tidal frame, low organic soil content, construction-related soil compaction, and the warm, dry conditions associated with Mediterranean summer. To ensure the generality of our findings and provide insight that can inform the design of other high marsh restoration projects, we tested seven plant species, including all taxa (other than the marsh dominant, *S. pacifica*) that make substantial contributions to high marsh cover in this watershed and other central California estuaries. This experiment employed over 17,000 transplants, making it one of the largest marsh restoration experiments to date, and its 3-year duration allowed us to assess restoration treatment effects on long-term cover as well as early survival and growth.

We asked: (Q1) Does early survival vary across elevation (i.e., moisture and salinity gradients), and do close neighbors improve survival where plants performed less well? (Q2) Do close neighbors or biochar addition treatments improve (a) plant growth or (b) later survival at high versus low elevation? (Q3) Do restoration plantings with close neighbors lead to greater restoration success in terms of (a) native or (b) exotic cover? Do patterns vary across elevation and/or species? (Q4) How do rainfall and seasonal trends in soil water potential, soil percent moisture, and soil temperature influence abiotic stress gradients in this system? (Q5) During summertime drought, do soil metrics differ under plant canopies compared with the open, suggesting a potential mechanism for facilitation between neighbors? The answers to these questions will contribute to our understanding of plant interactions in the high marsh and their influence on restoration success, informing the design and adaptive management of salt marsh restoration projects.

METHODS

Site description

In the Elkhorn Slough Estuary (Figure 1a), open exchange with Monterey Bay drives a daily average tidal range of 1.6 m and maintains estuarine salinity near 31 ppt. The central California coast has a mild Mediterranean climate with wet winters and dry summers, and infrequent inundation coupled with summertime drought can create hypersaline conditions in the high marsh (Callaway et al., 1990; Fresquez, 2014). Below Mean Higher High Water (MHHW), this system is dominated by *S. pacifica* (Chenopodiaceae) and lacks the *Spartina* species found in some California estuaries.

At higher elevations, the *S. pacifica* dominant can be interrupted by large patches of the perennial species *Distichlis spicata*, *Frankenia salina*, and *Jaumea carnosa*.

These high marsh specialists represent three plant families (Poaceae, Frankeniaceae, Asteraceae) and collectively may contribute up to 40% of high marsh cover

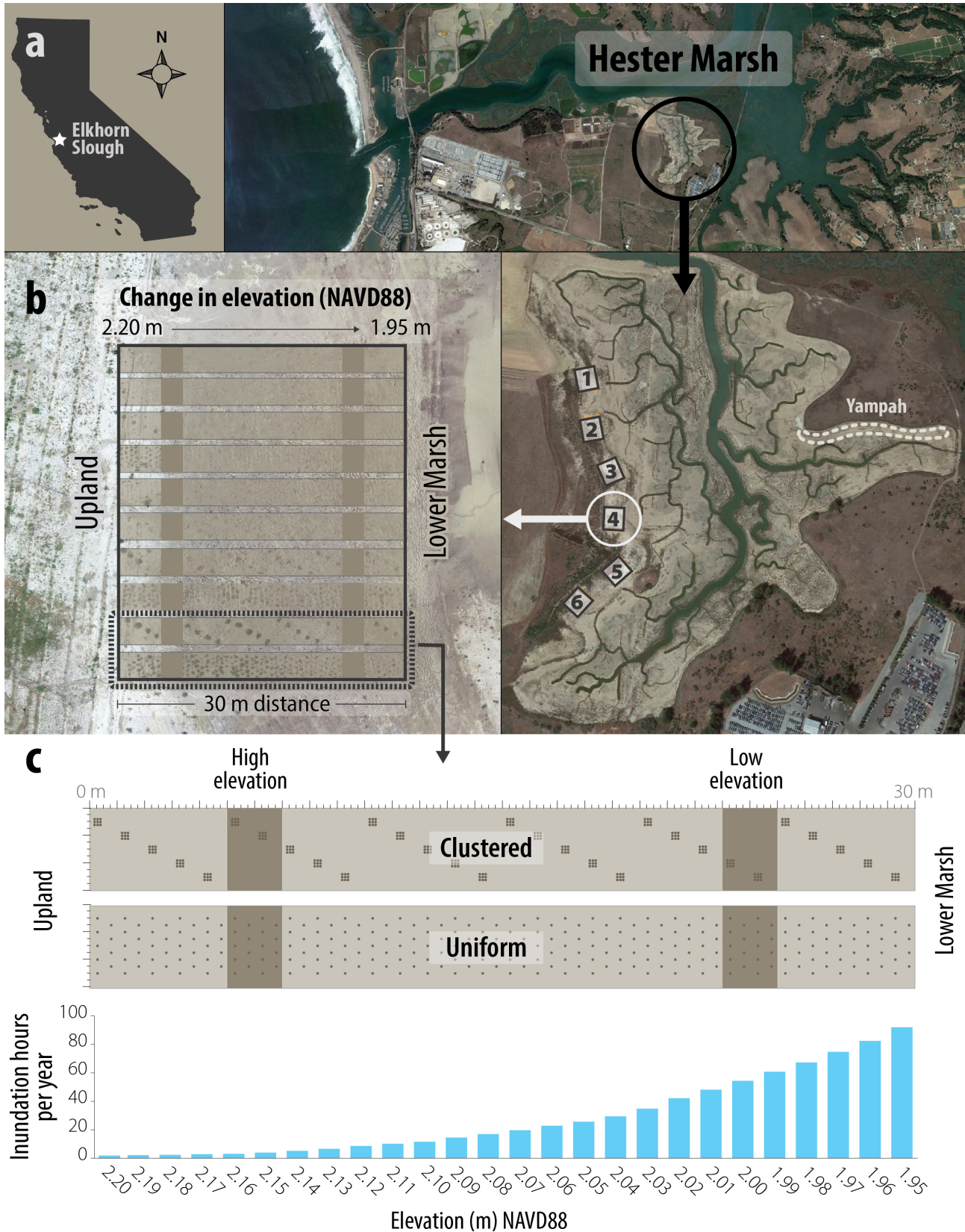


FIGURE 1 Legend on next page.

(Wasson & Woolfolk, 2011). Other high marsh perennials are less common in this system and include *Extriplex californica* (Chenopodiaceae), *Limonium californicum* (Plumbaginaceae), *Spergularia macrotheca* (Caryophyllaceae), and *Triglochin concinna* (Juncaginaceae). The patchy distribution of high marsh specialists in this system raises the question of whether close conspecific neighbors may have a facilitative effect in the high marsh.

Sediment addition and sediment removal were used in tandem to restore the 25-ha Hester Marsh site on the Elkhorn Slough National Estuarine Research Reserve (Fountain et al., 2019). During Phase I construction in 2018, soil was scraped from a hillside grassland bordering the estuary and pushed down into the marsh plain, raising it approximately 90 centimeters and setting it above MHHW under the current tidal regime. A 30-meter-wide band of the scraped hillside was then graded to a gentle slope of high marsh habitat sitting between 1.95 and 2.20 m North American Vertical Datum of 1988 (NAVD88), where experiments for this study were installed (Appendix S1: Figure S1). Soils in this constructed high marsh tended to be heterogenous after grading, and low in organic content because of their origin (i.e., subsurface layers of the hillside exposed via scraping). Low organic content coupled with higher temperature and evaporation rates on bare soils of the constructed high marsh may contribute to transplant stress, particularly during Mediterranean summer.

Our primary goal at Hester Marsh was to create diverse habitat that would remain resilient to a century of sea-level rise, and our secondary goal was to learn as much as possible about best practices for large-scale restoration work in this and similar systems. To that end, we built experiments into the project that would allow us to test the effectiveness of different restoration strategies for maximizing the growth and cover of a diverse suite of species. We allowed *S. pacifica* to colonize the site naturally (Shikuzawa et al., 2024; Zedler et al., 2001), and focused on planting less common high marsh specialists that were likely to be propagule-limited, particularly at higher elevations where seed would only disperse on rare king tides.

Propagation

Propagation success was low for two of the seven species studied here, so we revised our large-scale block planting design to focus on the remaining five species (Figure 2a; Appendix S1: Figure S1) and used the available stock of *L. californicum* and *T. concinna* in smaller scale experimental plantings adjacent to blocks (see Appendix S1: Section S1: Propagation for more details).

Experimental design

Overview

In the fall of 2018, we established six blocks for our main restoration planting in the high marsh elevation band (~1.95–2.20 m NAVD88). Blocks were ~30 m long from the landward to the seaward edge, ~35 m wide, and spaced 30–40 m apart (Figure 1b). Each block was subdivided into 10 columns, with 2 columns allocated to each primary species (*D. spicata*, *E. californica*, *F. salina*, *J. carnosa*, and *S. macrotheca*); one column in each pair was planted in the uniform treatment, and one in the clustered treatment (Figure 1c) (see Appendix S1: Section S2: Experimental design for more details). We also planted *L. californicum* and *T. concinna* in “wings” on either side of each block; wings were installed near the top of blocks because these species tend to occur at the upper edge of the high marsh in this watershed.

Planting treatments

In uniform columns, transplants were spaced 50 cm apart to limit interactions between neighbors. In clustered columns, groups of nine plants were installed 10 cm apart to promote interactions between neighbors (Figure 2b). This spacing was informed by previous work in this system (Tanner et al., 2022) and is similar to treatments applied in other studies (O'Brien & Zedler, 2006; Silliman et al., 2015). In January 2019, we planted 2700 seedlings in each block (540 seedlings for each of the five primary

FIGURE 1 (a) Location of the restored Hester Marsh in Elkhorn Slough Estuary in Monterey Bay, California, USA. (b) Six blocks (~30 × 35 m) were installed between 1.95 and 2.20 m NAVD88 on the gently sloping high marsh adjacent to the western hillside (the source of high marsh fill). Each block was subdivided into 10 planted columns, with a pair of columns assigned to each of the five primary species. The location of supplemental *Extriplex californica* plantings at Yampah is shown on the eastern side of the restored marsh (see dashed white line). (c) In each column pair, one column was planted in the clustered pattern and one in the uniform pattern of the assigned species. Darker brown bands show the location of marked 9-plant units at high and low elevation, where biochar was applied to half of the marked plants for each of the five primary species. Inundation time in planted columns ranged from ~2 h per year near the upland boundary of the block to ~92 h near the lower marsh boundary.

