

RESEARCH ARTICLE

Restoration of a marsh-upland ecotone specialist: the role of elevation, amendment, and facilitation

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Abstract

Introduction: Restoration of ecotone specialists can be challenging, since ecotones are defined by steep environmental and competition gradients. Restoration success is enhanced by understanding the factors that limit the range of ecotone specialists in the transition zone.

Methods: We examined conditions affecting the restoration success of coastal gumplant, *Grindelia stricta*, a salt marsh-upland ecotone specialist in California. We planted transplants in experiments testing the impacts of facilitation, soil amendment, and elevation on *Grindelia* survival and health. We also surveyed the seaward boundary of *Grindelia* at a restored versus natural marsh.

Results: We found that facilitation by *Salicornia pacifica* greatly improved outplanting success at stressful elevations, but that soil amendment had little impact. Restoration success appeared to be limited by physical stress at lower elevations and competition at higher elevations, as predicted by the stress gradient hypothesis. Our survey revealed that *Grindelia*'s lower limit is close to the king tide line.

Conclusions: This study provides a model of how restoration science and experiments can enhance the success of species living in ecotones. Results on this ecotone specialist delineate the zone of likely plant success and highlight the potential value of including facilitation to decrease the stressors near the edge of the ecotone.

Implications for Practice: This study provides several ways restoration practitioners can move forward with determining how to restore ecotonal species. Given the steep gradients in ecotones, we recommend conducting surveys of distributional limits of wild populations to first understand species tolerance limits. Restoration experiments manipulating physical conditions or neighbors can help determine what factors allow an ecotonal species to extend into stressful conditions. Facilitation may prove more effective than soil amendment at ameliorating stressful physical conditions at the edge of the physical tolerance limit of ecotonal species. Restoration of these species is possible with knowledge of their elevational distributions and the factors limiting their expansion.

Key words: ecotone, facilitation, nurse plant, restoration, salt marsh, stress gradient hypothesis, tidal marsh, transition zone

Introduction

Ecotones are the transition zone between ecosystems, usually occurring in a narrow area with strong physical and biological gradients (Delcourt & Delcourt 1992; Kark 2012). They often differ from bordering systems in species composition and biogeochemical characteristics and can support unique species (Attrill & Rundle 2002; Traut 2005; Kark 2012). Ecotones are especially important because they regulate and intensify flows of energy, nutrients, and organisms (Risser 1995; Traut 2005). As temperatures and sea levels rise, scientists increasingly focus on the movement of ecotones as a potential indicator of climate change impacts (Shadangi & Nath 2008; Wasson et al. 2013). Because ecotones can have drastic impacts on bordering systems and drive landscape changes (Peters et al. 2006), understanding their changes in location and learning to restore them is critical (Wasson et al. 2013).

One example of an ecotone with a steep gradient of physical conditions driven by variation in frequency of tidal inundation is the salt marsh-upland ecotone (Zedler & Cox 1984; Eicher 1987; Walker et al. 2003). This boundary zone between tidal wetlands and adjacent uplands harbors unique plant and

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animal communities and provides vital support to wildlife (James & Zedler 2000; Traut 2005; Rosencranz et al. 2019). Anthropogenic activities have led to extensive loss of salt marshes worldwide (Simas et al. 2001; Deegan et al. 2012), and restoration projects have been undertaken to restore them (Billah et al. 2022). Most restoration projects focus on generating conditions to favor the dominant mid- or low-marsh species (Callaway 2005; Billah et al. 2022), but the high marsh-upland ecotone is also threatened (Wasson & Woolfolk 2011). Therefore, there is a need to develop and test restoration strategies for the marsh-upland ecotone (James & Zedler 2000; Smith et al. 2001; Traut 2005).

Globally, salt marsh ecotone restoration success is impacted by physical and biological factors that correlate with elevation (Zedler & Cox 1984; James & Zedler 2000; Callaway 2005). This elevational gradient is driven by tidal elevation, which impacts salinity, inundation, and desiccation, all of which contribute directly to restoration success (Cui et al. 2011; Liu et al. 2020). Changes in these abiotic conditions also alter biotic interactions, which further impact restoration (Bockelmann et al. 2002; Cui et al. 2011; Derksen-Hooijberg et al. 2018; Zhu et al. 2019). Biological factors that impact plant zonation such as competition and facilitation are critical to ecotone ecology (Pennings & Callaway 1992; Derksen-Hooijberg et al. 2018) and are often determined by abiotic factors (Pennings & Callaway 1992; James & Zedler 2000; Cui et al. 2011). This is true in California, where the salt marsh-upland ecotone features differing biotic and abiotic conditions from the surrounding systems (Zedler & Cox 1984; James & Zedler 2000). The ecotone occurs at an elevation with periodic inundation during the highest tides of the year (Flick & Cayan 1985; James & Zedler 2000). Abiotic conditions influence the zonation of species in this system (Callaway 2005; Traut 2005), where the lower boundary of this ecotone with the salt marsh is influenced by physical limitations and competition (Wasson et al. 2013). Ecotone species may be outcompeted at lower elevations by salt marsh species with higher inundation and salinity tolerances. Dynamics at the upland boundary are similar—ecotone species may have a competitive advantage in areas with periodic inundation and higher salinity, but upland plants may outcompete ecotone species at higher elevations (Callaway et al. 1990; James & Zedler 2000; Wasson et al. 2013).

Restoration success can be further complicated by alterations to the natural environment occurring during the restoration process. Restoration sites may have stressful conditions for plant establishment if major construction disturbed the topsoil (Hart et al. 1999; Von Wilpert & Schäffer 2006). In salt marsh restoration, sites with sediment addition and disturbed topsoil often contain fewer nutrients and organic matter than the natural marsh. Soil amendments at marsh restoration sites can add organic matter to increase nutrient and water retention and can add nutrients directly (O'Brien & Zedler 2006; Sutton-Grier et al. 2009; Scott et al. 2020). Soil amendments and fertilizers are therefore used to establish plants at marsh restoration sites by alleviating soil compaction and topsoil removal and increasing nutrient availability (Broome et al. 1983; Sutton-Grier

et al. 2009; Wolf et al. 2019; Scott et al. 2020; Van Putte et al. 2022).

