Summer 2020

Integrating Field Methods, Remote Sensing and Modeling to Monitor Climate-Adapted Tidal Marsh Restoration

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INTEGRATING FIELD METHODS, REMOTE SENSING AND MODELING TO MONITOR CLIMATE-ADAPTED TIDAL MARSH RESTORATION

A Thesis Presented to the Faculty of the
Department of Applied Environmental Science
California State University Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Environmental Science

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by
Alexandra S. Thomsen
Summer 2020

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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ABSTRACT

Integrating Field Methods, Remote Sensing and Modeling to
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by
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Master of Science in Environmental Science
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Sea level rise threatens coastal wetlands worldwide. In response, wetland restoration projects are implementing strategies that decrease vulnerability to this threat. Vegetation monitoring at sites employing new restoration strategies, including determination of appropriate and efficient monitoring techniques, is critical to improve understanding of factors leading to restoration success and maximize benefits of future projects. In Central California, sediment addition raised a degraded marsh plain to a high elevation expected to be resilient to sea level rise over the next century. We conducted area searches of plant survival and modeled effects of nine predictors on new vegetation cover using two monitoring strategies: 1) transect surveys, and 2) unmanned aircraft systems (UAS) imagery. We conducted targeted sediment sampling to examine additional chemical or physical sediment properties contributing to vegetation patterns. Limited vegetation survived sediment addition, likely due to the thickness and placement method. Cover reached 8-14% in the initially-bare area after one year. Elevation and inundation frequency were particularly critical to understanding restoration success, with greatest cover in high-elevation areas tidally-inundated < 0.85% of the time. Sediment analysis suggested greater salinity stress and ammonia levels in poorly-vegetated compared to well-vegetated areas at the same elevation, which may be driven by variation in physical sediment properties. Similar modeling results indicate both transect and UAS methods were suitable for monitoring this site. Field transects may provide the best approach for tracking vegetation colonization if resources are limited, but UAS can complement this to provide landscape perspective.

ACKNOWLEDGEMENTS

I would like to thank my committee members for their support and guidance throughout my thesis research. Dr. Arlene Haffa’s flexibility and unwavering support have made my accomplishments as a graduate student possible. Dr. Suzanne Worcester provided valuable perspective on how to make my research and presentations as strong and clear as possible. I would not be here without Dr. Kerstin Wasson, whose early support set me on this path of marsh restoration research, whose mentorship has helped me build confidence, and who inspires me to continuously strive to be a better researcher.

I would also like to thank the Elkhorn Slough National Estuarine Research Reserve (ESNERR) for taking me in as part of the team, and for providing data, advice, input on research questions, and more: Charlie Endris, John Haskins, Alex Lapides, Andrea Woolfolk, Monique Fountain, and Dr. Rikke Jeppesen. Thank you to non-ESNERR collaborators for their contributions as well: Dr. Karen Tanner (who assisted with vegetation data collection and provided additional mentorship), Dr. Elizabeth Watson, Johannes Krause (who collected field conductivity/salinity data), Monica Appiano (who assisted with field sediment sampling and conducted a set of sediment analyses), and Dr. Ivano Aiello. I’m very grateful to the NOAA Center for Coastal and Marine Ecosystems at CSUMB for funding this work, and to Drs. Corey Garza and Laura Good for helping me navigate the fellowship. I also want to thank the CSUMB Environmental Science program: particularly Drs. John Olson and Fred Watson for enabling me to refine aspects of this research through their courses and for providing additional advising outside of class, and my fellow graduate students Ruby Kwan-Davis and Jazmine Mejia-Muñoz for assessing different image classification methods with me.

This publication was made possible by the *National Oceanic and Atmospheric Administration, Office of Education Educational Partnership Program award* (NA16SEC4810009). Its contents are solely the responsibility of the award recipient and do not necessarily represent the official views of the *U.S. Department of Commerce, National Oceanic and Atmospheric Administration*.