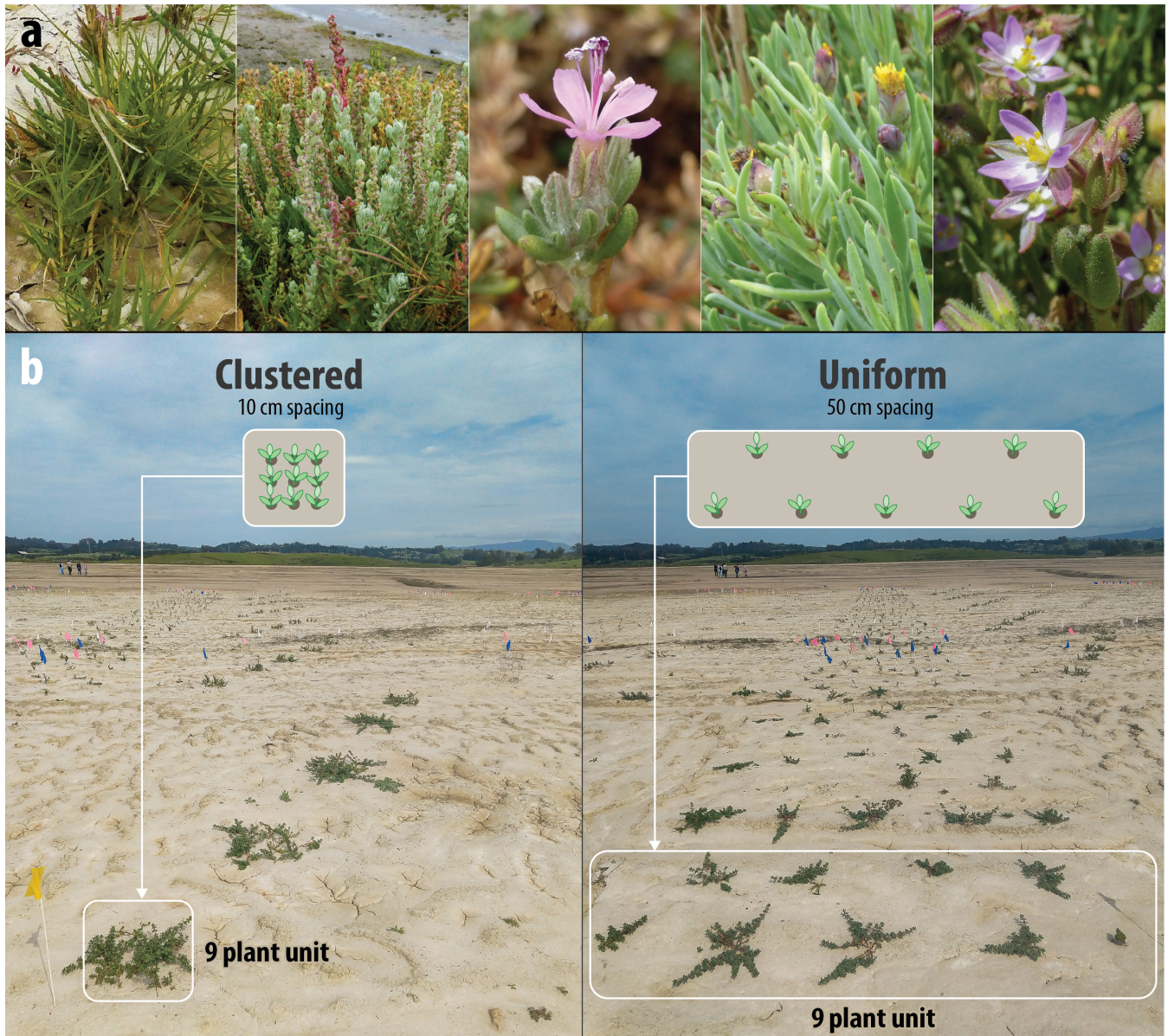


FIGURE 2 (a) The five species used in large-scale block plantings: *Distichlis spicata*, *Extriplex californica*, *Frankenia salina*, *Jaumea carnosa*, and *Spergularia macrotheca* (left to right). (b) Each column was planted with 270 individuals of the assigned species. In clustered columns, nine-plant units were planted with 10 cm spacing between individuals. In uniform columns, all plants were evenly distributed using 50 cm spacing. Flags indicate marked nine-plant units at high and low elevation where survival and growth were measured in the biochar treatment (blue flags) and the control treatment (pink flags). Photos of columns planted with *F. salina* in (b) were taken from the upland edge of the planted block, looking across the main channel of the restored marsh toward Yampah Island. Photo credits: Karen E. Tanner, 2019 and 2020.

species, with 270 seedlings per column). We marked nine-plant units at “high elevation” (~2.16 m NAVD88) and “low elevation” (~2.0 m NAVD88) in each column (Figure 1c). These marked nine-plant units ($n = 48$ per species) were used for growth and survival surveys that would be too intensive to carry out across the entire planted block (see Appendix S1: Section S2: Experimental design for more details). In the wings near the top of the blocks, we planted nine-plant units of *L. californicum* and *T. concinna* in each planting pattern as limited

transplant stock allowed ($n = 18$ replicates for *L. californicum* and $n = 6$ replicates for *T. concinna*).

Biochar addition treatment

We developed a biochar addition treatment to test whether invasive blue gum (*Eucalyptus globulus*) felled on Reserve lands could be beneficially used as a soil amendment to promote transplant establishment at the

Hester Marsh restoration site (see Appendix S1: Section S3: Biochar, Table S1 for more details). We assigned half of all the marked nine-plant units at high and low elevation to the biochar treatment (see Appendix S1: Section S2: Experimental design for more details). We added 18 mL of biochar (~14% by volume) to dibbler holes before installing plants assigned to this treatment group. Due to limited transplant stock, we did not include *L. californicum* or *T. concinna* in the biochar addition experiment.

Supplemental *E. californica* plantings at Yampah

In the spring of 2019, high *E. californica* mortality near the bottom of planted blocks was associated with compacted soils and standing water. These conditions only occurred in a subset of blocks, likely related to differences in soil texture and/or paths traveled by vehicles during construction. A trend for higher survival in clustered plantings under these conditions motivated a second clustering experiment using leftover stock of *E. californica*, installed in December 2019. This supplemental experiment was carried out at Yampah Island on the eastern side of the restored Hester Marsh (Figure 1b), where sediment was added to raise marsh elevation and heavy equipment compacted soils. At each Yampah plot ($n = 20$ total), we installed one nine-plant unit in the uniform pattern and one nine-plant unit in the clustered pattern. No biochar treatment was applied in this experiment.

Inundation during the study period

Tidal inundation data from the Reserve's nearby water quality monitoring station were used to estimate hours of inundation across elevation for the period August 2018–August 2021, from the end of Phase 1 site construction through final cover surveys (Figure 1c) (see Appendix S1: Section S4: Tidal inundation and rainfall for more details).

DATA COLLECTION

Overview

We relied on two data collection strategies: surveys on transects across the full elevation gradient in planted columns, and measurements at marked nine-plant units in designated high-elevation and low-elevation locations (Figure 1c) where biochar addition treatments were also applied (see Appendix S1: Section S5: Data collection for more details).

Q1: Early survival across the elevation gradient (9 weeks after planting)

Following planting, we observed high *E. californica* and *S. macrotheca* mortality near the bottom of some planted blocks, where soils were compacted and waterlogged from tides and heavy rains. This mortality occurred during the first few weeks after transplanting and affected plants at lower elevations than the nine-plant units we had marked to track long-term growth and survival in the “low elevation” group. We therefore conducted a one-time survival survey on transects across the full elevation gradient in planted blocks to quantify early mortality (see Appendix S1: Section S5.1 for more details).

Q2a: Plant volume at high versus low elevation (14 weeks after planting)

We compared growth at nine-plant units in the clustered versus uniform planting treatments at high and low elevation (Figure 1c) in May of 2019, using maximum height and diameter measurements to estimate plant volume (see Appendix S1: Sections S2: Experimental design and S5.2 for more details).

Q2b: Survival at high versus low elevation (18 weeks after planting)

Main planting

We assessed survival in clustered versus uniform nine-plant units at high and low elevation (Figure 1c) (see Appendix S1: Section S2: Experimental design for more details). Individuals in clusters became more difficult to distinguish as plants grew, so we carried out our final survey in June of 2019. To accommodate the nonindependence of plants in clusters, we counted the number of plants still alive in each marked clustered or uniform unit and divided by the total originally planted (typically nine plants—in rare cases where transplants of the incorrect species were discovered in plantings and were removed, the original total was decremented).

Supplemental *E. californica* plantings at Yampah (installed December of 2019)

We assessed the survival of all *E. californica* in nine-plant units on a monthly basis for the duration of the experiment.

Q3: Percent cover across the elevation gradient (2019, 2020, 2021)

We assessed cover in summer because it is an active growing period for most perennial natives planted in our restored high marsh. Surveys carried out in June (2019) or July (2020 and 2021) were also early enough to capture cover of annual exotic species, which tend to senesce during the dry season. We marked a starting point at the top of the block (2.2 m NAVD88) and an endpoint at the bottom of the block (1.95 m NAVD88) in each planted column and collected presence/absence data on these transects each year (see Appendix S1: Section S5.3 for more details). Forty-one distinct taxa were observed on the initial survey in June of 2019, including 11 natives and 30 exotic species (see Appendix S1: Table S2 for a complete list); a subset of these same species were observed on July surveys in subsequent years. By July, senescent exotic annuals could be difficult to identify to the species level but could still be easily distinguished from high marsh natives and from each other. We therefore assessed exotic cover on the basis of the total unique exotics encountered.

Q4: Rainfall and seasonal trends in soil water potential and percent moisture in the open (2019)

We used records from a nearby weather station to report rainfall during the planting year (2019), and to calculate average rainfall for the 20-year period, January 2001–January 2020 (see Appendix S1: Section S4: Tidal inundation and rainfall for more details).

To track changes in percent moisture and soil water potential over time, we collected soil samples in the open at all blocks (see Appendix S1: Section S5.4, Table S3 for more details).

Q4 and Q5: Seasonal trends in soil temperatures in the open and under plant canopies (2019–2020)

To compare soil temperatures in the open and underneath plant canopies, we installed Thermochron iButton units (model DS1921G, Maxim Integrated, San Jose, California, USA) at each block. Units were installed in the open ($n = 6$ across blocks) and underneath canopies of extra transplants alongside each planted block ($n = 1$ iButton unit per species per

block) (see Appendix S1: Section S5.5 for more details).

Q5: Soil water potential and percent moisture in the open and under plant canopies during summertime drought (35 weeks after planting)

Near the end of the first dry season (September 2019), we collected soil cores underneath plant canopies to compare with soil cores taken in the open (see Appendix S1: Section S5.6 for more details). Sample sizes were $n = 6$ cores each for *E. californica*, *F. salina*, and *S. macrotheca*; $n = 4$ cores for *J. carmosa* (two individuals died); and $n = 4$ cores for *D. spicata* (one individual died and one core classified as having light cover was dropped prior to analysis).

STATISTICAL ANALYSES

Overall approach

All analyses were carried out in R version 4.3.2 (R Core Team, 2023). We used the lme4 package (Bates et al., 2014) to build linear models, linear mixed-effects models, or generalized linear mixed-effects models (GLMMs) as needed, choosing the most appropriate family for each data set. We used the Anova function from the car package (Fox & Weisberg, 2011) to extract p values from all models (we chose the Type III approach to accommodate unbalanced data). In models including elevation as a numerical covariate, we removed nonsignificant interactions to avoid compromising the calculation of Type III SS, reporting results using the reduced model. For all analyses, we used the DHARMA package (Hartig, 2021) to generate model diagnostic plots and test for deviations from model assumptions. We inspected quantile–quantile plots, applying a Kolmogorov–Smirnov test for uniformity as well as dispersion and outlier tests on the overall models. We also tested models for zero inflation, and tested within categorical predictors for violations of uniformity and homogeneity of variance (Levene's test). Unless otherwise stated below, models met all assumptions.

Q1: Early survival across the elevation gradient (9 weeks after planting)

We used binomial generalized linear models (GLMs) to assess survival across elevation by planting treatment for each species. Models included elevation (continuous) and

planting pattern (clustered vs. uniform) as fixed effects. We also chose to include block as a fixed effect because we observed clear differences in survival among the three blocks surveyed, but the low number of blocks made a random block effect inappropriate. Diagnostic plots revealed a minor deviation from the expected quantiles for *E. californica* but did not suggest a serious problem in model fit for this species.

Q2a: Plant volume at high versus low elevation (14 weeks after planting)

We chose to model volume using natural log-transformed data after inspecting the shape of raw and transformed data sets by species. Linear mixed models for the five primary species included planting pattern (clustered vs. uniform), elevation (high vs. low), the interaction between planting pattern \times elevation, and block as a random effect for all species except *J. carnosa*, where including block triggered a singular fit error (likely due to low between-block variation). We also built linear models using natural log-transformed volume data for *L. californicum* and *T. concinna*, including only the planting pattern as a fixed effect (again dropping the random block effect to avoid overfitting). The biochar predictor had no significant effect on plant volume for the five primary species and was dropped from all models. Homogeneity of variance was violated for the planting pattern predictor in the *J. carnosa* model ($p = 0.018$), so results for this species should be considered approximate.