One salt marsh-upland ecotone species prevalent in Pacific salt marshes is *Grindelia stricta* (coastal gumweed, henceforth referred to as *Grindelia*). *Grindelia* is a sub-shrub plant common on the Pacific coast of North America that has relatively high salinity and drought tolerance (Steyermark 1937). It is known for colonizing new and open habitats, success in dry areas, and a tendency to grow in highly saline soils (Steyermark 1937). *Grindelia stricta* is often highlighted as an iconic salt marsh transition zone species in the San Francisco Bay region, where its yellow blooms are conspicuous along channel and creek banks, and where it provides roosting, foraging, and breeding habitat to salt marsh birds, including species of concern such as endemic tidal marsh sparrow subspecies, black rail, and clapper rail (Garcia 1995; Takekawa et al. 2011; Wood et al. 2012; Vasey & Baye 2018). It can be an indicator of higher marsh and is at its healthiest in the ecotone (Traut 2005). More than half the variation in plant community structure of the high marsh in northern California is explained by abiotic factors including elevation and salinity (Traut 2005).

This study aims to inform salt marsh-upland ecotone restoration in California by testing restoration strategies for *Grindelia stricta* and determining conditions that limit establishment. We conducted this study at a large marsh restoration in Elkhorn Slough estuary. Most Elkhorn Slough marshes are low and drowning, and *Grindelia* is not often observed along creeks and channels, but the restoration site was constructed higher than surrounding marshes, and so there was a potential opportunity to provide *Grindelia* habitat along creeks and channels such as is observed in San Francisco Bay (Vasey & Baye 2018; the suggestion was made by M. Vasey, personal communication). Specifically, the goal was to determine factors enhancing *Grindelia*'s growth and survival in restoration conditions, optimal planting elevations for restoration, and elevation tolerances. Because facilitation and competition play a key role in ecotone ecology, and because edaphic conditions impact both restoration success and the lower limit of the ecotone (Traut 2005), these factors were a key aspect of this study. By understanding what factors and conditions limit or enhance the growth of *Grindelia*, we can gain a better understanding of what conditions are needed for ecotone restoration in general, and for restoration using *Grindelia* in particular.

Methods

Study System

Elkhorn Slough is a eutrophic estuary in Monterey Bay, Central California, U.S.A., with a Mediterranean climate and semidiurnal tides (Caffrey et al. 2002). This study focuses on two interconnected salt marshes along the slough, Hester Marsh and Yampah Marsh (Fig. 1), both part of the Elkhorn Slough National Estuarine Research Reserve. Hester Marsh is the site of a recent sediment addition project that raised the elevation of a formerly diked marsh that had subsided to mudflat elevation, using low organic (~2%) and low nutrient soil scraped

from the adjacent hillside, and resulted in compacted soils (Thomsen et al. 2022). Yampah Marsh is a natural marsh adjacent to Hester Marsh. In this estuary, the marsh-upland ecotone occurs between mean higher high water (MHHW) and the highest tides, or about 1.6 to 2.2 m NAVD88 (Wasson et al. 2013). The dominant species in the marsh is *Salicornia pacifica* (henceforth *Salicornia*), while key ecotone plants include *Distichlis spicata*, *Frankenia salina*, *Jaumea carnosa*, *Atriplex prostrata*, and *Grindelia stricta* (Wasson & Woolfolk 2011). Since *Grindelia* is slow to establish at marsh restoration sites naturally (Williams & Faber 2004), the Elkhorn Slough Reserve is planting this species in the high marsh and adjacent coastal uplands as a part of restoration.

Facilitation and Soil Amendment Experiment

To test the effect of interspecific facilitation on *Grindelia* seedling success, we planted transplants either in the midst of established *Salicornia pacifica* patches or in adjacent bare patches. We planted directly at the seaward marsh edge with encouragement from marsh experts on the Elkhorn Slough marsh advisory group, since *Grindelia* thrives along high channel banks in San Francisco Bay. We planted along a higher channel edge (mean elevation 2.09 m NAVD88) and a lower creek edge (mean elevation 2.02 m NAVD88) in the same area (Fig. 1B). In order to determine whether soil amendments affected *Grindelia* seedling success, we compared transplants planted in ambient soil (low organic and low nutrient) versus those planted in potting soil (high organic and high nutrient). This experiment thus had three treatments: (1) Facilitation (creek $n = 11$, channel $n = 17$) with

a *Salicornia* neighbor and ambient soil, (2) Control (creek $n = 9$, channel $n = 23$) with no *Salicornia* neighbor and ambient soil, and (3) Amendment (creek $n = 10$, channel $n = 22$) with no *Salicornia* neighbor and potting soil. We hypothesized that facilitation treatments would perform better than control due to facilitation effects from the neighboring *Salicornia* plant. We hypothesized that amendment treatments would perform better than control due to higher organic and nutrient content in the soil providing nutrients and retaining moisture.

We planted *Grindelia* greenhouse-grown transplants in late January of 2023. *Grindelia* seeds were collected from sites in the Elkhorn Slough marsh-upland ecotone. Seedlings were raised in the Elkhorn Slough Reserve native plant nursery, grown in “stubby conetainers” (100 mL soil volume). With volunteer teams, we dug holes 10 cm deep and 10 cm in diameter, put the plants in the hole, and filled any space not taken up by roots with either potting soil or ambient soil. Foxfarm Ocean Forest organic potting soil was used (ingredients: composted forest humus, sphagnum peat moss, Pacific Northwest sea-going fish emulsion, crab meal, shrimp meal, earthworm castings, sandy loam, perlite, bat guano, granite dust, Norwegian kelp, and oyster shell). Plants were each watered with 120 mL fresh water upon planting, and received 120 mL fresh water every week for the first month and a half after planting unless it rained. We checked for *Grindelia* survival in April, July, and September 2023. In September we also evaluated two metrics of plant health, height and a visual estimate of percent green. We also took elevation readings at the base of each plant using a Reach RS2 RTK unit (1.0–1.5 cm horizontal and vertical accuracy).