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CHAPTER 1 – INTRODUCTION

Salt marshes and other wetlands provide numerous benefits to wildlife and humans (Barbier et al. 2011; Mitsch et al. 2015), yet over 50% of global wetland area has been lost in the past century and future losses are anticipated due to threats such as sea level rise, diminished sediment inputs, and eutrophication (Deegan et al. 2012; Kirwan et al. 2013; Weston 2014; Watson et al. 2017; Li et al. 2018). Some areas, including parts of China, the Netherlands, and the U.S., have had particularly substantial marsh and wetland area loss, primarily due to diking and draining for land reclamation (Li et al. 2018). Many human benefits are lost as marsh area declines, including buffering from flooding, biodiversity support for fisheries and tourism, and carbon sequestration (Barbier et al. 2011). In order to reverse the historical trend of marsh loss and maintain the value of these areas for their ecosystem functions and services, the number and scale of restoration projects has been increasing in recent decades, and new techniques are being tested.

Marshes occupy a narrow vertical range in the intertidal zone, between about Mean High Water to the king tide line (Larson 2001). Reduced riverine sediment supplies and subsidence due to groundwater overdraft or diking have resulted in marsh elevation loss relative to sea level (Kennish 2001). In combination with these other impacts, accelerating sea level rise further decreases the relative elevation of marshes, making them vulnerable to drowning (Kirwan et al. 2013). Sediment placement on degrading marshes is a restoration technique intended to build the “elevation capital” of marshes to increase their resilience to sea level rise (Mendelssohn and Kuhn 2003; Cahoon et al. 2019). These projects have typically used thin applications of sediment to allow for survival and vertical growth of marsh vegetation through the added sediment, with new colonization by seed supplementing growth of surviving vegetation to restore marsh cover (Raposa et al. 2020). Utilizing a thick layer of sediment addition on highly degraded and subsided marshes is relatively novel, and redevelopment of vegetation cover will likely rely more on colonization by seed than on vegetation survival (Mendelssohn and Kuhn 2003)

Monitoring of restoration sites is essential to improve understanding of the criteria that make marsh restoration successful and inform planning for future projects (Williams and Faber 2001). Vegetation cover is typically used as a metric for monitoring restoration progress, as this represents establishment of the foundation species that other marsh species depend on. Monitoring of natural vegetation establishment is particularly critical at restoration sites designed at high elevation using sediment addition due to the relative novelty of this approach at large scales and in marshes not dominated by *Spartina* (Mendelssohn and Kuhn 2003; La Peyre et al. 2009). Innovative methods, such as using imagery collected by unmanned aircraft systems (UAS), are also being examined to help researchers keep up with an increasing scale and frequency of restoration projects and often-limited monitoring budgets and staff (Shuman and Ambrose 2003; Callaway et al. 2011). Remote sensing methods like UAS may be advantageous over traditional field survey methods, like transect sampling, because they minimize trampling of newly established vegetation and can cover large areas in a short period of time (Shuman and Ambrose 2003; Tuxen et al. 2008). While UAS monitoring of wetland restoration is an emerging trend (Chabot and Bird 2013), its utility in monitoring and understanding early vegetation colonization at restoration sites requires further study.

Both biotic and abiotic factors are known to influence marsh vegetation. Biotic factors are not expected to be major drivers of colonization at restoration sites that lack existing vegetation and animals, though competition, facilitation, and herbivory have been found to influence distribution of halophytes in marshes (Bakker et al. 1993; Ungar 1998; Noe and Zedler 2001a; Jefferies et al. 2006; Bertness et al. 2014; Alberti et al. 2015). Many abiotic factors can influence marsh vegetation distribution by influencing (1) tidally-dispersed seed delivery, and (2) seed germination and seedling survival.

Tidal inundation is linked to both seed delivery and the abiotic stressors that influence seedling germination and survival. Seed delivery in coastal marshes is mainly influenced by the tides, which transport seeds from nearby established marshes in the water and attached to wrack (Huiskes et al. 1995; Morzaria-Luna and Zedler 2007). Temporal variation can affect seed delivery and resulting colonization patterns, as seed release varies seasonally (Thompson et al. 1979; Mayer 1987). King tides during times of high seed availability may be particularly important in setting the upper marsh boundary. In addition to a lack of seed delivery, low moisture in areas above the king tide line can inhibit seed germination (Noe and Zedler 2000). In low-elevation, frequently-inundated areas (below Mean High Water), vegetation growth may be suppressed by excessive waterlogging (Mahall and Park 1976). Therefore, inundation can help us understand both the landward and seaward boundaries of marsh vegetation and the overall patterns of new colonization.