Q2b: Survival at high versus low elevation (18 weeks after planting)

We used binomial geGLMMs or GLMs to assess the proportion of plants surviving for six of the seven species studied here (because 99% of marked *J. carnosa* individuals survived in all treatments, we do not report statistical tests for that species). For the remaining species, we used the total number of individuals planted in each clustered or uniform unit (usually nine plants) as a weighting factor in the model. We built GLMMs for *D. spicata*, *E. californica*, and *S. macrotheca*, including planting pattern (clustered vs. uniform), elevation (high vs. low), the interaction between planting pattern \times elevation, and block as a random effect. We used the glmmTMB package (Brooks et al., 2017) to extend the *S. macrotheca* model to correct for zero inflation identified in DHARMA diagnostics. We dropped the random block effect from the *F. salina* model to avoid overfitting (likely caused by

low between-block variation given the high survival of this species), using a binomial GLM instead. The biochar predictor had no significant effect on the survival of any species tested, and was dropped from all models. Finally, we built binomial GLMs to model *L. californicum* and *T. concinna* survival at high elevation, including only planting pattern as a fixed effect (block was dropped from models to avoid overfitting).

Q3a: Percent transplant cover across the elevation gradient (2019, 2020, 2021)

We tested the effect of planting treatment on cover in each year, choosing a binomial approach for presence/absence data on transplanted species. For all species and years but one, we built binomial GLMMs including elevation (continuous gradient), planting pattern (clustered vs. uniform), the elevation \times planting pattern interaction, and block as a random effect. Nonsignificant interaction terms involving the elevation covariate were dropped from final models, as described above. We also dropped the random block effect from the 2019 *D. spicata* cover analysis to avoid model overfitting (likely caused by low variation between blocks). Homogeneity of variance was violated for the planting pattern predictor in the *S. macrotheca* 2019 model ($p = 0.021$), and diagnostic plots revealed a minor deviation from the expected quantiles for *S. macrotheca* in 2020, so results for this species should be considered approximate.

Q3b: Percent exotic cover across the elevation gradient (2019, 2020, 2021)

Because most exotic annuals encountered were upland species, and even salt-tolerant exotics do not occur at the lowest elevations studied here, we dropped data points below 2.035 m NAVD88 (near the low elevation location shown in Figure 1c) before carrying out analyses. This reduced the 2019 and 2020 data sets from 149 to 99 sampling points per transect and reduced the 2021 data set from 59 to 39 sampling points per transect. We then summed the number of unique exotic species encountered at each sampling point (pin drop). We chose a Poisson approach as most appropriate for these count data, building GLMMs including planting pattern (clustered vs. uniform), elevation (continuous gradient), the elevation \times planting pattern interaction, and block as a random effect. Nonsignificant interaction terms involving the elevation covariate were dropped from final models, as described above. Models passed zero-inflation and overdispersion tests for most species and years, but

DHARMA diagnostics revealed numerous deviations from uniformity and homogeneity of variance in 2020 models (see Appendix S1: Section S6: Statistical analysis of exotic cover for details). Despite these deviations, patterns in quantile–quantile plots did not suggest serious problems with model fit.

Q4 and Q5

See Appendix S1: Section S7: Statistical analyses of soil data for details on how soil temperature, soil water potential, and soil percent moisture data were analyzed and assessed for model fit.

RESULTS

Q1: Does early survival vary across the elevation gradient, and do close neighbors improve survival where plants performed less well (9 weeks after planting)?

Plant survival to 9 weeks was high for *D. spicata*, *F. salina*, and *J. carnosa*, while *E. californica* and *S. macrotheca* suffered substantial mortality during this period (Figure 3; Appendix S1: Figure S2a). Elevation was a significant predictor of survival for *E. californica*, *J. carnosa*, and *S. macrotheca*, with more transplants surviving at higher elevations (Figure 3b,d,e; Appendix S1: Table S4b,d,e; $p < 0.031$ for all three species). Planting pattern had no significant effect on survival of any species, but marginally significantly ($p = 0.051$) more *E. californica* individuals survived in clustered plantings (Figure 3b; Appendix S1: Table S4b). Survival of *D. spicata* and *F. salina* was unaffected by elevation, planting pattern, or block (Figure 3a,c; Appendix S1: Table S4a,c). Block had a significant effect on *E. californica* and *S. macrotheca* survival only ($p < 0.001$ and $p = 0.002$, respectively; Appendix S1: Table S4b,e).

Q2a: Do close neighbors or biochar addition improve plant volume at high versus low elevation (14 weeks after planting)?

Plant volume across the five primary species was strongly and significantly affected by both elevation and planting pattern (Figure 4, left panels; Table 1). Plants were consistently larger at higher elevation and in the uniform plantings ($p < 0.022$ for both predictors,

all species). Only *E. californica* showed a significant effect of the planting pattern \times elevation interaction, where plant size increased more strongly at high elevation in the uniform plantings (Figure 4b; Table 1b). The biochar predictor had no significant effect on plant volume for the five primary species (Appendix S1: Tables S1 and S5). *L. californicum* and *T. concinna* planted at high elevation were also significantly larger in uniform plantings (Appendix S1: Figure S3a, Table S6; $p < 0.001$ and $p = 0.013$, respectively).

Q2b: Do close neighbors or biochar addition improve survival at high versus low elevation?

Main planting

Plant survival to 18 weeks was significantly greater at high versus low elevation for *E. californica* and *S. macrotheca* (Figure 4g,j; Table 2b,d, $p < 0.002$ for both species). Survival of *E. californica* was also marginally significantly higher in clustered plantings (Table 2b, $p = 0.074$). A significant effect of elevation ($p = 0.006$) and a marginally significant effect of planting pattern ($p = 0.054$) on *D. spicata* survival (Figure 4f; Table 2a) were driven by two locations where survival was $< 30\%$; if these data points were dropped, only a marginally significant planting pattern \times elevation interaction remained ($p = 0.067$). Elevation, planting pattern, and their interaction had no effect on the survival of *F. salina* (Figure 4h; Table 2c), and 99% of *J. carnosa* individuals survived across all treatments (Figure 4i). The biochar predictor had no significant effect on the survival of any of the species tested in planted blocks (Appendix S1: Table S7). At high-elevation plantings in block wings, *L. californicum* survival was significantly higher in uniform plantings (Appendix S1: Figure S3b, Table S8a, $p = 0.003$), but planting pattern had no effect on the survival of *T. concinna* (Appendix S1: Table S8b, $p = 0.236$).

Supplemental *E. californica* planting at Yampah (high elevation only)

On the first survival survey 8 weeks after planting, in January 2020, we found only a handful of seedlings alive and in poor condition. By the end of February 2020, we observed complete mortality across both the uniform and clustered planting treatments at Yampah.

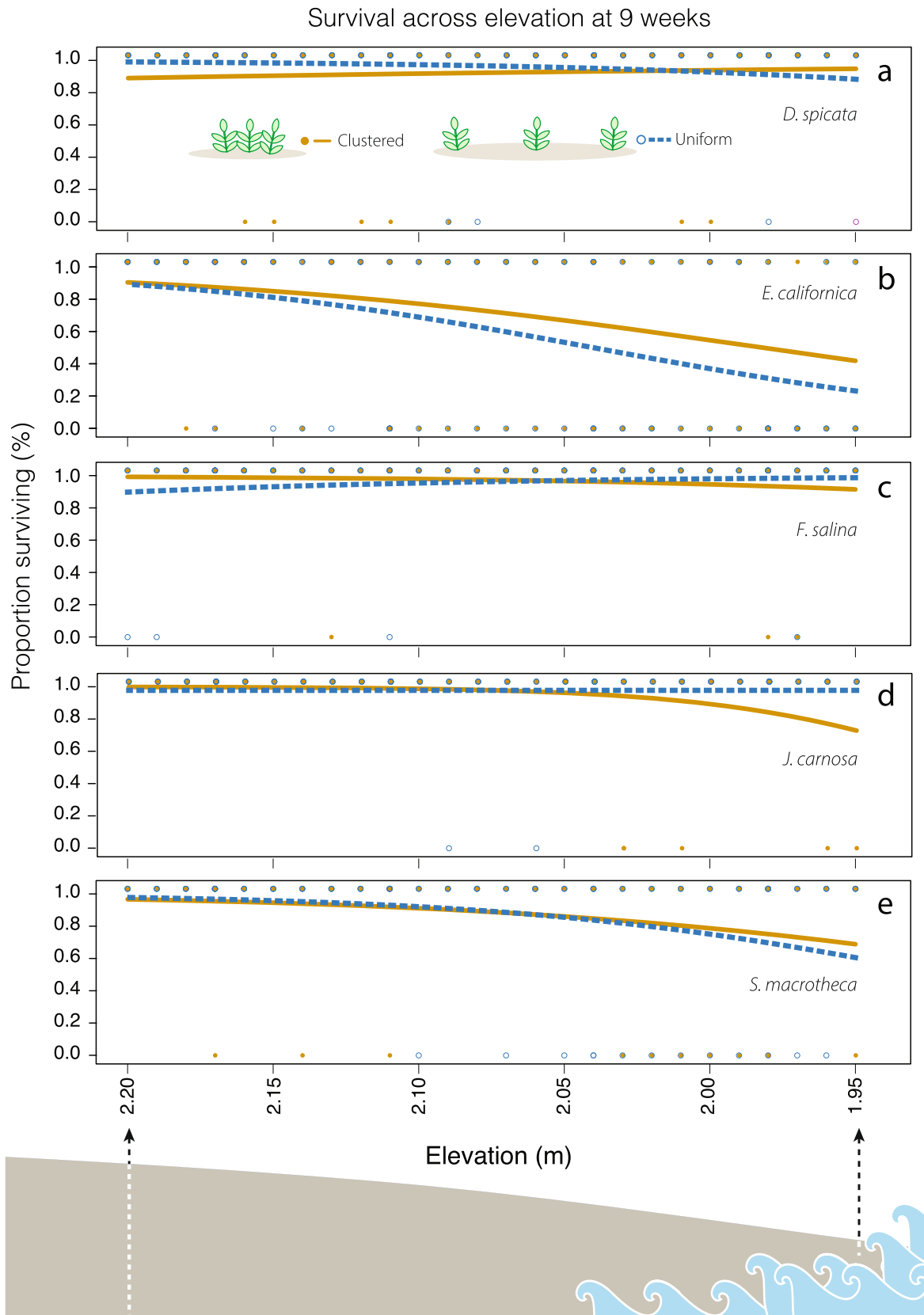


FIGURE 3 Legend on next page.

Q3a: Do restoration plantings with close neighbors lead to greater restoration success in terms of native cover (2019, 2020, 2021)?

Planted species cover generally increased across elevation (Figure 5), and increased with each growing season for *D. spicata*, *F. salina*, and *J. carnososa* (Appendix S1: Figures S4 and S5). The cover of *E. californica* (Figure 5b) and *S. macrotheca* (Figure 5e) was more variable over space and time, especially for the latter, which attained high cover in the first growing season but declined thereafter (Appendix S1: Figure S4). Clustering never had a positive effect and instead suppressed cover when main planting pattern effects were significant (Table 3). A significant planting pattern \times elevation interaction for *D. spicata* cover in 2019 suggested a subtle switch in neighbor effects across elevation, with minor effects on cover. Otherwise, significant planting pattern \times elevation interactions indicated a stronger benefit of the uniform planting as elevation increased (e.g., *F. salina* and *S. macrotheca* in 2019; Figure 5c,e), but could also signal a weakening negative effect of neighbors at some elevations, resulting in similar performance in both treatments (e.g., *S. macrotheca* in 2021; Figure 5e). By the 2021 growing season, cover was significantly lower in clustered plantings for all species (Figure 5; Table 3).

Q3b: Do restoration plantings lead to greater restoration success in terms of exotic cover (2019, 2020, 2021)?