Figure 1. Map of experimental transplants and survey points. Green circles are creek transplants, pink circles are channel transplants, blue circles are levee transplants, green triangles are naturally growing *Grindelia*, and orange squares are seeded *Grindelia*.

We conducted a series of statistical analyses to determine differences between treatments. These and all other statistics were run in R (R Core Team 2021). We used a Kruskal–Wallis test to compare plant height and greenness at the time of final sampling in September 2023, and ran a Dunn test for pairwise comparisons between treatments using the `dunn.test` package in R (Dinno 2017). For this and following Dunn tests, we report unadjusted p values. Because all the creek transplants had died by September 2023, we limited the analysis to the channel transplants. To determine the impact of treatment on *Grindelia* survival over time, we ran Cox proportional hazards regressions separately for the creek and channel transplants using the `coxme` package in R (Therneau 2015). Pairwise comparisons were done using the `emmeans` function from the `emmeans` package in R (Lenth 2022).

Elevation and Soil Amendment Experiment

In our second experiment, we tested the effects of elevation and soil amendment on *Grindelia* transplant success. Our primary objective was to identify the optimal elevational zone for restoration plantings, and whether this varies with soil amendments. We planted transplants ($n = 90$) along a levee at one edge of Hester Marsh. We planted at five elevations from high marsh to low upland elevations in nine transects perpendicular to the marsh edge (Fig. 2). We also included a soil treatment, comparing ambient sediment versus potting soil amendment. This resulted in 10 total treatments: elevations 1–5 with and without potting soil amendment. We hypothesized that *Grindelia* at the lowest elevation would perform worse than *Grindelia* planted at the middle elevations due to inundation and salinity, and that *Grindelia* planted at the highest elevation would perform worse than *Grindelia* at the middle elevations due to competition with established upland plants. We also hypothesized that *Grindelia* in potting soil would perform better than *Grindelia* in ambient soil.

These plantings and monitoring were done at the same time and with the same methods as the plantings for the facilitation and soil amendment experiment described above. We also took soil cores at five of the levee transects ($n = 25$) to

determine salinity, water content, and organic matter content across elevation gradients. Soil cores were taken using a push corer and stored in sealed ziplock bags until the end of the day. Samples were weighed, dried in a drying oven, and weighed again to determine gravimetric water content. The samples were then ground and homogenized, and subsampled for organic matter and salinity. Organic matter subsamples of 10 g were placed in a muffle furnace at 500°C for 4 hours and then weighed to determine organic matter content. A separate 2.5 g subsample was diluted with DI water at a 1:10 ratio and tested for specific conductivity and salinity (ppt) using a YSI ProDSS.

To determine differences in plant health among treatments at the end of the experiment in September, we ran a non-generalized linear mixed model (GLMM) using the `glmmTMB` package in R (Brooks et al. 2017) with elevation and amendment as fixed effects and transect as a random effect. Initial models had elevation and amendment as interactive effects, but no interactions were significant, so they were not included in the final model. We used a binomial family for plant greenness and a gamma family with a log link for plant height. 100% green values were adjusted to 99.9% to fit the gamma family. Pairwise comparisons were done using the `emmeans` function. To determine differences in survival over time among treatments, we ran a cox proportional hazards regression using the same model structure described above. Here we use the `Anova` function in R to determine the significance of model effects (elevation and soil). To determine differences in abiotic conditions (elevation and soil salinity, water content, and organic matter) across the five elevation treatments, potential drivers of *Grindelia* distribution, we used Kruskal–Wallis tests and Dunn tests for pairwise comparisons.

Surveys of Elevations in Restored Versus. Natural Marshes

In order to determine the difference in seaward elevational limit of *Grindelia* in natural, unrestored marshes versus seeded and transplanted *Grindelia* in restored marshes, we sampled naturally growing *Grindelia* in two nearby marshes (Fig. 1), Yampah Marsh, a natural marsh ($n = 34$ plants across about 500 m of

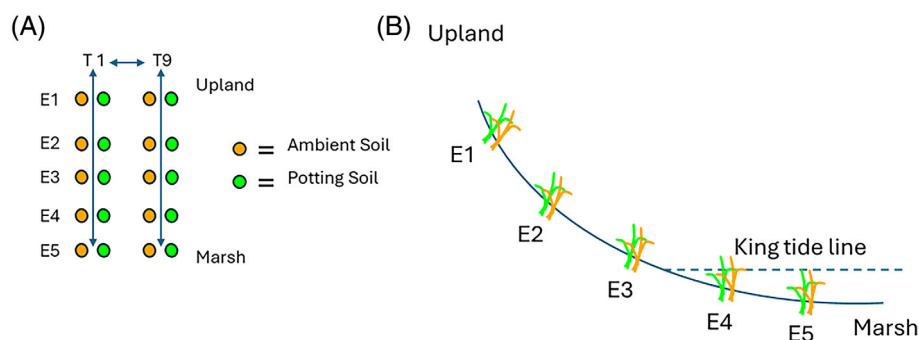


Figure 2. Elevation and soil amendment experimental design. (A) Diagram of the experimental design as viewed from above with both ambient and potting soil treatments at each of five elevations. (B) Side view of one transect showing elevation treatments. There were nine of these transects.

hillslope) and Hester Marsh, a restored marsh ($n = 28$ plants across around 200 m of hillslope). Within Hester Marsh, we compared seeded *Grindelia* to naturally occurring *Grindelia* to determine impacts of life history on tolerances. We were further motivated to explain our findings that *Grindelia* did not thrive on the creek or channel edge in Elkhorn Slough. To do this, we sampled both areas where *Grindelia* dispersed down from a hillside into the marsh from existing wild plants and areas where *Grindelia* seed was added to the hillside as a part of restoration. We conducted a visual search of the area to locate the most seaward *Grindelia* along the ecotone, sampling *Grindelia* plants at least 2 m apart. To measure their elevation, we used a Reach RS2 RTK (5 averaged positions per point) and recorded elevations in NAVD 88 m. We also took soil cores at selected ($n = 6$) plants in Yampah Marsh to compare edaphic conditions between successful levee elevation treatments and naturally growing *Grindelia* in the hope of determining drivers of *Grindelia* distribution. To test for differences in the elevational limit between *Grindelia* life histories, we used a Kruskal–Wallis test and ran a Dunn test for pairwise comparisons using the dunn.test package (Dinno 2017).