Tidal creek network structure, including distance to tidal creeks and the size of nearby creeks, influences marsh species distributions, likely due to the influence of creeks on soil conditions (Zedler et al. 1999; Sanderson et al. 2001). Creek proximity has been associated with improved plant growth, potentially due to flushing of salts and other toxins from the soil (Schile et al. 2011). High salinity is likely to suppress marsh plant establishment by limiting seed germination and seedling survival (Shumway and Bertness 1992; Noe and Zedler 2000; Noe and Zedler 2001a; Woo and Takekawa 2012). Additional factors related to sediment addition can also affect marsh plant survival and colonization. Plants can survive both natural and human-placed sediment addition, but may not survive high levels of sediment addition (Stagg and Mendelssohn 2010; Walters and Kirwan 2016). Properties of the added sediment, like grain size, can impact new colonization by influencing physical and chemical parameters including moisture, salinity, and nutrient concentrations (Reimold et al. 1978; Wigand et al. 2016).

Recently, a major project was undertaken in Elkhorn Slough, an estuary in Central California, to restore a formerly diked and degraded salt marsh using substantial sediment addition to create a high-elevation marsh plain. Limited vegetation was present before construction of the restoration site, and one area of interest was whether some of it would survive sediment addition. However, the major focus was on examining new colonization via seeds. The unusually high elevation of the new site (mostly above Mean Higher High Water) made expectations for natural colonization uncertain. How would the rate of colonization compare with similar sediment addition projects? Would any species other than the marsh dominant, *Salicornia pacifica* (perennial pickleweed), colonize the site? What factors are associated with natural colonization, and how can knowledge of these factors inform future projects? The initially-bare state and lack of seed bank at this site provide a unique opportunity to study these questions. We used a combination of data collected through area searches, transect-based field surveys, UAS monitoring, and targeted sediment sampling to assess restoration progress and evaluate the potential factors influencing early marsh vegetation colonization. We expected that vegetation development would depend on factors related to elevation and inundation, tidal creek influence, the sediment addition process, and sediment properties.

Overall, our goal was to improve understanding of the fate of vegetation following large-scale sediment addition and the process of natural colonization by new vegetation at a high marsh restoration site, which may become a more common restoration technique in the future as managers consider sea level rise in project planning. Evaluation of the important drivers of natural colonization will reveal the types of areas most easily colonized by new vegetation and potential stressors inhibiting colonization, informing adaptive management and planning of future restoration sites. Comparison of field- and UAS-based methods will inform future monitoring and analysis. The lessons learned from this project about vegetation colonization and monitoring methodology can be applied to future marsh restoration projects in many different regions, by indicating the most important factors to consider when designing high marsh restoration projects and the relative benefits of different monitoring strategies.

CHAPTER 2 – METHODS

SITE DESCRIPTION

We conducted this research at a recently restored 25-hectare marsh in Elkhorn Slough (Fig. 1). Located in Monterey Bay in Central California, Elkhorn Slough is one of California's largest estuaries and harbors the state's largest salt marsh area south of San Francisco Bay. Marsh vegetation in the Slough supports hundreds of species of wildlife, stores carbon, and filters water, yet many of these valuable marshes have been converted for agriculture or other development. Historical marsh loss in Elkhorn Slough has paralleled the global decline, with approximately 50% of vegetated marsh area lost in the past 150 years (Van Dyke and Wasson 2005). Much of the remaining vegetated marsh area may drown due to sea level rise in the next century, and is also vulnerable to additional stressors like eutrophication (Wasson et al. 2012; Wasson et al. 2017).

The Elkhorn Slough National Estuarine Research Reserve (ESNERR) launched an ecosystem-based management initiative in 2004 to engage stakeholders and decision-makers in strategic planning for the estuary, which resulted in prioritization of salt marsh restoration (Wasson et al. 2015). ESNERR's Hester Marsh project is restoring 19 hectares of degraded marsh that had been diked and farmed, then subsided and degraded to mudflat. Upland grading of former agricultural land added six hectares of new marsh area and will facilitate upland migration in response to anticipated sea level rise. This project involved substantial sediment addition followed by reconstruction of historical tidal creeks to raise the marsh plain by an average of 69 cm to an elevation that would be resilient to sea level rise for at least 100 years. Between December 2017 and August 2018, approximately 176,000 cubic meters of sediment were moved in order to restore the formerly degraded marsh, and create additional marsh area, at a target elevation of 1.89 m NAVD88 (Fountain et al. 2019). Because of variation in elevation across the landscape prior to restoration (e.g. high berms, low mudflats and basins) the amount of sediment addition varied across the site, and some high areas had sediment removed ("scraped"), rather than added, to meet the target marsh elevation. The sediment added to the degraded marsh was a combination of dredge material from the Pajaro River Bench Excavation Project and upland soil from former farmland on an adjacent hillside (Fountain et al. 2019). Placement of sediment from these sources resulted in a new site that lacked a seed bank and was virtually bare when it was opened to tidal exchange in August 2018. Six blocks were actively planted on the western side of the site (Appendix C), and were excluded from analyses of natural colonization (Fig. 1).