Most exotic invaders in planted areas were upland species, and exotic cover significantly increased with elevation in all years (Figure 6). Significant effects of planting pattern on cover were relatively rare and varied with the species planted. Exotic cover in *D. spicata* columns was unaffected by planting pattern (Table 4a; Figure 6a). In areas planted with *E. californica*, a significant elevation \times planting pattern interaction reflects a switch from higher exotic cover in the clustered treatment at mid-elevations to higher exotic cover in the uniform treatment at the highest elevations (Table 4b; Figure 6b). Exotic cover tended to be

higher in clustered plantings of *F. salina* across the elevation gradient (Table 4c; Figure 6c). Exotic cover in columns planted with *J. carnososa* or *S. macrotheca* was variable across years, tending to be higher in clustered plantings at mid-elevation, but higher in uniform plantings near the upland transition (Table 4d,e; Figure 6d,e).

Q4: How do rainfall and seasonal trends in soil water potential, soil percent moisture, and soil temperature influence abiotic stress gradients in this system (2019)?

The weather followed a characteristic Mediterranean pattern in the first growing season, with a cool wet winter and warm dry summer. Following planting, rainfall was above the 20-year average in February and May (Appendix S1: Figure S6a). Soil moisture content ranged from a summertime low of $\sim 2\%$ to more than 25% during the wet season, was highly variable across blocks, and followed a general pattern of greater moisture near the bottom of blocks where inundation was more frequent (Appendix S1: Figure S6b). Soil water potential during the wet season ranged from nearly zero (the maximum value possible) at the upland edge of the block to -40 MPa at the lower marsh boundary near the end of the dry season (Appendix S1: Figure S6c). The most negative soil water potential values were observed at lower elevations, where frequent inundation likely maintained more saline conditions. Soil temperatures in the open ranged from a mean high of 33°C in September to a mean low of 17°C in December (Appendix S1: Figure S7a).

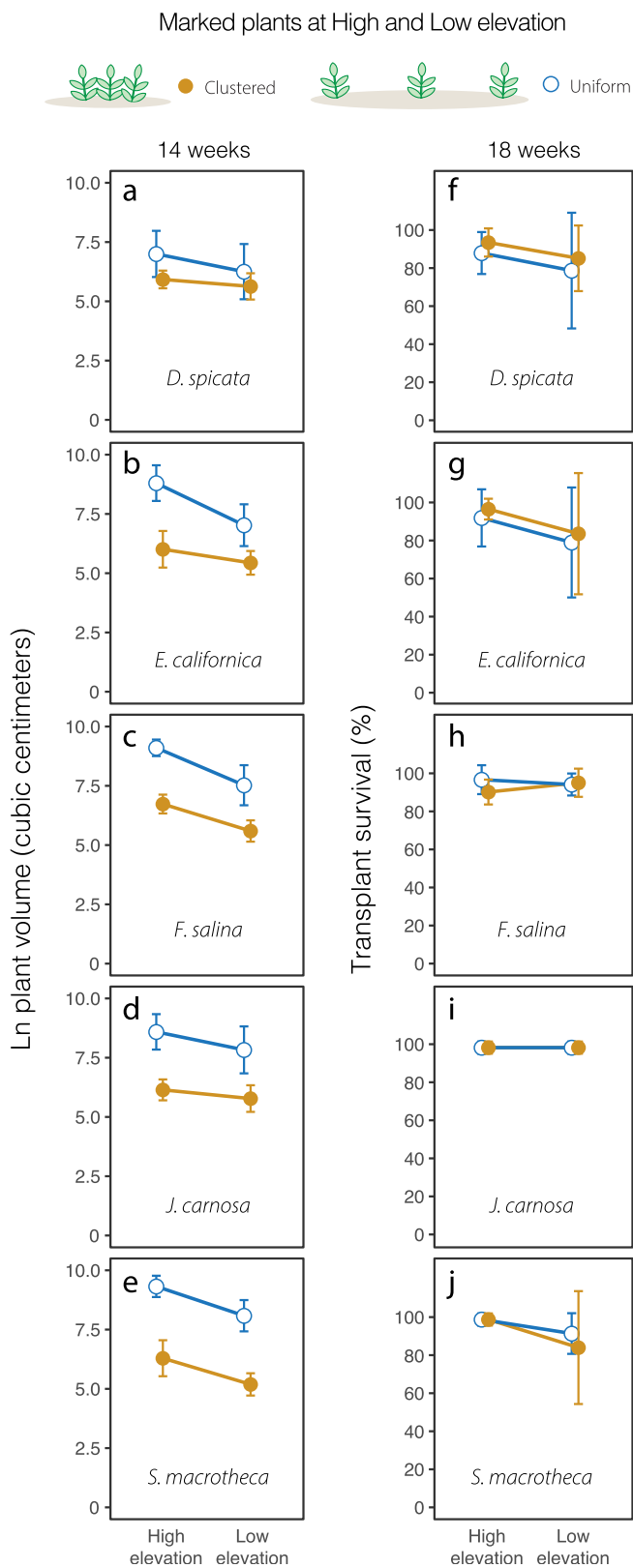
Q5: During summertime drought, do soil metrics differ under plant canopies compared with the open (35 weeks after planting)?

Sampling location (in the open vs. under plant canopies) had no effect on soil water potential near the end of the dry season (Appendix S1: Figure S7c, Table S9). In contrast, soil moisture was significantly higher under plant canopies (Appendix S1: Figure S7b, Table S10a). Post hoc tests

FIGURE 3 The proportion of transplants surviving to 9 weeks in the clustered and uniform planting pattern, on transects across the full elevation gradient in three planted blocks: (a) *Distichlis spicata*, (b) *Extriplex californica*, (c) *Frankenia salina*, (d) *Jaumea carnososa*, (e) *Spergularia macrotheca*. Individual plants at each elevation are visualized as dots at position 1.0 on the y axis (live plants) or position 0.0 on the y axis (dead plants). Filled orange dots indicate plants in the clustered planting pattern, and open blue dots indicate plants in the uniform planting pattern; because three individuals per planting treatment were surveyed at each elevation, up to six dots may be stacked at each elevation (for example, when all plants in both treatments survived at a given elevation, six stacked dots appear at position 1.0). Linear survival trends in the clustered planting pattern are shown in orange, and survival trends in the uniform planting pattern are shown in blue.

revealed that this effect was largely driven by the difference in soil moisture under *F. salina* canopy versus bare soil (Appendix S1: Table S10b). Soil temperatures were also coolest under *F. salina* canopy (Appendix S1: Figure S7a).

Soil temperatures differed in the open versus under plant canopies (Appendix S1: Table S11). Temperatures in the open and under the relatively sparse canopies of *D. spicata* and *J. carnosa* canopies were higher, especially during warmer months, while temperatures under the denser canopies of *E. californica*, *F. salina*, and *S. macrotheca* tended to be cooler (Appendix S1: Figure S7a, Table S12).



DISCUSSION

Intraspecific interactions in restoration

Facilitation has been advanced as an important tool to reduce stress at restoration sites, but we found little evidence of positive interactions between plants in our restored salt marsh. In our main restoration planting, we found that close neighbors slightly improved survival of a single species (*E. californica*), but this benefit was strongly outweighed by competition for space as plants grew. For the remaining species, we found that clustering did not benefit plant performance in any way, and in fact close neighbors strongly suppressed growth and cover for all five species in planted blocks, as well as growth of two additional species planted in block wings. Our supplemental restoration planting at Yampah the following year was designed as a second test of neighbor effects on *E. californica* under stressful conditions, but in this case, clustering conferred no survival benefit (all transplants died in clustered as well as uniform plantings). We also found no benefit of clustering on *F. salina* and *J. carnosa* performance in an earlier plot-scale experiment at a restored lagoon in the Elkhorn Slough complex (Tanner et al., 2022). Given our efforts to detect intraspecific facilitation in restoration plantings that collectively cover seven species, three independent experiments in separate years, and tests at both the plot and landscape scale, we conclude that close conspecific neighbors do not improve high marsh restoration outcomes in this estuary—and likely will not benefit restoration efforts in similar systems.

Our results were surprising because positive interactions between plants that mitigate stress have been

FIGURE 4 Performance of marked plants in the clustered and uniform planting patterns at high and low elevation: Left panels (a–e) show natural log-transformed plant volume at 14 weeks, and right panels (f–j) show percent transplant survival at 18 weeks. The clustered planting pattern is shown in orange, and the uniform planting pattern is shown in blue. Error bars show one SD. See Figure 1c for the position of the high- and low-elevation locations within planted blocks.

TABLE 1 Linear mixed-effects model and linear model results evaluating the effects of planting pattern (clustered vs. uniform), high versus low elevation, and the planting pattern \times elevation interaction on natural log-transformed plant volume for the 5 primary species: (a) *Distichlis spicata*, (b) *Extripes californica*, (c) *Frankenia salina*, (d) *Spergularia macrotheca*, and (e) *Jaumea carnosa*.

Model type and species	Predictor	F	df	Residual df	SS	p
Linear mixed-effects model						
(a) <i>D. spicata</i> (n = 47)	(Intercept)	1290.39	1	5.00		<0.001
	Planting pattern	14.21	1	38.09		0.001
	Elevation	5.74	1	38.09		0.022
	Planting pattern \times Elevation	1.16	1	38.09		0.288
(b) <i>E. californica</i> (n = 48)	(Intercept)	1339.29	1	5.00		<0.001
	Planting pattern	142.51	1	39.00		<0.001
	Elevation	40.95	1	39.00		<0.001
	Planting pattern \times Elevation	10.75	1	39.00		0.002
(c) <i>F. salina</i> (n = 48)	(Intercept)	3595.69	1	5.00		<0.001
	Planting pattern	224.40	1	39.00		<0.001
	Elevation	89.43	1	39.00		<0.001
	Planting pattern \times Elevation	2.35	1	39.00		0.133
(d) <i>S. macrotheca</i> (n = 47)	(Intercept)	3630.48	1	4.99		<0.001
	Planting pattern	321.48	1	38.11		<0.001
	Elevation	50.38	1	38.11		<0.001
	Planting pattern \times Elevation	0.15	1	38.11		0.704
Linear model						
(e) <i>J. carnosa</i> (n = 48)	(Intercept)	4704.85	1		2409.36	<0.001
	Planting pattern	118.62	1		60.74	<0.001
	Elevation	7.44	1		3.81	0.009
	Planting pattern \times Elevation	0.91	1		0.46	0.346

Note: Results when including the nonsignificant biochar treatment predictor are presented in Appendix S1: Table S5. Bold values indicate significant effects ($p \leq 0.05$).

demonstrated in both natural and restored systems. Once the SGH (Bertness & Callaway, 1994) laid out a relationship between neighbor interaction patterns and stress, this framework was validated by theoretical modeling efforts (Travis et al., 2005, 2006) and empirical studies in alpine systems (Callaway et al., 2002; Cavieres et al., 2006), deserts (McAuliffe, 1986; Nobel, 1980), grasslands (Greenlee & Callaway, 1996), oak woodlands (Callaway, 1992; Callaway & D'Antonio, 1991), salt marshes (Bertness, 1991; Bertness & Shumway, 1993; Bertness & Yeh, 1994), and intertidal zones (Bertness, 1989; Leslie, 2005). The broad evidence for positive neighbor effects in a range of natural systems (He et al., 2013) prompted scientists to propose that facilitation should be incorporated into restoration designs for stressful habitat (Halpern et al., 2007; Padilla & Pugnaire, 2006). Positive interactions that improve restoration outcomes have previously been demonstrated in coastal systems. In a test of interspecific facilitation including three taxa studied here

(*F. salina*, *J. carnosa*, and *L. californicum*), O'Brien and Zedler (2006) found that more transplants tended to survive sediment smothering and salinity stress when planted in tight clusters. Studies focused on intraspecific interactions have also found positive effects on restoration outcomes; Bos and Van Katwijk (2007) found that clustered eelgrass plantings were able to withstand greater hydrodynamic stress, and Silliman et al. (2015) demonstrated that clumping buffers anoxia and erosion stress for *Spartina* transplants in the low marsh. At our restoration site, we hypothesized that conspecific neighbors with the same stress tolerance and resource needs could still drive a benefit via shading effects on soil moisture and plant water relations. Yet, plants in the uniform treatment performed best, suggesting that any benefit of shading in the clustered treatment was outweighed by competition for belowground resources (e.g., water) or aboveground resources (e.g., space). As a result, intraspecific facilitation does not appear to be an effective tool for improving restoration success in this

TABLE 2 Generalized linear mixed-effects model and generalized linear model results evaluating the effects of planting pattern (clustered vs. uniform), high versus low elevation, and the planting pattern × elevation interaction on transplant survival to 18 weeks for four of the five primary species: (a) *Distichlis spicata*, (b) *Extriplex californica*, (c) *Frankenia salina*, and (d) *Spergularia macrotheca* (statistical tests for *Jaumea carnosa* are not presented because marked plant survival was 99% across all treatments). Results when including the nonsignificant biochar treatment predictor are presented in Appendix S1: Table S5.