Results

Facilitation and Soil Amendment Experiment

In this experiment, facilitation resulted in statistically significant differences in survival, while soil amendment had no impact (Table S1). Survival was much lower in the lower elevation creek transplants than in the higher elevation channel transplants (Fig. 3A & 3B). Treatment impacts are hard to determine in creek transplants because all plants died regardless of treatment by 8 months (Fig. 3B). Differences in survival at the channel demonstrate a strong positive effect of facilitation relative to the control (Fig. 3A, $p = 0.008$). The impact was large, with facilitation decreasing the chances of plant mortality by around 80% according to our model (Table S1). Conversely, soil amendment had no significant impact on plant survival (Table S1, Fig. 3B).

Plant health metrics are only available at the channel, where there were statistically significant differences between treatments in plant height (Kruskal–Wallis H -statistic = 10.286, $df = 2$, $p = 0.006$), but not in percent green (Kruskal–Wallis H -statistic = 3.64, $df = 2$, $p = 0.16$). Facilitation impacted

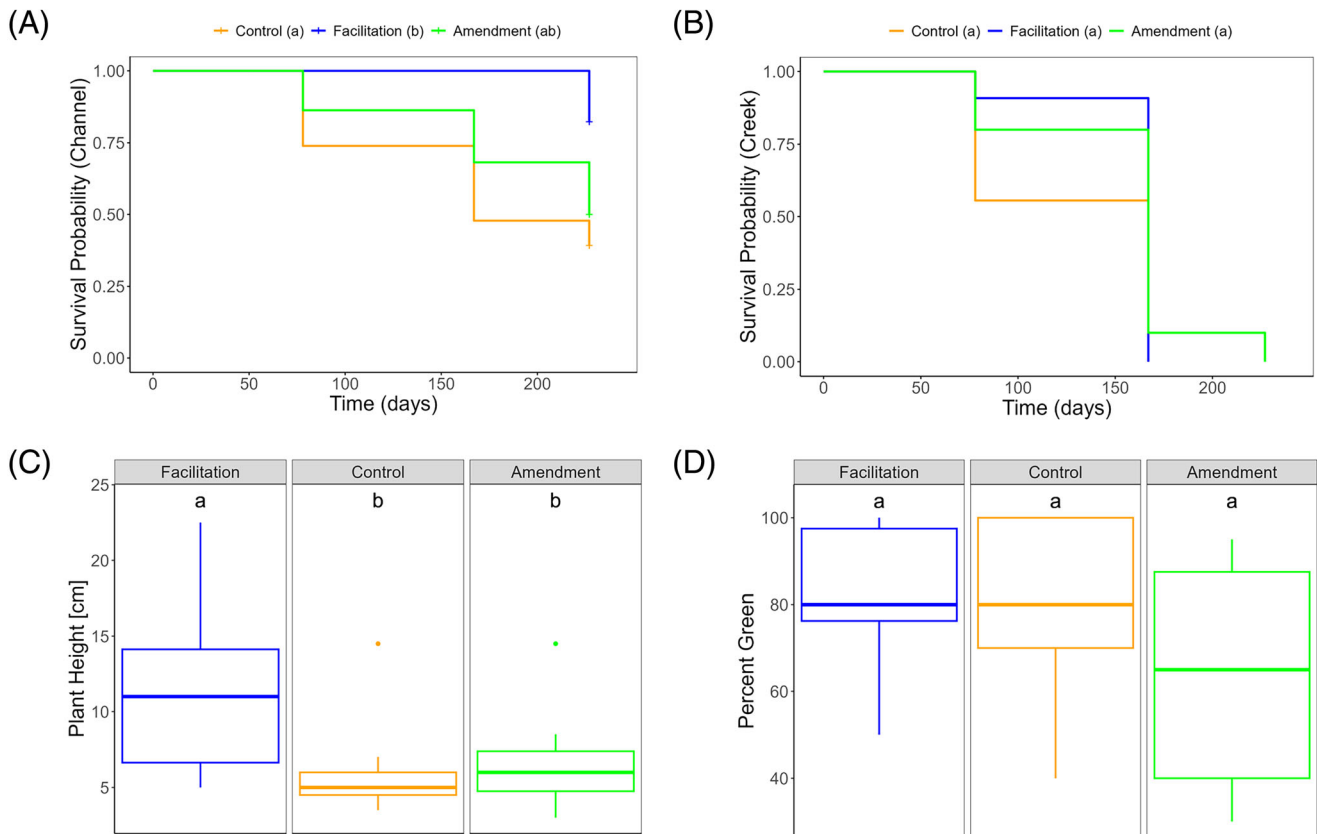


Figure 3. Facilitation and soil amendment experiment results. (A) Survival over time among channel transplants, showing improved survival in facilitation treatment. (B) Survival over time among creek transplants, showing initially improved survival in facilitation treatment, but all transplants died by the end of the study period. (C) Plant height of surviving plants 8 months after planting. (D) Percent green of surviving plants 8 months after planting. (C) and (D) represent results from the channel transplants only because all creek transplants were dead before plant health sampling. Treatments not sharing any letter in (C) and (D) are significantly different in pairwise comparisons determined using Dunn tests.

plant health, increasing plant height but not percent green. Conversely, soil amendment had no significant impact on plant health.