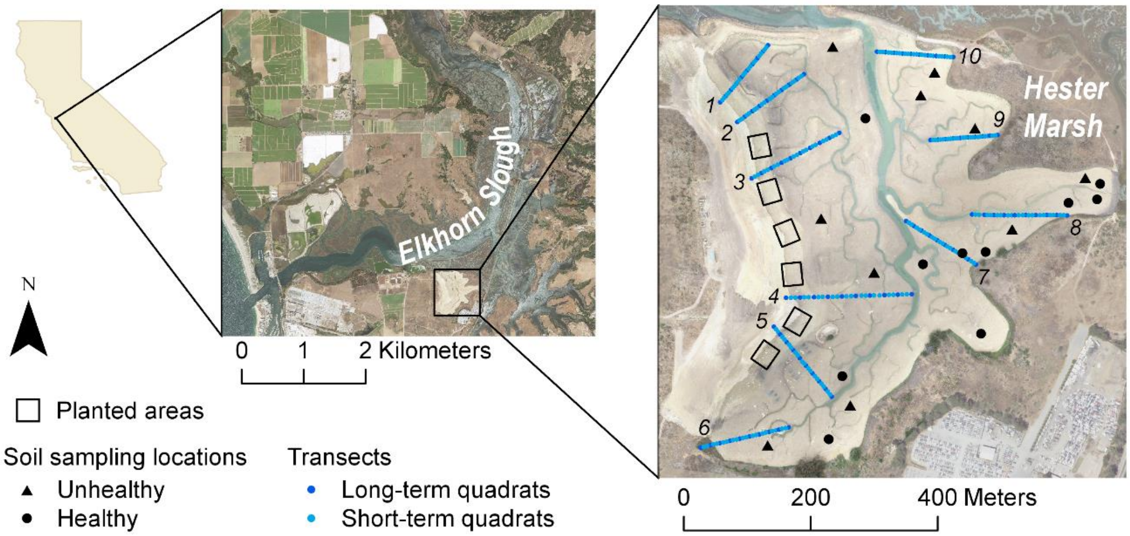

Figure 1. Geographic location and site map of Hester Marsh, located on the southern side of Elkhorn Slough in Central California, USA. Vegetation metrics, elevation, and salinity were examined in quadrats along 10 transects at Hester. Each transect has 28 evenly spaced quadrats, 18 of which are for short-term monitoring and 10 of which will be monitored for several decades. Active planting experiments occurred in six blocks on the western side, which were excluded from natural colonization analyses. Sediment sampling was carried out at 10 well-vegetated and 10 poorly-vegetated sites across the marsh to identify additional factors that may be influencing vegetation colonization and growth.

ESTIMATING HISTORICAL VEGETATED AREA

To quantify baseline conditions at the restoration site, we estimated vegetated marsh cover based on earliest available aerial imagery and recent UAS imagery prior to restoration. We digitized georeferenced aerial imagery from 1931 in ArcGIS software as vegetated marsh, unvegetated mudflat/basin, and tidal creeks (pixel size = 0.63 m, collected by Western Gulf Oil Co., part of the Fairchild Aerial Surveys, Inc. collection). We calculated the "historical vegetated area" as the vegetated area in 1931 within the restoration project footprint, which was the area below an elevation of 2.3 m NAVD88 in August 2018 according to a UAS-derived digital elevation model (DEM). We also digitized georeferenced UAS imagery from October 2015 in ArcGIS software as vegetated marsh, unvegetated mudflat/basin, tidal creeks, vegetated berms, grassland, and other unvegetated areas which included berms and roads. We calculated the vegetated area prior to restoration as the area in 2015 that had marsh vegetation (including vegetated berms) within the restoration project footprint. To estimate the vegetated area when the restored marsh plain is fully vegetated, we used the restoration project footprint area excluding tidal creeks.