Model type and species	Predictor	χ^2	df	<i>p</i>
GLMM (binomial)				
(a) <i>D. spicata</i> (<i>n</i> = 48)	(Intercept)	40.01	1	<0.001
	Planting pattern	3.73	1	<i>0.054</i>
	Elevation	7.58	1	0.006
	Planting pattern × Elevation	0.14	1	0.704
(b) <i>E. californica</i> (<i>n</i> = 48)	(Intercept)	15.68	1	<0.001
	Planting pattern	3.20	1	<i>0.074</i>
	Elevation	18.09	1	<0.001
	Planting pattern × Elevation	0.54	1	0.461
(c) <i>F. salina</i> (<i>n</i> = 48)	Planting pattern	1.47	1	0.226
	Elevation	0.00	1	0.956
	Planting pattern × Elevation	2.75	1	<i>0.097</i>
GLM (zero-inflated binomial)				
(d) <i>S. macrotheca</i> (<i>n</i> = 48)	(Intercept)	49.96	1	<0.001
	Planting pattern	0.01	1	0.925
	Elevation	9.93	1	0.002
	Planting pattern × Elevation	0.01	1	0.925

Abbreviation: GLMM, generalized linear mixed-effects model. Bold values indicate significant effects ($p \leq 0.05$); italic values indicate marginally significant effects ($p \leq 0.10$).

central California high marsh. Many of the species studied here are widely distributed in marsh communities on the US West Coast (Janousek et al., 2019), and previous work has identified strong similarities between marsh communities on the California coast and in the Mediterranean region (Peinado et al., 1995). Where high marsh floristic composition and climate regime are similar to the system studied here, we predict that close conspecific neighbors will suppress restoration success. Clustered plantings using different species may yield better outcomes in the high marsh, particularly when those species differ in abiotic tolerance and competitive ability (Maestre et al., 2009).

Physical stressors affecting restoration outcomes

Stress can make revegetation of restoration sites challenging, and the ability to identify and mitigate stressors is key to enhancing restoration success (Beheshti et al., 2023; Brooks et al., 2015; O’Brien & Zedler, 2006). Stress mitigation may be particularly important on constructed

habitat, where heavy equipment can compact soil and grading creates large swathes of bare earth where exposure stress can be high (Mossman et al., 2012; Thomsen et al., 2022; Zedler et al., 2003). We observed clear evidence of stress in some planted blocks, and in the supplemental experiment at Yampah. In particular, early survival of *E. californica* was highly variable across planted blocks (ranging from 35% to 91%) and appeared to be related to local soil conditions. *S. macrotheca* also experienced patchy mortality, particularly in one block where 24% of transplants died during the first 10 weeks. At the Yampah site where we planted only *E. californica*, all transplants died during the first few weeks after planting. For effective adaptive management of this and other similar restoration projects, it is critical to characterize the stressors present and explore solutions for decreasing them (Zedler, 2017).

We observed clear differences in plant performance across elevation, with impacts on mortality and/or growth and cover depending on species. Transplant performance generally declined downslope, and natural recruitment of *S. pacifica* was also lower near the bottom boundary of the high marsh (Thomsen et al., 2022). Although hypoxia is known to impair salt marsh plant

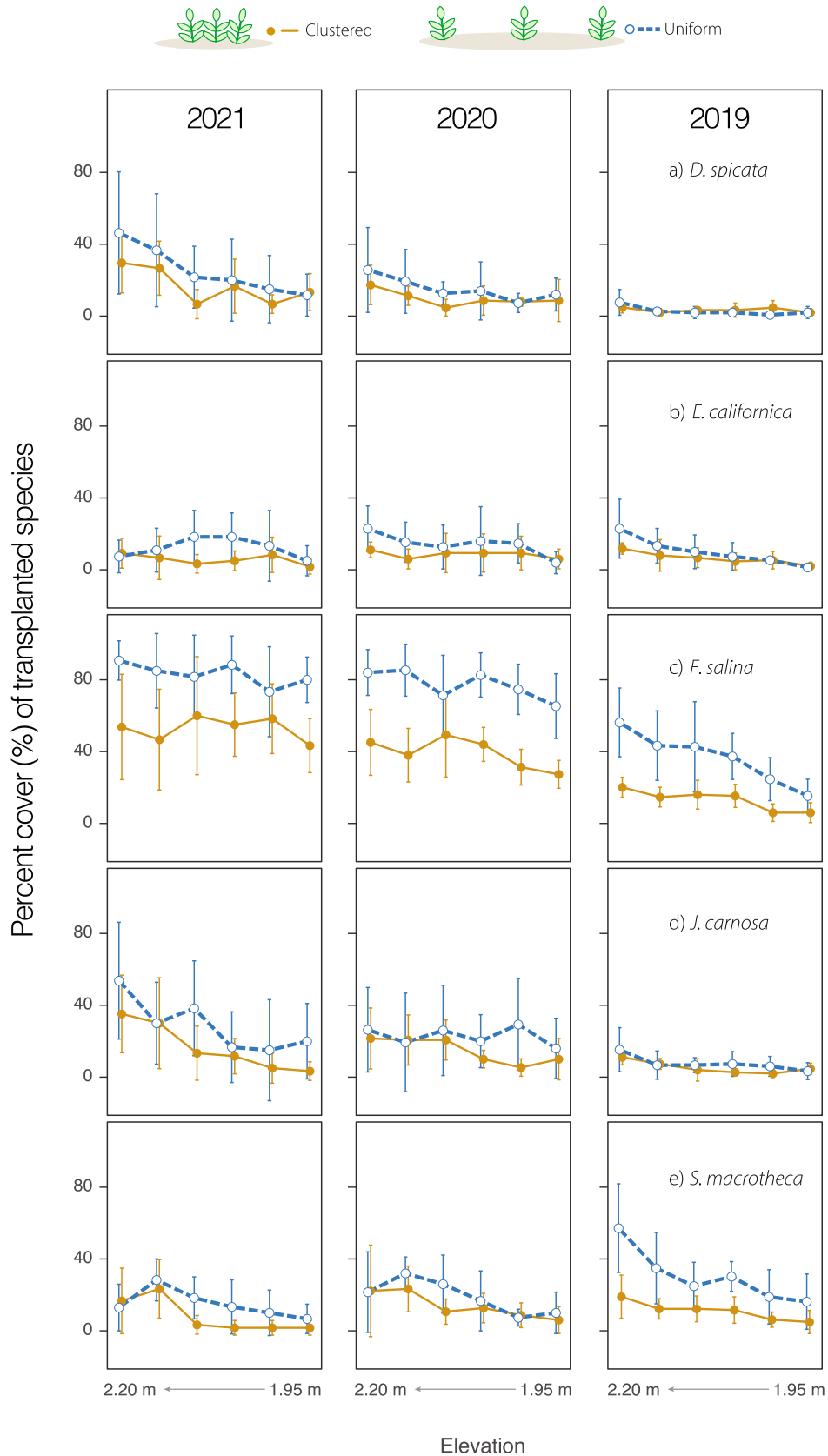


FIGURE 5 Percent cover of the five primary species, surveyed across the full elevation gradient in all blocks for 3 years (2019, 2020, 2021). Years are ordered from right to left to show trends for increasing cover across both years and elevation. Each row of panels shows the cover of a single species across 3 years, starting in the top row with (a) *Distichlis spicata* and ending with (e) *Spergularia macrotheca*. The clustered planting pattern is shown in orange, and the uniform planting pattern is shown in blue. Error bars show one SD.

TABLE 3 Transplant cover in 2019, 2020, 2021: Results from binomial generalized linear mixed-effects models and a generalized linear model evaluating the effects of elevation, planting pattern (clustered vs. uniform), and the elevation × planting pattern interaction in block columns planted with each of the five primary species: (a) *Distichlis spicata*, (b) *Extripes californica*, (c) *Frankenia salina*, (d) *Jaumea carnosa*, and (e) *Spergularia macrotheca*.

Species and predictor	2019 native cover			2020 native cover			2021 native cover		
	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>
(a) <i>D. spicata</i>									
(Intercept)	25.53	1	<0.001	37.82	1	<0.001
Elevation	5.49	1	0.019	17.19	1	<0.001	32.73	1	<0.001
Planting pattern	5.92	1	0.015	12.16	1	<0.001	8.42	1	0.004
Elevation × Planting pattern	5.84	1	0.016
(b) <i>E. californica</i>									
(Intercept)	45.44	1	<0.001	11.03	1	0.001	2.22	1	0.137
Elevation	34.83	1	<0.001	5.62	1	0.018	0.69	1	0.406
Planting pattern	6.15	1	0.013	6.71	1	0.010	9.25	1	0.002
Elevation × Planting pattern	6.63	1	0.010	7.40	1	0.007
(c) <i>F. salina</i>									
(Intercept)	60.61	1	<0.001	14.12	1	<0.001	0.76	1	0.385
Elevation	51.28	1	<0.001	16.19	1	<0.001	1.48	1	0.224
Planting pattern	3.72	1	<i>0.054</i>	2.72	1	<i>0.099</i>	2.83	1	<i>0.093</i>
Elevation × Planting pattern	5.33	1	0.021	4.83	1	0.028	3.91	1	0.048
(d) <i>J. carnosa</i>									
(Intercept)	23.27	1	<0.001	18.30	1	<0.001	50.44	1	<0.001
Elevation	15.48	1	<0.001	12.07	1	0.001	45.14	1	<0.001
Planting pattern	2.65	1	0.103	5.07	1	0.024	17.35	1	<0.001
Elevation × Planting pattern	4.41	1	0.036
(e) <i>S. macrotheca</i>									
(Intercept)	75.88	1	<0.001	64.17	1	<0.001	28.53	1	<0.001
Elevation	63.54	1	<0.001	52.35	1	<0.001	24.23	1	<0.001
Planting pattern	98.48	1	<0.001	8.61	1	0.003	5.94	1	0.015
Elevation × Planting pattern	5.59	1	0.018

Note: The sample size for each species in 2019 and 2020 was $n = 1788$; the sample size for each species in 2021 was $n = 708$. A generalized linear model was used for *D. spicata* in 2019 to avoid overfitting. Nonsignificant interaction terms involving the elevation covariate were dropped from the final models (see [Methods: Statistical analyses](#) for more details). Bold values indicate significant effects ($p \leq 0.05$); italic values indicate marginally significant effects ($p \leq 0.10$).

performance (Bertness & Ellison, 1987; Davy et al., 2011; Janousek & Mayo, 2013), it seems unlikely to be the culprit here; lower elevations of the high marsh are inundated more frequently, but still rarely at this site because the entire marsh was constructed to sit high in the tidal frame (Fountain et al., 2019). However, microtopography and sediment properties could still create waterlogged conditions at unexpected elevations (Crooks et al., 2002). Measurements of soil water potential declined at lower elevations while soil moisture content increased, indicating that salinity may have a stronger influence than moisture on soil water potential measurements. Although this finding suggests that salinity may be an important

driver of stress in this system, a study of soil salinity at this site carried out in 2019 found that soil salinities in the high marsh were not extreme (Thomsen et al., 2022). We were also surprised to find an apparent lack of stress at upper elevations in the high marsh, where we thought drought would have a strong influence on plant performance in this Mediterranean system. However, plentiful rainfall in late winter and spring of 2019 may have allowed transplants sufficient time to establish and become resilient to dry summertime conditions. Although soil cores spanned the full rooting zone for seedlings at the time of planting, root growth beyond that zone may have allowed transplants to tap into sources of