Elevation and Soil Amendment Experiment

The Cox model revealed that elevation had a significant effect on plant survival (Table S2, $p < 0.001$), while soil amendment had no significant effect (Table S2, $p = 0.33$). *Grindelia* survival was highest at middle elevations (Fig. 4A), and differences in survival could be extreme with small changes in elevation—a 0.11-m average difference between elevations 2 and 3 doubled the survival rate.

Grindelia health also differed by elevation, both in plant height and percent green (Table S3, $p < 0.001$ and 0.008, respectively). Surviving plants were significantly taller and greener at higher elevations, with a drop-off in both metrics below the highest three elevations (Fig. 4B & 4C). Surviving plants were significantly taller and greener at higher elevations, with a drop-off in both metrics below the highest three elevations (Fig. 4B & 4C).

Elevation also had a large impact on soil conditions—elevation, organic content, soil moisture, and salinity differed significantly by elevation (Fig. 5). Salinity and water content decreased with elevation, while organic matter was lowest at high elevations but peaked above the lowest. Salinity and water content changed dramatically between elevations 3 and 4 (Fig. 5). Elevations 1 and 2, above the king tide line, had similar soil conditions, while elevations with differing inundation frequency had stronger differences in abiotic conditions.

Surveys of Elevations in Restored Versus Natural Marshes

Our surveys of Yampah and Hester Marshes revealed that the lower limit of *Grindelia* was broadly similar across all areas and management histories we sampled. The average elevation among naturally growing *Grindelia* plants on the lower limit of establishment was 2.3 m in Yampah Marsh, 2.2 m in naturally growing *Grindelia* in Hester Marsh, and 2.2 m in seeded *Grindelia* in Hester Marsh. The seaward limit was significantly lower in restored, unseeded marsh than natural marsh (Fig. 6). This was not the case when compared to previous studies, in

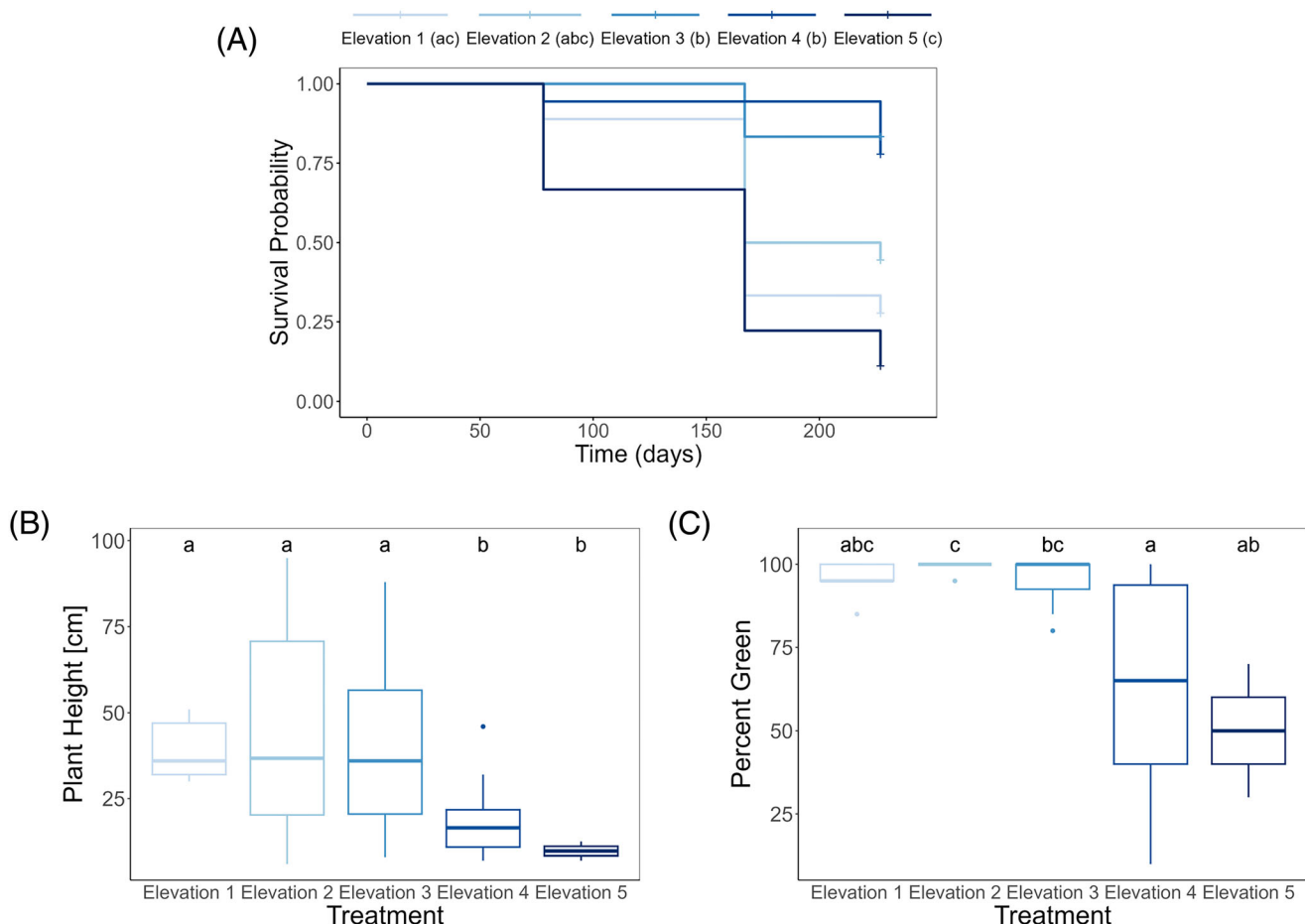


Figure 4. Plant response variables show strong contrasts across elevations. We show results for both soil treatments combined because soil treatment was not significant (Table S2). (A) Survival over time. (B) Plant height of surviving plants 8 months after planting. (C) Percent green of surviving plants 8 months after planting. Treatments not sharing any letters are significantly different in pairwise comparisons (Tables S4–S6).