INITIAL AREA SEARCHES OF SURVIVING MARSH VEGETATION

To examine plant survival following construction, we conducted area searches of the site in Fall 2018 (between October 10 and November 13). We surveyed only the sediment addition/removal area during these area searches rather than the entire project footprint, which includes historically-existing marsh vegetation on the eastern and southern edges that was not buried or scraped. To quantify the historically-existing marsh vegetation on the edges, we digitized this area from UAS imagery collected in August 2018. During area surveys of the sediment addition/removal area, we logged points where we found plants on the marsh plain using a handheld GPS (Trimble Juno 3B, Trimble Inc., Sunnyvale, CA), with each point representing the approximate number of plants for each species found within a 1-m diameter area. We did not include vegetation on tidal creek banks because some surveys occurred during high tides, when creeks were filled with water. Creek bank vegetation did not appear to be a major component of surviving vegetation.

To calculate cover of surviving vegetation found during area searches in the sediment addition/removal area, we multiplied the estimated number of individuals of each species by the approximate size of an individual of that species. Based on ground truthing during field surveys, we assumed an area of 64 cm^2 for each *Distichlis* individual, 100 cm^2 for *Jaumea* and *Frankenia*, 225 cm^2 for *Salicornia* and *Spergularia*, and 400 cm^2 for unidentified weeds. While it was difficult to distinguish whether plants in one location were many small individuals or one large one, these approximate area estimates were used in the field to determine the number of individuals to log at each location. We estimated the total vegetated marsh area in 2018 as the sum of this surviving vegetation cover and the digitized historically-existing vegetation on site edges.

To evaluate conditions under which marsh vegetation survived, we examined these points in relation to the digitized 2015 imagery showing where vegetation existed before construction and an elevation change raster showing the amount of sediment added or removed during construction (calculated by subtracting a pre-construction, October 2015 DEM from a post-construction, August 2018 DEM). If vegetation was present in areas that were vegetated in 2015 imagery and that had positive elevation change, we assumed the plants survived sediment addition. If vegetation was present in areas of elevation loss that were vegetated in 2015, we assumed the plants survived scraping (sediment removal which was undertaken to incorporate formerly high areas like berms into the restored marsh). If vegetation was present near (within five meters of) those formerly vegetated and scraped areas, we considered those plants as potentially originating from the scraped sediment. Plants that did not meet these criteria were included in estimated numbers and cover of initial vegetation, but their mechanism of survival is unknown. Weeds were included in these initial estimates, but were not assumed to be survivors. We are fairly certain that the native marsh plants we found were survivors and not new colonists, because these species do not typically germinate until the winter (Mayer 1987, Noe and Zedler 2001b).

TRANSECT MONITORING OF VEGETATION COLONIZATION

We monitored vegetation, elevation, and associated parameters over time along 10 permanent transects established by ESNERR. These transects were spread fairly evenly across the restoration footprint, though they were limited to areas that could be traversed on foot without crossing tidal creeks (Fig 1). Transect length ranged from 117 m to 198 m. Each transect had 10 quadrats spread uniformly from the seaward marsh boundary at the edge of a tidal creek to the landward marsh boundary approximately at king tide elevation. These 100 quadrat locations were marked with PVC or conduit pipe as fixed points at which ESNERR will track long-term changes for the next several decades. The landward end of five of the transects started in historically-existing marsh vegetation that was not scraped or buried during construction.

This research examines the first 12 months of data collected approximately quarterly at these transects (August 2018, October 2018, April 2019, August 2019). Because cover of new plants was initially so low, we added two evenly spaced temporary quadrats between each of the long-term ones, resulting in 28 quadrats per transect (280 total quadrats) monitored in April and August 2019. We monitored vegetation cover for each encountered species at all quadrats. For the long-term quadrats, we also measured canopy height of *Salicornia* (the dominant vegetation), elevation, and salinity.