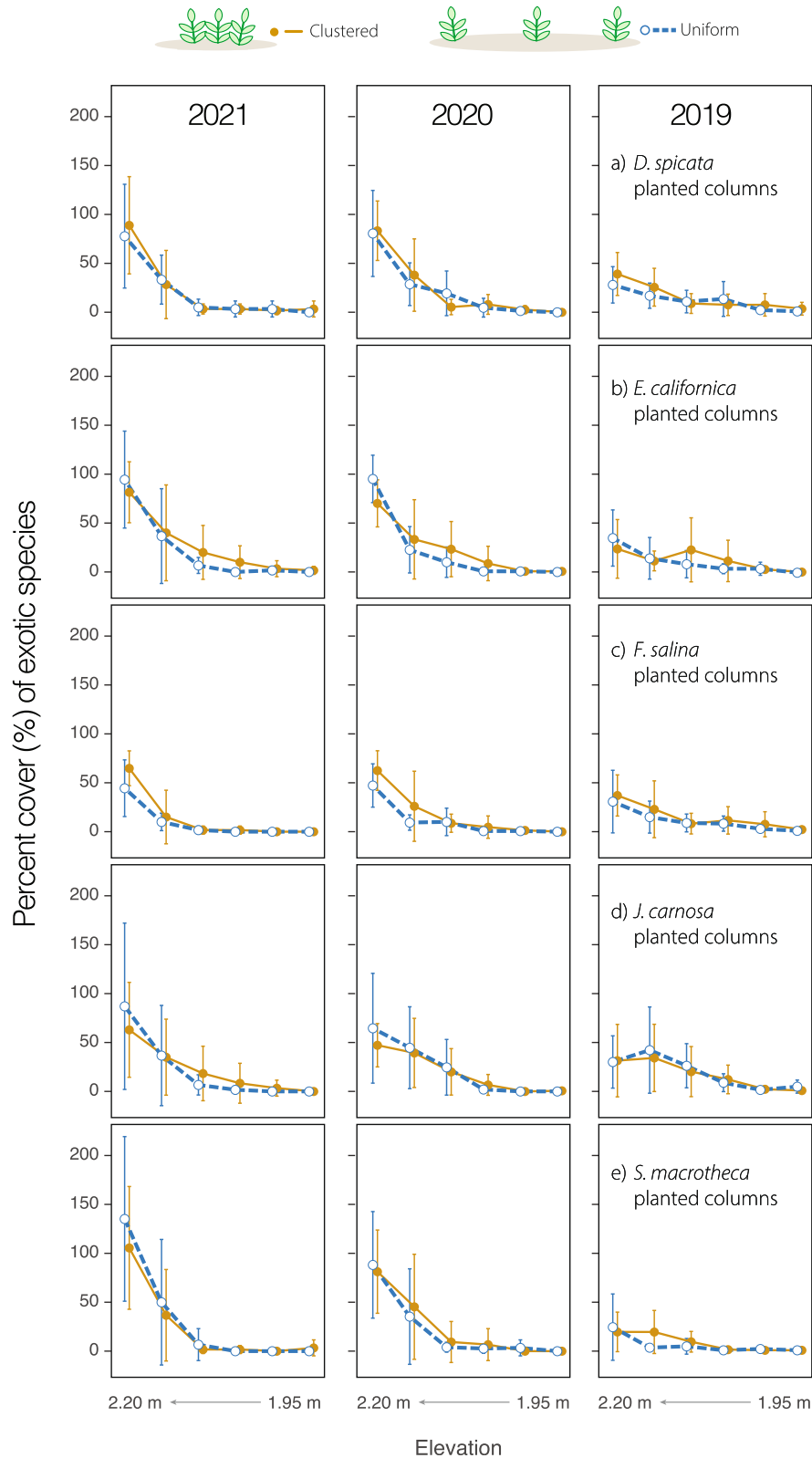


FIGURE 6 Percent exotic cover in columns planted with the five primary species in the clustered or uniform pattern, surveyed across the full elevation gradient in all blocks for 3 years (2019, 2020, 2021). Years are ordered from right to left to show trends for increasing exotic cover over time in columns planted with some species (most exotic plants in this watershed are upland species, so exotic cover also increases with elevation). Each row of panels shows exotic cover in columns planted with a single native species, starting in the top row with (a) *Distichlis spicata* and ending with (e) *Spergularia macrotheca*. Exotic cover in the clustered planting pattern is shown in orange, and the uniform planting pattern is shown in blue; cover can exceed 100% where multiple exotic species were encountered on point intercepts. Error bars show one SD.

TABLE 4 Exotic cover in 2019, 2020, 2021: Results from Poisson generalized linear mixed effects models evaluating the effects of Elevation, Planting pattern (Clustered vs. Uniform), and the Elevation × Planting pattern interaction in block columns planted with each of the 5 primary species: (a) *D. spicata*, (b) *E. californica*, (c) *F. salina*, (d) *J. carnos*a, and (e) *S. macrotheca*.

Species and predictor	2019 exotic cover			2020 exotic cover			2021 exotic cover		
	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>
<i>(a) D. spicata</i> planted columns									
(Intercept)	61.66	1	<0.001	241.74	1	<0.001	111.89	1	<0.001
Elevation	54.00	1	<0.001	234.13	1	<0.001	109.17	1	<0.001
Planting pattern	9.93	1	0.002	0.01	1	0.919	0.03	1	0.863
Elevation × Planting pattern	10.09	1	0.001
<i>(b) E. californica</i> planted columns									
(Intercept)	53.57	1	<0.001	249.03	1	<0.001	107.22	1	<0.001
Elevation	45.49	1	<0.001	242.61	1	<0.001	104.50	1	<0.001
Planting pattern	15.31	1	<0.001	26.34	1	<0.001	8.27	1	0.004
Elevation × Planting pattern	15.19	1	<0.001	26.30	1	<0.001	8.22	1	0.004
<i>(c) F. salina</i> planted columns									
(Intercept)	64.52	1	<0.001	182.23	1	<0.001	74.20	1	<0.001
Elevation	56.40	1	<0.001	174.59	1	<0.001	72.68	1	<0.001
Planting pattern	3.17	1	0.075	10.47	1	0.001	2.89	1	0.089
Elevation × Planting pattern
<i>(d) J. carnos</i> a planted columns									
(Intercept)	47.83	1	<0.001	156.20	1	<0.001	91.98	1	<0.001
Elevation	40.28	1	<0.001	147.30	1	<0.001	88.41	1	<0.001
Planting pattern	0.67	1	0.412	2.98	1	0.084	5.80	1	0.016
Elevation × Planting pattern	5.83	1	0.016
<i>(e) S. macrotheca</i> planted columns									
(Intercept)	71.90	1	<0.001	274.68	1	<0.001	163.93	1	<0.001
Elevation	66.25	1	<0.001	267.70	1	<0.001	162.17	1	<0.001
Planting pattern	8.18	1	0.004	0.91	1	0.340	3.62	1	0.057
Elevation × Planting pattern	8.02	1	0.005

Note: Data points below 2.035 m NAVD88 were dropped prior to this analysis because nearly all exotics in this system are upland species and none occur at the lowest elevations in planted blocks. The sample size for each species in 2019 and 2020 was *n* = 1188; the sample size for each species in 2021 was *n* = 468.

Nonsignificant interaction terms involving the elevation covariate were dropped from the final models (see *Methods: Statistical analyses* for more details). Bold values indicate significant effects (*p* ≤ 0.05); italic values indicate marginally significant effects (*p* ≤ 0.10).

moisture that we could not detect—including a potential influx of groundwater from the adjoining scraped hillside (Montalvo et al., 2024).

We also observed high mortality in localized areas of the main restoration planting, particularly in low-elevation areas with visibly compacted soil that also accumulated salt deposits during the dry season. Compaction can limit establishment of salt marsh vegetation (Callaway, 2001), and we speculate that soil compaction in these locations may have exacerbated flooding or salinity stress, with patchy but strong negative effects on early survival of *E. californica* and *S. macrotheca*. Subtle variations in microtopography can have a strong influence on salt

marsh plant performance (Xie et al., 2019), and soil texture interacts with tidal regime to drive changes in soil water content and salinity that can favor or suppress particular species (Moffett et al., 2010). Clearly, environmental conditions near the bottom of some blocks were not favorable for survival of *E. californica* or *S. macrotheca*. At Yampah, where sediment was added to build up lost elevation, conditions appeared to be uniformly stressful, and all supplemental plantings of *E. californica* died. This area has remained much more bare than planted blocks on the western side of the site—and areas that have remained bare are also more saline (Pausch, 2024; Thomsen et al., 2022), further hindering plant colonization.

Managers should consider actions that could mitigate these stressors in similar systems. None of the strategies that we tested at this large-scale restoration site were effective at reducing stress. In our main restoration planting, biochar soil amendment did not improve plant survival or growth, aligning with findings from a separate sediment treatment study carried out at Elkhorn Slough and seven other reserves (Raposa et al., 2023). In that study, the authors found that biochar addition did not affect vegetation cover or sediment salinity but did promote drainage and oxygenation. However, such benefits may be of limited value in the high marsh, where inundation (and anoxic conditions) is relatively rare. Our clustering treatment had a mild positive effect on early survival of *E. californica*, but it ultimately had a strong negative effect on growth or cover of all species. These outcomes may be explained if stress is primarily driven by salinity or compaction, which is unlikely to be buffered by close neighbors or the modest soil amendment treatments applied here. However, mortality of *E. californica* and *S. macrotheca* within the first 9 weeks of planting occurred during a period of heavy rainfall, which could be expected to mitigate excess soil salinity. Moreover, given the elevated position of the constructed marsh in the tidal frame and breaching of the site in August of 2018, the high marsh had undergone relatively few cycles of inundation by the time of restoration planting. We therefore suspect that soil compaction drove stressful conditions in areas of localized mortality. Regardless of the exact mechanisms at play in constructed marsh habitat, smaller test plantings across broader areas and multiple years will mitigate the risks posed by variable weather and spatially patchy soils. Active intervention may be required to jump-start colonization in persistently bare areas; the combination of freshwater addition and decompaction has proved effective in other restored salt marsh systems that have been slow to recover (Beheshti et al., 2023).

Learning from large-scale restoration experiments

Large-scale restoration projects provide invaluable opportunities to test and refine restoration practices (Zedler, 2017). Guidance on the most effective strategies is lacking in many systems, and this makes restoration practice inherently experimental—yet restoration projects are rarely designed as experiments (Zedler, 2005). Experiments that test different restoration treatments can shed light on mechanisms that govern the assembly and structure of restored communities (Beheshti et al., 2023; Doherty et al., 2011; Zedler, 2017). Identifying these

mechanisms allows development of best practices to enhance restoration success in similar systems, and to fine-tune these practices for particular sites—where outcomes are influenced by the specific combination of topography, abiotic characteristics, and species present. Long-term monitoring of restoration experiments is also needed to distinguish successful strategies from unsuccessful ones (Wolters et al., 2005)—yet monitoring is typically limited to a brief window following restoration efforts. We designed the Hester Marsh restoration project as a suite of restoration experiments coupled with long-term monitoring on an unprecedented scale. We learned from these experiments while also revegetating a formerly bare marsh.

Using multiple species lends powerful generality to our findings. We tested the effects of conspecific clustering on seven species from different plant families, including all species that make substantial contributions to high marsh cover (aside from the dominant *S. pacifica*, which tends to recruit well at restored sites in this system). We also tested biochar addition effects on five of these species in the main restoration planting. This approach allows us to make a clear and strong recommendation that practitioners should space plants apart to minimize competition in similar marsh restoration projects, and that biochar amendment is unnecessary. However, we still found differences in plant performance among species. *F. salina* and *S. macrotheca* were fast growers and reached >30% cover in the first 5 months, when other species remained at 10% or less cover. Once established, *L. californicum* appeared to flourish in this system, while none of the *T. concinna* transplants survived. *D. spicata* and *J. carnosus* grew very slowly and contributed little cover in the first year, but steadily increased to >20% cover on average by the third year. *F. salina* was clearly best suited to growing conditions at our site, consistently providing the most cover among planted species in each year and increasing in cover year over year. We recommend this species as a top performer for this and similar systems, as did a related study (Shikuzawa et al., 2024).