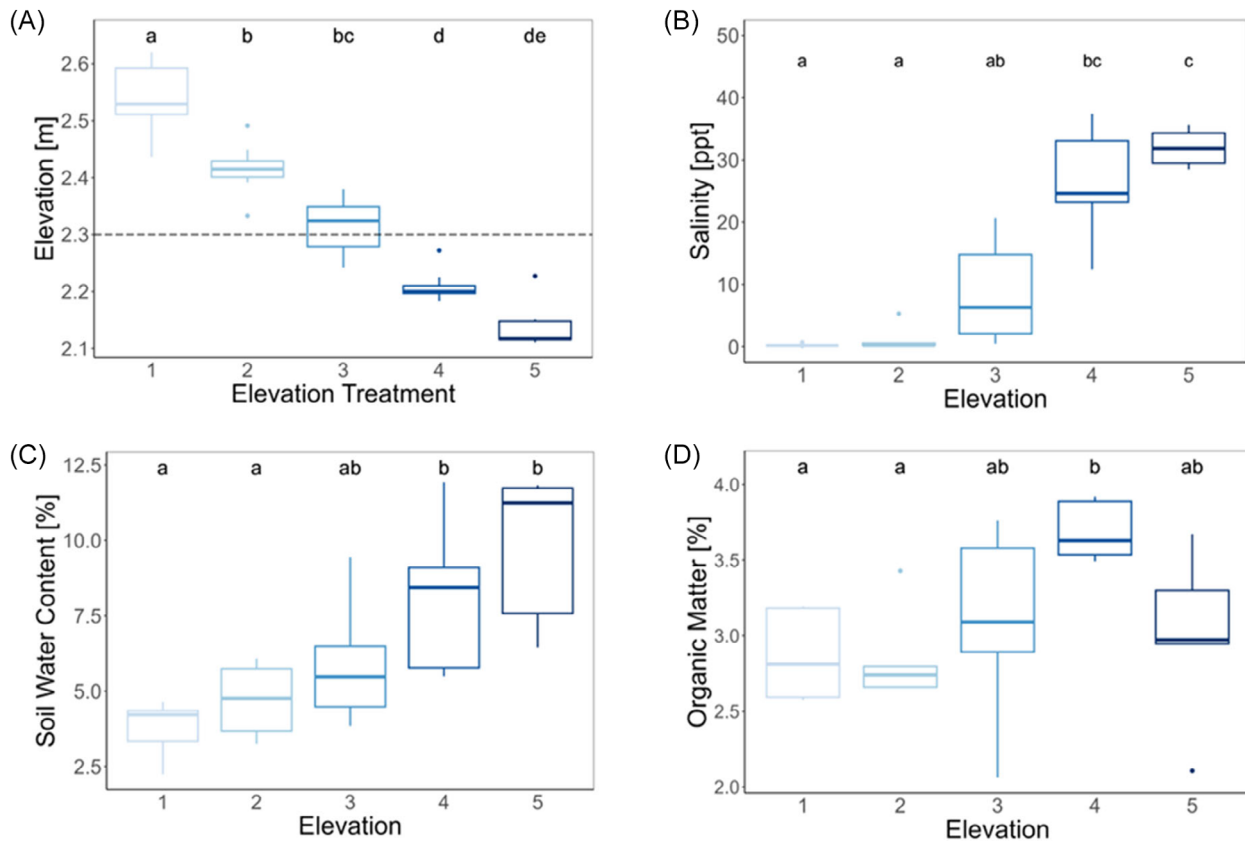


Figure 5. Abiotic conditions across elevations, with a strong correlation between inundation-impacted conditions and elevation. Statistical results reported represent Kruskal–Wallis tests on the differences between elevation treatments. (A) Elevations of levee transplants ($p < 0.001$, $df = 4$, H -statistic = 82.49), with the dashed line representing the king tide line at Hester Marsh (Tanner et al. 2023). (B) Salinity conditions of ambient soil at these elevations ($p < 0.001$, $df = 4$, H -statistic = 20.03). (C) Gravimetric soil water content of ambient soil at these elevations ($p = 0.0049$, $df = 4$, H -statistic = 14.92). (D) Organic matter content of ambient soil at these elevations ($p = 0.044$, $df = 4$, H -statistic = 9.81). Treatments not sharing any letters are significantly different in pairwise comparisons determined using Dunn tests.

which there was significant variation in the seaward boundary of *Grindelia* (Table 1). Soil cores at some Yampah Marsh plants (natural marsh) represent average soil conditions at the lowest *Grindelia* plants in the natural marsh, with a soil salinity of 4.16 ppt, 7.7% gravimetric soil water content, and 8.1% soil organic matter.

Discussion

Ecotone restoration success can be enhanced by a better understanding of ecotone dynamics and plant tolerances. Here, we determined the elevation tolerances of *Grindelia*, a marsh-upland ecotone specialist, and tested restoration techniques based on ecological theory. We used surveys to determine that *Grindelia* elevation tolerances at a restoration site are similar to natural limits and used experiments to improve understanding of ecotone dynamics impacting these limits. Soil amendment failed to aid *Grindelia* restoration, while elevation was a critical predictor of survival and health. Additionally, we found evidence of facilitation effects that can enhance restoration success under physically stressful conditions.