We measured vegetation cover at each quadrat using a 50 cm by 50 cm PVC frame, elevated off the ground to prevent damage to marsh vegetation. The quadrat frame had a grid of strings running across it, creating 16 intercepts where the strings cross. At each intercept, we dropped a metal rod and recorded all vegetation species that touched the rod. If no living plant touched the intercept rod, the intercept was recorded as "bare." We calculated percent cover for a given species within each quadrat as the number of intercepts where that species was recorded divided by the total number of intercepts, multiplied by 100. This had the potential to result in percent cover exceeding 100% when calculated for multiple vegetation species combined, which represents canopy layering by the different species. We collected canopy height data for *Salicornia* in each quadrat by measuring the tallest stem within a 10 cm radius at each of three marked intercepts. We estimated *Salicornia* biomass for each quadrat by multiplying the average of the three canopy heights by percent cover of *Salicornia*.

We monitored elevation at the 100 long-term quadrats during each of the quarterly vegetation surveys except October 2018, and at all 280 long-term and temporary quadrats in August 2019. We used RTK GPS (EOS Arrow 200 with ArcGIS Collector) to establish baseline elevations of the long-term quadrats in August 2018, and a combination of Terrestrial Laser Scanning (TLS) and laser leveling (using a Sprinter 150) for later elevation surveys. All elevations are reported in meters referenced to the North American Vertical Datum of 1988 (NAVD88). We calculated salinity based on apparent conductivity measurements at all 280 long-term and temporary quadrats at the end of the dry season in September 2019. We collected field measurements of apparent conductivity using a Geonics Model EM38 MK2 Conductivity Meter (Geonics Ltd., Mississauga, Ontario, Canada) and recorded the readings on a handheld GPS (Garmin GPSMAP 64ST, Garmin Ltd., Olathe, KS). We used a calibration function derived from 22 soil samples collected at the time of the conductivity survey to model salinity at each quadrat based on apparent conductivity (Krause 2020).

We examined nine potential factors influencing native marsh vegetation cover during the first growing season using August 2019 transect data (Table 1). Values for these predictors were derived from field and unmanned aircraft systems (UAS) surveys, including digital elevation models (DEMs) and imagery. We used random forest modeling to examine these variables due to the strength of this regression tree method in modeling many different predictors and complex, nonlinear relationships (Cutler et al. 2007). We performed modeling using the *randomForest* package (v. 4.6-14; Liaw and Wiener 2002) in R software (v. 3.5.1, R Core Team 2018; number of trees = 1500, apply correction bias, other parameters left at defaults). To reduce the number of variables to examine and discuss further, we started by running a full model with all nine predictors and then removed one variable at a time, starting with the least important, and evaluated model performance based on out-of-bag data at each iteration. We excluded variables when their inclusion did not increase the percentage of variance explained by the model. We report the importance of individual variables in the final vegetation cover model as the percentage increase in Mean Squared Error (MSE), which represents reduction in model performance, when the values of the predictor are randomly permuted (Cutler et al. 2007).

Table 1. Predictors examined in transect and site-wide UAS analyses of vegetation cover.

Variable	Source for transect analysis	Source for site-wide UAS analysis
Elevation post-restoration (m)	Measured using TLS/laser leveling in August 2019	August 2018 DEM (pixel size = 3.3 cm)
Inundation (% time)	Calculated using ESNERR Vierra Marsh tide data (Aug 2018-May 2019) and field-measured elevation	Calculated using ESNERR Vierra Marsh tide data (Aug 2018-May 2019) and May 2019 DEM (pixel size = 3.3 cm)
Elevation change over first year of restoration (m)	Calculated by subtracting August 2018 DEM from May 2019 DEM (pixel size = 3.3 cm)	Calculated by subtracting August 2018 DEM from May 2019 DEM (pixel size = 3.3 cm)
Salinity (ppm)	Calibrated from apparent conductivity readings and soil samples (Sept 2019)	Modeled using *Forest-Based Regression* in ArcGIS (pixel size = 3.3 cm)
Creek distance (m)	Calculated using *Euclidean Distance* from polygon feature	Calculated using *Euclidean Distance* from polygon feature (pixel size = 25 cm)
Sediment source (categorical)	Digitized from mid-construction UAS imagery (Feb 2018)	Digitized from mid-construction UAS imagery (Feb 2018)
Sediment addition/removal (categorical)	Categorical elevation change raster (Oct 2015 DEM subtracted from Aug 2018 DEM)	Categorical elevation change raster (Oct 2015 DEM subtracted from Aug 2018 DEM)
Elevation pre-restoration (m)	Oct 2015 DEM (pixel size = 6 cm)	Oct 2015 DEM (pixel size = 6 cm)
Former habitat type (categorical)	Digitized 2015 habitat map	Digitized 2015 habitat map