Recognizing that it can be expensive and time-consuming to incorporate monitoring into restoration projects, we tracked different metrics to assess which provided the most insight into restoration outcomes over our 3-year period of study. Given that restoration projects often set goals that relate directly to cover, and that clustered planting designs may trade off survival and subsequent growth and cover (Duggan-Edwards et al., 2020), it is important to monitor more than early survival. Cover across elevation is the most important variable to monitor for tidal marsh restoration (Wolters et al., 2005), and doing this just once a year is more informative for

managers than focusing on time-consuming parameters like individual plant size or survival during the first growing season. If our experiments had considered a more limited time period or spatial area, we likely would have missed strong spatial patterns in plant performance in response to elevation and local soil characteristics over time. If we had just tracked outcomes in the main restoration planting during the first growing season, we would have ranked *S. macrotheca* as much more successful than *D. spicata* or *J. carnosa*. However, despite excellent performance in the first growing season, *S. macrotheca* cover dropped drastically in subsequent years while the cover of *D. spicata* and *J. carnosa* continued to increase steadily. We also likely would have concluded that neighbor facilitation can improve restoration outcomes for *E. californica*—but in the long run, neighbors were not beneficial. Moreover, the supplemental *E. californica* planting installed in a different year and area of the restoration site suffered total mortality, showing how variable success can be. Taken together, these results highlight that it is wise to avoid drawing conclusions from restoration outcomes over limited temporal and spatial scales (Witman et al., 2015). Planning restoration work in phases that span different growing seasons and areas of a restoration site provides more opportunities to learn about the factors that govern restoration success (Zedler, 2017).

Our experiments were designed to test the effectiveness of different restoration strategies over broad spatial and temporal scales that are relevant for large-scale restoration projects. This design is important because much guidance for restoration comes from small plot-scale experiments that focus on early performance and may not be informative for practitioners who need to operate at landscape scales. The insights gained by building well-designed experiments and long-term monitoring into large restoration projects can be applied to enhance outcomes of future restoration phases and to identify best practices for other, similar systems.

AUTHOR CONTRIBUTIONS

Karen E. Tanner, Kerstin Wasson, Ingrid M. Parker, and Monique C. Fountain conceived and designed the research. Karen E. Tanner and Kerstin Wasson led the fieldwork, with contributions from all authors. Data analysis and interpretation were led by Karen E. Tanner, with input from Ingrid M. Parker and Kerstin Wasson. The manuscript was drafted by Karen E. Tanner, with extensive input from Ingrid M. Parker and Kerstin Wasson. Editorial contributions were made by all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Tanner et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.kwh70rzd9>.

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REFERENCES

- Agegnehu, G., A. K. Srivastava, and M. I. Bird. 2017. "The Role of Biochar and Biochar-Compost in Improving Soil Quality and Crop Performance: A Review." *Applied Soil Ecology* 119: 156–170.
- Ali, S., M. Rizwan, M. F. Qayyum, Y. S. Ok, M. Ibrahim, M. Riaz, M. S. Arif, F. Hafeez, M. I. Al-Wabel, and A. N. Shahzad. 2017. "Biochar Soil Amendment on Alleviation of Drought and Salt Stress in Plants: A Critical Review." *Environmental Science and Pollution Research* 24: 12700–12712.
- Armitage, A. R., K. E. Boyer, R. R. Vance, and R. F. Ambrose. 2006. "Restoring Assemblages of Salt Marsh Halophytes in the Presence of a Rapidly Colonizing Dominant Species." *Wetlands* 26: 667–676.
- Bangert, R., S. M. Ferrier, L. Evans, K. Kennedy, K. C. Grady, E. Hersch-Green, G. J. Allan, and T. G. Whitham. 2013. "The Proportion of Three Foundation Plant Species and their Genotypes Influence an Arthropod Community: Restoration Implications for the Endangered Southwestern Willow Flycatcher." *Restoration Ecology* 21: 447–456.
- Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. "The Value of Estuarine and Coastal Ecosystem Services." *Ecological Monographs* 81: 169–193.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.48550/arXiv.1406.5823>.

- Baur, B. 2014. "Dispersal-Limited Species – A Challenge for Ecological Restoration." *Basic and Applied Ecology* 15: 559–564.
- Bayraktarov, E., M. I. Saunders, S. Abdullah, M. Mills, J. Beher, H. P. Possingham, P. J. Mumby, and C. E. Lovelock. 2016. "The Cost and Feasibility of Marine Coastal Restoration." *Ecological Applications* 26: 1055–74.
- Beheshti, K. M., S. C. Schroeter, A. A. Deza, D. C. Reed, R. S. Smith, and H. M. Page. 2023. "Large-Scale Field Studies Inform Adaptive Management of California Wetland Restoration." *Restoration Ecology* 31: e13936.
- Bertness, M. D. 1989. "Intraspecific Competition and Facilitation in a Northern Acorn Barnacle Population." *Ecology* 70: 257–268.
- Bertness, M. D. 1991. "Interspecific Interactions among High Marsh Perennials in a New England Salt Marsh." *Ecology* 72: 125–137.
- Bertness, M. D., and R. Callaway. 1994. "Positive Interactions in Communities." *Trends in Ecology & Evolution* 9: 191–93.
- Bertness, M. D., and A. M. Ellison. 1987. "Determinants of Pattern in a New England Salt Marsh Plant Community." *Ecological Monographs* 57: 129–147.
- Bertness, M. D., and P. J. Ewanchuk. 2002. "Latitudinal and Climate-Driven Variation in the Strength and Nature of Biological Interactions in New England Salt Marshes." *Oecologia* 132: 392–401.
- Bertness, M. D., and S. D. Hacker. 1994. "Physical Stress and Positive Associations among Marsh Plants." *The American Naturalist* 144: 363–372.
- Bertness, M. D., and G. H. Leonard. 1997. "The Role of Positive Interactions in Communities: Lessons from Intertidal Habitats." *Ecology* 78: 1976–89.
- Bertness, M. D., and S. W. Shumway. 1993. "Competition and Facilitation in Marsh Plants." *The American Naturalist* 142: 718–724.
- Bertness, M. D., and S. M. Yeh. 1994. "Cooperative and Competitive Interactions in the Recruitment of Marsh Elders." *Ecology* 75: 2416–29.
- Bos, A., and M. Van Katwijk. 2007. "Planting Density, Hydrodynamic Exposure and Mussel Beds Affect Survival of Transplanted Intertidal Eelgrass." *Marine Ecology Progress Series* 336: 121–29.
- Brooks, K. L., H. L. Mossman, J. L. Chitty, and A. Grant. 2015. "Limited Vegetation Development on a Created Salt Marsh Associated with Over-Consolidated Sediments and Lack of Topographic Heterogeneity." *Estuaries and Coasts* 38: 325–336.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. "glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *The R Journal* 9: 378–400.
- Callaway, J. C. 2001. "Hydrology and Substrate." In *Handbook for Restoring Tidal Wetlands*, edited by J. Zedler, 89–118. Boca Raton, FL: CRC Press.
- Callaway, R. M. 1992. "Effect of Shrubs on Recruitment of *Quercus douglasii* and *Quercus lobata* in California." *Ecology* 73: 2118–28.
- Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, et al. 2002. "Positive Interactions among Alpine Plants Increase with Stress." *Nature* 417: 844–48.
- Callaway, R. M., and C. M. D'Antonio. 1991. "Shrub Facilitation of Coast Live Oak Establishment in Central California." *Madrono* 38: 158–169.
- Callaway, R. M., S. Jones, W. R. Ferren, Jr., and A. Parikh. 1990. "Ecology of a Mediterranean-Climate Estuarine Wetland at Carpinteria, California: Plant Distributions and Soil Salinity in the Upper Marsh." *Canadian Journal of Botany* 68: 1139–46.
- Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perring, P. Venail, A. Narwani, et al. 2012. "Biodiversity Loss and Its Impact on Humanity." *Nature* 486: 59–67.
- Cavieres, L. A., E. I. Badano, A. Sierra-Almeida, S. Gómez-González, and M. A. Molina-Montenegro. 2006. "Positive Interactions between Alpine Plant Species and the Nurse Cushion Plant *Laretia acaulis* Do Not Increase with Elevation in the Andes of Central Chile." *New Phytologist* 169: 59–69.
- Chazdon, R. L., D. A. Falk, L. F. Banin, M. Wagner, S. J. Wilson, R. C. Grabowski, and K. N. Suding. 2021. "The Intervention Continuum in Restoration Ecology: Rethinking the Active–Passive Dichotomy." *Restoration Ecology* 32: e13535.
- Clausing, R. J., G. De La Fuente, A. Falace, and M. Chiantore. 2023. "Accounting for Environmental Stress in Restoration of Intertidal Foundation Species." *Journal of Applied Ecology* 60: 305–318.
- Crooks, S., J. Schutten, G. D. Sheern, K. Pye, and A. J. Davy. 2002. "Drainage and Elevation as Factors in the Restoration of Salt Marsh in Britain." *Restoration Ecology* 10: 591–602.
- Davy, A. J., M. J. H. Brown, H. L. Mossman, and A. Grant. 2011. "Colonization of a Newly Developing Salt Marsh: Disentangling Independent Effects of Elevation and Redox Potential on Halophytes." *Journal of Ecology* 99: 1350–57.
- Doherty, J. M., J. C. Callaway, and J. B. Zedler. 2011. "Diversity–Function Relationships Changed in a Long-Term Restoration Experiment." *Ecological Applications* 21: 2143–55.
- Duggan-Edwards, M. F., J. F. Pagès, S. R. Jenkins, T. J. Bouma, and M. W. Skov. 2020. "External Conditions Drive Optimal Planting Configurations for Salt Marsh Restoration." *Journal of Applied Ecology* 57: 619–629.
- Ehrenfeld, J. G. 2000. "Defining the Limits of Restoration: The Need for Realistic Goals." *Restoration Ecology* 8: 2–9.
- Fountain, M., C. Jeppesen, C. Endris, A. Woolfolk, E. Watson, I. Aiello, S. Fork, J. Haskins, K. Beheshti, and K. Wasson. 2019. "Hester Marsh Restoration: Annual Report." Elkhorn Slough National Estuarine Research Reserve. <https://elkhornslough.org/reserve/tidal-wetland-program/hester-marsh/>.
- Fowler, N. 1986. "The Role of Competition in Plant Communities in Arid and Semiarid Regions." *Annual Review of Ecology and Systematics* 1: 89–110.
- Fox, J., and S. Weisberg. 2011. *An R Companion to Applied Regression*. Thousand Oaks, CA: Sage Publications, Inc.
- Fresquez, C. C. 2014. "The Ecological Factors Influencing the Marsh-Upland Ecotonal Plant Community and Their Use as Part of an Effective Restoration Strategy." PhD diss., University of California.
- Gedan, K. B., B. R. Silliman, and M. D. Bertness. 2009. "Centuries of Human-Driven Change in Salt Marsh Ecosystems." *Annual Review of Marine Science* 1: 117–141.
- Goldberg, D. E., and A. M. Barton. 1992. "Patterns and Consequences of Interspecific Competition in Natural Communities:

- A Review of Field Experiments with Plants.” *The American Naturalist* 139: 771–801.
- Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. “Applying Plant Facilitation to Forest Restoration: A Meta-Analysis of the User of Shrubs as Nurse Plants.” *Ecological Applications* 14: 1128–38.
- Greenlee, J. T., and R. M. Callaway. 1996. “Abiotic Stress and the Relative Importance of Interference and Facilitation in Montane Bunchgrass Communities in Western Montana.” *The American Naturalist* 148: 386–396.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. “Community Structure, Population Control, and Competition.” *The American Naturalist* 94: 421–25.
- Halpern, B. S., B. R. Silliman, J. D. Olden, J. P. Bruno, and M. D. Bertness. 2007. “Incorporating Positive Interactions in Aquatic Restoration and Conservation.” *Frontiers in Ecology and the Environment* 5: 153–160.
- Hammer, E. C., M. Forstreuter, M. C. Rillig, and J. Kohler. 2015. “Biochar Increases Arbuscular Mycorrhizal Plant Growth Enhancement and Ameliorates Salinity Stress.” *Applied Soil Ecology* 96: 114–121.
- Hartig, F. 2021. “DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.” R Package Version 0.4.3. <https://CRAN.R-project.org/package=DHARMA>.
- He, Q., M. D. Bertness, and A. H. Altieri. 2013. “Global Shifts towards Positive Species Interactions with Increasing Environmental Stress.” *Ecology Letters* 16: 695–706.
- Holl, K. D., and T. M. Aide. 2011. “When and Where to Actively Restore Ecosystems?” *Forest Ecology and Management* 261: 1558–63.
- Hughes, A. R., J. H. Grabowski, H. M. Leslie, S. Scyphers, and S. L. Williams. 2018. “Inclusion of Biodiversity in Habitat Restoration Policy to Facilitate Ecosystem Recovery.” *Conservation Letters* 11: e12419.
- Janousek, C. N., and C. Mayo. 2013. “Plant Responses to Increased Inundation and Salt Exposure: Interactive Effects on Tidal Marsh Productivity.” *Plant Ecology* 214: 917–928.
- Janousek, C. N., K. M. Thorne, and J. Y. Takekawa. 2019. “Vertical Zonation and Niche Breadth of Tidal Marsh Plants along the Northeast Pacific Coast.” *Estuaries and Coasts* 42: 85–98.
- Langis, R., M. Zalejko, and J. B. Zedler. 1991. “Nitrogen Assessments in a Constructed and a Natural Salt Marsh of San Diego Bay.” *Ecological Applications* 1: 40–51.
- Leslie, H. M. 2005. “Positive Interspecific Effects Trump Negative Effects in High-Density Barnacle Aggregations.” *Ecology* 86: 2716–25.
- Lindig-Cisneros, R., and J. B. Zedler. 2002. “Halophyte Recruitment in a Salt Marsh Restoration Site.” *Estuaries* 25: 1174–83.
- Liu, Z., S. Fagherazzi, Q. He, O. Gourgue, J. Bai, X. Liu, C. Miao, Z. Hu, and B. Cui. 2024. “A Global Meta-Analysis on the Drivers of Salt Marsh Planting Success and Implications for Ecosystem Services.” *Nature Communications* 15: 3643.
- Luo, X., G. Liu, Y. Xia, L. Chen, Z. Jiang, H. Zheng, and Z. Wang. 2017. “Use of Biochar-Compost to Improve Properties and Productivity of the Degraded Coastal Soil in the Yellow River Delta, China.” *Journal of Soils and Sediments* 17: 780–89.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. “Refining the Stress-Gradient Hypothesis for Competition and Facilitation in Plant Communities.” *Journal of Ecology* 97: 199–205.
- Mahall, B. E., and R. B. Park. 1976. “The Ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in Salt Marshes of Northern San Francisco Bay: II. Soil Water and Salinity.” *Journal of Ecology* 64: 793.
- McAtee, K. J., K. M. Thorne, and C. R. Whitcraft. 2020. “Short-Term Impact of Sediment Addition on Plants and Invertebrates in a Southern California Salt Marsh.” *PLoS One* 15: e0240597.
- McAuliffe, J. R. 1986. “Herbivore-Limited Establishment of a Sonoran Desert Tree, *Cercidium microphyllum*.” *Ecology* 67: 276–280.
- Meli, P., M. Martínez-Ramos, and J. M. Rey-Benayas. 2013. “Selecting Species for Passive and Active Riparian Restoration in Southern Mexico.” *Restoration Ecology* 21: 163–65.
- Mendelssohn, I. A., and N. L. Kuhn. 2003. “Sediment Subsidy: Effects on Soil-Plant Responses in a Rapidly Submerging Coastal Salt Marsh.” *Ecological Engineering* 21: 115–128.
- Moffett, K. B., D. A. Robinson, and S. M. Gorelick. 2010. “Relationship of Salt Marsh Vegetation Zonation to Spatial Patterns in Soil Moisture, Salinity, and Topography.” *Ecosystems* 13: 1287–1302.
- Montalvo, M. S., E. Grande, A. E. Braswell, A. Visser, B. Arora, E. C. Seybold, C. Tatariw, et al. 2024. “A Fresh Take: Seasonal Changes in Terrestrial Freshwater Inputs Impact Salt Marsh Hydrology and Vegetation Dynamics.” *Estuaries and Coasts* 47: 2389–2405. <https://doi.org/10.1007/s12237-024-01392-1>.
- Mossman, H. L., M. J. H. Brown, A. J. Davy, and A. Grant. 2012. “Constraints on Salt Marsh Development Following Managed Coastal Realignment: Dispersal Limitation or Environmental Tolerance?” *Restoration Ecology* 20: 65–75.
- Nobel, P. S. 1980. “Morphology, Nurse Plants, and Minimum Apical Temperatures for Young *Carnegiea gigantea*.” *Botanical Gazette* 141: 188–191.
- O’Brien, E. L., and J. B. Zedler. 2006. “Accelerating the Restoration of Vegetation in a Southern California Salt Marsh.” *Wetlands Ecology and Management* 14: 269–286.
- Padilla, F. M., and F. I. Pugnaire. 2006. “The Role of Nurse Plants in the Restoration of Degraded Environments.” *Frontiers in Ecology and the Environment* 4: 196–202.
- Pausch, R. 2024. “Testing Strategies to Enhance Transplant Success under Stressful Conditions at a Tidal Marsh Restoration Project.” *Restoration Ecology* 32: e14117. <https://doi.org/10.1111/rec.14117>.
- Peinado, M., F. Alcaez, J. L. Aguirre, J. Delgadillo, and J. Alvarez. 1995. “Similarity of Zonation within Californian-Baja Californian and Mediterranean Salt Marshes.” *The Southwestern Naturalist* 40: 388–405.
- R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Raposa, K. B., A. Woolfolk, C. A. Endris, M. C. Fountain, G. Moore, M. Tyrrell, R. Swerida, et al. 2023. “Evaluating Thin-Layer Sediment Placement as a Tool for Enhancing Tidal Marsh Resilience: A Coordinated Experiment across Eight US National Estuarine Research Reserves.” *Estuaries and Coasts* 46: 595–615.
- Rey Benayas, J. M., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. “Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis.” *Science* 325: 1121–24.

- Schoener, T. W. 1983. "Field Experiments on Interspecific Competition." *The American Naturalist* 122: 240–285.
- Shikuzawa, J., E. B. Watson, K. Tanner, B. Wilburn, S. K. Fork, S. Larson, M. C. Fountain, A. Thomsen, and K. Wasson. 2024. "Ecosystem Functions of Plant Diversity: Comparisons from a Large-Scale Marsh Restoration Experiment in California, USA." *Ecosphere* 15: e4742.
- Shimamoto, C. Y., A. A. Padiá, C. M. Da Rosa, and M. C. M. Marques. 2018. "Restoration of Ecosystem Services in Tropical Forests: A Global Meta-Analysis." *PLoS One* 13: e0208523.
- Silliman, B. R., E. Schrack, Q. He, R. Cope, A. Santoni, T. Van Der Heide, R. Jacobi, M. Jacobi, and J. Van De Koppel. 2015. "Facilitation Shifts Paradigms and Can Amplify Coastal Restoration Efforts." *Proceedings of the National Academy of Sciences of the United States of America* 112: 14295–300.
- Stachowicz, J. J. 2001. "Mutualism, Facilitation, and the Structure of Ecological Communities." *BioScience* 51: 235.
- Stagg, C. L., and I. A. Mendelsohn. 2010. "Restoring Ecological Function to a Submerged Salt Marsh." *Restoration Ecology* 18: 10–17.
- Tanner, K., I. Parker, M. Fountain, A. Thomsen, and K. Wasson. 2024. "Performance of Seven Species in Clustered Versus Uniform Plantings in a Large-Scale High Marsh Restoration Project." Dataset. Dryad. <https://doi.org/10.5061/dryad.kwh70rzd9>.
- Tanner, K. E., K. Wasson, and I. M. Parker. 2022. "Competition Rather than Facilitation Affects Plant Performance across an Abiotic Stress Gradient in a Restored California Salt Marsh." *Restoration Ecology* 31: e13746.
- Thomsen, A. S., J. Krause, M. Appiano, K. E. Tanner, C. Endris, J. Haskins, E. Watson, A. Woolfolk, M. C. Fountain, and K. Wasson. 2022. "Monitoring Vegetation Dynamics at a Tidal Marsh Restoration Site: Integrating Field Methods, Remote Sensing and Modeling." *Estuaries and Coasts* 45: 523–538.
- Travis, J. M. J., R. W. Brooker, E. J. Clark, and C. Dytham. 2006. "The Distribution of Positive and Negative Species Interactions across Environmental Gradients on a Dual-Lattice Model." *Journal of Theoretical Biology* 241: 896–902.
- Travis, J. M. J., R. W. Brooker, and C. Dytham. 2005. "The Interplay of Positive and Negative Species Interactions across an Environmental Gradient: Insights from an Individual-Based Simulation Model." *Biology Letters* 1: 5–8.
- Wasson, K., and A. Woolfolk. 2011. "Salt Marsh-Upland Ecotones in Central California: Vulnerability to Invasions and Anthropogenic Stressors." *Wetlands* 31: 389–402.
- Witman, J. D., R. W. Lamb, and J. E. K. Byrnes. 2015. "Towards an Integration of Scale and Complexity in Marine Ecology." *Ecological Monographs* 85: 475–504.
- Wolters, M., A. Garbutt, and J. P. Bakker. 2005. "Salt-Marsh Restoration: Evaluating the Success of De-Embankments in North-West Europe." *Biological Conservation* 123: 249–268.
- Xie, T., B. Cui, S. Li, and J. Bai. 2019. "Topography Regulates Edaphic Suitability for Seedling Establishment Associated with Tidal Elevation in Coastal Salt Marshes." *Geoderma* 337: 1258–66.
- Yando, E. S., M. J. Osland, S. F. Jones, and M. W. Hester. 2019. "Jump-Starting Coastal Wetland Restoration: A Comparison of Marsh and Mangrove Foundation Species." *Restoration Ecology* 27: 1145–54.
- Zedler, J. B. 2005. "Restoring Wetland Plant Diversity: A Comparison of Existing and Adaptive Approaches." *Wetlands Ecology and Management* 13: 5–14.
- Zedler, J. B. 2017. "What's New in Adaptive Management and Restoration of Coasts and Estuaries?" *Estuaries and Coasts* 40: 1–21.
- Zedler, J. B., J. C. Callaway, and G. Sullivan. 2001. "Declining Biodiversity: Why Species Matter and How Their Functions Might Be Restored in Californian Tidal Marshes." *BioScience* 51: 1005.
- Zedler, J. B., and S. Kercher. 2005. "Wetland Resources: Status, Trends, Ecosystem Services, and Restorability." *Annual Review of Environment and Resources* 30: 39–74.
- Zedler, J. B., H. Morzaria-Luna, and K. Ward. 2003. "The Challenge of Restoring Vegetation on Tidal, Hypersaline Substrates." *Plant and Soil* 253: 259–273.
- Zhang, Y., W. Cioffi, R. Cope, P. Daleo, E. Heywood, C. Hoyt, C. Smith, and B. Silliman. 2018. "A Global Synthesis Reveals Gaps in Coastal Habitat Restoration Research." *Sustainability* 10: 1040.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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