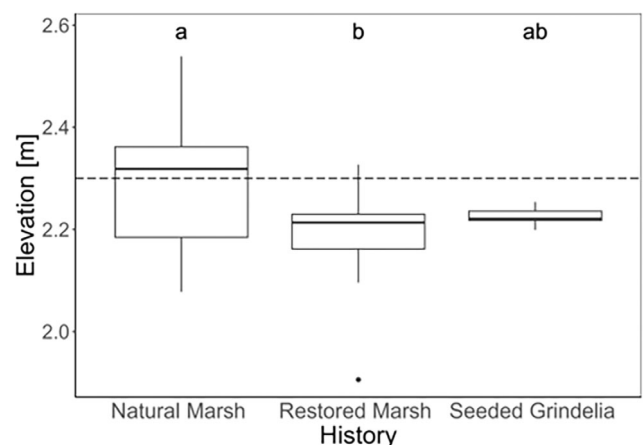


Figure 6. Elevation ranges of lowest growing *Grindelia* differed significantly by management history. Significance comparisons represent pairwise comparisons determined using Dunn tests, pulled from the results of a Kruskal–Wallis test of differences in elevation range between management histories (H -statistic = 11.80, $df = 2$, $p = 0.0027$). The dashed line represents the king tide line at Hester Marsh (Tanner et al. 2023).

Table 1. The elevation of the lowest growing *Grindelia* in different marshes in California. Z^* was calculated using the formula (field measurement – mean tide level)/(mean higher high water – mean tide level), with all four measurements provided in NAVD88. On this scale, mean tide level is 0 and mean higher high water is 1.

Source	Location, Region	Longitude	Latitude	Lowest <i>Grindelia</i> Elevation	
				(NAVD88)	Z^*
Thorne (2015)	Humboldt Bay	–124.15	40.86	1.91	0.98
Eicher (1987)	Humboldt Bay	–124.15	40.86	2.26	1.30
Rankin et al. (2023)	Gambinini Marsh, San Pablo Bay	–122.58	38.21	1.69	0.70
J. Collins—personal communication	Petaluma Marsh, San Pablo Bay	–122.56	38.20	2.00	1.10
Rankin et al. (2023)	Petaluma Marsh, San Pablo Bay	–122.55	38.19	1.72	0.77
Rankin et al. (2023)	Raccoon Island, San Pablo Bay	–122.32	38.19	1.69	0.73
Rankin et al. (2023)	Rush Ranch, Suisun Bay	–122.02	38.19	1.86	0.89
Rankin et al. (2023)	Sonoma Creek, San Pablo Bay	–122.41	38.14	1.82	0.96
Rankin et al. (2023)	Black John Marsh, San Pablo Bay	–122.52	38.13	1.53	0.55
Rankin et al. (2023)	Strip Marsh, San Pablo Bay	–122.35	38.13	1.77	0.91
Rankin et al. (2023)	Sonoma Bay, San Pablo Bay	–122.47	38.12	1.52	0.59
Rankin et al. (2023)	Tolay/Tolay Creek San Pablo Bay	–122.44	38.12	1.38	0.42
Rankin et al. (2023)	Martinez, Suisun Bay	–122.14	38.02	1.65	0.64
J. Collins—personal communication	China Camp, San Pablo Bay	–122.49	38.01	1.93	1.11
Rankin et al. (2023)	China Camp, San Pablo Bay	–122.49	38.01	1.51	0.53
Rankin et al. (2023)	Corte Madera, Central SF Bay	–122.51	37.93	1.62	0.71
Thorne (2015)	Bolinas Bay	–122.68	37.92	1.73	1.12
Rankin et al. (2023)	Audubon West/Dumbarton Marsh, South SF Bay	–122.10	37.51	2.17	0.99
Rankin et al. (2023)	Laumeister, South SF Bay	–122.12	37.47	1.15	–0.05
Orlando et al. (2005)	Palo Alto Baylands, South SF Bay	–122.11	37.46	2.00	0.86
This paper	Hester Marsh, Elkhorn Slough	–121.76	36.81	2.20	1.69

Most tidal marsh restoration has focused on the low marsh, often a monoculture of one or two species. However, rarer species that are limited to the marsh-upland ecotone also merit attention. Environmental gradients are very steep as the high marsh slopes to upland, for example, in our system transitioning from saline to fresh soil salinity in just a few horizontal meters. Our study illustrates the value of surveying the elevational distribution of ecotone species and physical stressors that may limit it, which allows practitioners to focus restoration efforts in the zone where success is most likely. Our experiments also show the value of pilot transplanting across elevations to ensure the zone with best survival and growth at the restoration site is identified. Pilot experiments can also help practitioners determine whether facilitation (e.g. using nurse plants) or soil amendments (e.g. adding organic-rich soil) may decrease the stressors at the edge of the tolerance zone of the marsh-upland ecotone. Thus, our investigation provides a model of how restoration science and experiments can enhance the success of species living in the sharp environmental gradients of ecotones.

Facilitation Along a Stress Gradient

Positive interactions among plants are powerful in many systems (Stachowicz 2001), and facilitation can help restoration success in harsh environments (Silliman et al. 2015; Derksen-Hooijberg et al. 2018). In salt marshes, previous studies have found a facilitation effect through predator and heat stress protection, shading, sediment deposition, and oxygenation (Bertness 1984; Bertness & Shumway 1993; Silliman et al. 2015; Bilkovic et al. 2017). The

stress gradient hypothesis predicts positive interactions in stressful conditions and negative interactions in less stressful ones (Bertness & Callaway 1994). Facilitation has successfully increased low marsh restoration success on the American and European Atlantic coasts (Silliman et al. 2015; Derksen-Hooijberg et al. 2018). However, results are mixed in California high marshes, with examples of facilitation, competition, and alterations in the direction of species interactions depending on the combinations of plants present (Pennings & Callaway 1992; Callaway & Pennings 2000). *Grindelia* specifically has had mixed results in the high marsh in previous studies, with *Frankeniania salina* and *Jaumea carnosa* having a positive impact on *Grindelia* success and *Salicornia pacifica* and *Spartina foliosa* having a negative impact in the San Francisco Bay Estuary (Lewis & Thornton 2013). While competition in the high marsh has been confirmed in Elkhorn Slough, where intraspecific competition outweighs intraspecific facilitation (Tanner et al. 2023, 2025), potential for facilitation has also been found with enhanced soil water potentials around *Frankeniania salina* and *Jaumea carnosa* transplants (Tanner et al. 2023) and reduction of soil temperatures and porewater salinity by *Salicornia* (Whitcraft & Levin 2007).

Unlike prior studies (Lewis & Thornton 2013), we found that *Salicornia* facilitates *Grindelia* establishment and survival in the high marsh. Facilitation effects were strong and represent the first demonstration that pickleweed can serve as a nurse plant for *Grindelia*. *Salicornia* may shade *Grindelia*, preventing desiccation and mitigating high temperatures, or shelter *Grindelia* from wave and wind impacts, both of which are established facilitation mechanisms in other plant communities

(Callaway 2007). The discrepancy between our results of *Salicornia* facilitation and prior results of *Salicornia* competition (Lewis & Thornton 2013) may be explained by position in the ecotone. At higher elevations above the ecotone, *Grindelia* appeared to be out-competed by upland neighbors in our elevation experiment. We further observed *Grindelia* extending to higher elevations in areas of the restoration site where sediment had been scraped from the hillside, removing competitors. We therefore hypothesize that neighbors may facilitate *Grindelia* at the lower end of its distribution in the high marsh, where physiological conditions are more stressful. This finding of facilitation at the lower, more physically stressful end of *Grindelia*'s elevational range but competition at the higher end supports the stress gradient hypothesis.

Our finding demonstrates that facilitation can be incorporated into the design of salt marsh ecotone restoration, and that *Salicornia* can be used to establish *Grindelia* near its seaward tolerance limit in California salt marshes. But facilitation can only mitigate stress up to a point—at the lowest elevation we tested, all *Grindelia* transplants died regardless of whether they had neighbors. Additionally, while we found evidence for *Salicornia* facilitation, other studies show that it can compete with subordinates (Noto & Shurin 2017). On-the-ground, site-specific, pre-implementation studies should be conducted to inform local restoration approaches, particularly those involving species interactions.

Soil Amendment

Hester Marsh had highly compacted soils following construction (Thomsen et al. 2022), and while soils were de-compacted in the planting process, the ambient soil likely recompacted due to rain and overtopping more so than the larger grained potting soil. Ambient soil had lower nutrients and lower organic matter (~2–4% in our samples) than the potting soil. Nevertheless, we found no evidence that soil amendment improved the success of our *Grindelia* transplants at Hester Marsh in any experiment or at any elevation despite harsh soil conditions and organic matter lower than experienced by naturally growing *Grindelia* in Yampah Marsh. Perhaps salinity and moisture were the main driving factors for plant success and outweighed any potential benefits from soil amendment. These results indicate that soil amendment is not a worthwhile management strategy for restoration of this ecotone specialist even in restoration projects where soils are low in nutrients and organics.

Physical Stress Along an Elevation Gradient

Ecotones occur along steep environmental gradients (Risser 1993). In the salt marsh-upland ecotone, stress comes from the frequency and duration of tidal inundation, which impacts both moisture and salinity (Cui et al. 2011), and can be predicted by elevation. Knowing elevation tolerances is therefore a key first step towards informed restoration (Callaway 2005). The presence of a clear ecotone in California salt marshes with variations in abiotic and biotic factors is known (Zedler & Cox 1984; James & Zedler 2000; Traut 2005), but generally less is known about the tolerances of marsh-upland

biota (Janousek et al. 2019). A seaward limit preventing expansion into the low marsh has been confirmed for other ecotone species in this system (Janousek & Mayo 2013).

We found that elevation is a very strong predictor of *Grindelia* distribution and identified the contour line of its lower limit at around 2.2 m NAVD 88, near the landward boundary of the salt marsh, close to the king tide level. This limit is similar between natural and restored marshes and between *Grindelia* established from wild recruitment of seeds, from seeds sown for restoration, and from greenhouse-grown transplants. Older established populations in the natural marsh were found slightly higher than those at the restoration site, perhaps because the restoration site had not yet been impacted by rare, unusually high king tides that only occur on a decadal scale. Elevation could explain the discrepancy between the channel and creek transplants—channel transplants were at a slightly higher elevation, putting them high enough to avoid about half of the inundation events that affected the creek transplants (Tanner et al. 2023).

While tolerant of high salinities, *Grindelia* requires a salinity lower than 23 ppt to germinate and is impacted by inundation, indicating a low elevation limit preventing expansion into the lower salt marsh (Wayne 1995; Janousek & Mayo 2013; Lewis & Thornton 2013). Our results imply that salinity could be the mechanism inhibiting *Grindelia* growth at lower elevations. The seaward boundary of *Grindelia* at Elkhorn Slough appears to be higher than other estuaries in northern California. As the most southern site of those examined, Elkhorn Slough receives less rain, and the estuary has a very strong marine influence due to an artificial harbor mouth—Elkhorn Slough has very saline salt marsh communities relative to some Bay area marshes (Watson et al. 2011). These saline marsh soils may limit marshward expansion of *Grindelia*. Important to note here is the variety of subspecies of *Grindelia stricta*. Different subspecies, like the *var. angustifolia* common in the San Francisco Bay area tidal marshes, may have different salinity tolerances, which could explain some discrepancies seen between estuaries. Subspecies are challenging to identify and are inconsistently listed in field data, so this hypothesis could not be confirmed. The differences in elevational distribution of this ecotone specialist, and potential differences depending on subspecies, highlight the importance of local data in successful ecotone restoration.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Facilitation and soil amendment experiment Cox proportional hazard results.

Table S2. Summary of levee Cox proportional hazard results.

Table S3. Elevation and soil amendment experiment GLMMs.

Table S4. Summary of pairwise comparisons from elevation and soil amendment experiment Cox model.

Table S5. Summary of pairwise comparisons from elevation and soil amendment experiment plant height GLMM.

Table S6. Summary of pairwise comparisons from elevation and soil amendment experiment percent green GLMM.

Table S7. Exact values from Figure S2.

Figure S1. Survival over time in the elevation and soil amendment experiment.

Figure S2. Elevations of *Grindelia* planted/surveyed at each location for comparison.

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