CHARACTERIZATION OF INUNDATION ACROSS ELEVATIONS

To understand how inundation varies across the different elevations at Hester Marsh and influences vegetation patterns, we used ESNERR's permanent water quality monitoring sonde at nearby Vierra Marsh, leveled in to NAVD88, to track water levels every 15 minutes from August 2018 to May 2019. Tide ranges and timing are nearly identical throughout the Elkhorn Slough estuary due to strong tidal forcing, so data from this nearby station was expected to be accurate for Hester Marsh. We confirmed the accuracy by monitoring the areas inundated on several high tides (both in the field and in UAS imagery), determining the elevation ranges of the inundated areas using digital elevation models (DEMs), and comparing the inundated elevations with the Vierra tide data. We calculated percent time inundated as total hours a given elevation was inundated divided by total hours recorded by the sonde, multiplied by 100.

To evaluate the influence of tides on the upper marsh boundary, we identified the most landward *Salicornia* plant near the top of each of the five initially-bare western transects and the five southern and eastern transects that started in historically-existing vegetation. We estimated the elevation of each of these plants using an August 2019 DEM, and compared the *Salicornia* elevations with tide levels to examine whether the upper marsh boundary differs between new and historically-existing vegetation. Based on the tidal dispersal mechanism of seeds (Huiskes et al. 1995; Morzaria-Luna and Zedler 2007) and seasonal variation in seed abundance (Mayer 1987), we identified the "main seed dispersal area" as all elevations below the highest tide level that occurred between October 2018 and March 2019. We predicted that new marsh colonization would be limited to this main seed dispersal area. We expected that if the highest tide during this seed dispersal period was lower than historical king tides, the upper elevational limit of newly-colonized *Salicornia* would be lower than that of historically-existing *Salicornia*.

SITE-WIDE UAS MONITORING OF VEGETATION COLONIZATION

We monitored vegetation development and elevation changes for the first year of restoration approximately monthly using unmanned aircraft systems (UAS) imagery. We analyzed factors influencing vegetation presence based on high-resolution imagery collected in October 2019, at the end of the first growing season. We operated a DJI Phantom 4 Pro quadcopter drone (SZ DJI Technology Co., Ltd., Shenzhen, China) to collect red, green, and blue (RGB) data with a 20 megapixel camera and near infrared (NIR) and red-edge data with a Sentera Double 4k sensor (Sentera Inc., Minneapolis, MN). We analyzed vegetation in October 2019 imagery using only RGB data due to incomplete NIR coverage, which seemed sufficient for detecting plants due to the high resolution of the RGB imagery (pixel size = 0.79 cm). We collected October imagery under clear conditions, at a flight altitude of 30 m, with 75% frontal and 70% side overlap. We selected this flight altitude as a balance between image resolution (0.79 cm) and flight time (2.5 hours) based on prior experimentation at the site. A total of 50 white, 30-cm round bucket lids were anchored to the marsh plain as ground control points (GCPs) for drone data processing. GCPs were surveyed similarly to quadrat locations, using RTK GPS for an initial August 2018 survey to establish baseline positions and elevations and TLS/laser leveling for later surveys. We used DroneDeploy for flight planning and Agisoft Metashape and Sentera FieldAgent platforms for processing orthomosaics and DEMs (RMSE of DEM vertical accuracy was approximately 3 cm).

We created a classified image of vegetated and unvegetated areas using October 2019 imagery in ArcGIS software (v. 10.7, ESRI 2019) and used this classified image to determine total vegetated area in 2019 and percent vegetation cover in 1-m^2 cells. We used stratified random sampling to randomly sample low-cover and high-cover cells for site-wide modeling of factors influencing vegetation cover, using the average nearest neighbor index to determine a number of randomly sampled cells that minimizes autocorrelation.

We compared two supervised classification methods: a pixel-based approach with a maximum likelihood classifier and an object-based approach with a support vector machine classifier. For both classifications, we initially used three classes, then merged the two unvegetated classes together to achieve an image of vegetation presence/absence (unvegetated mud, n = 34 training samples; unvegetated shadows, n = 9 training samples; vegetation, n = 10 training samples). While our training sample size was small, it performed better than several larger sample sizes, likely due to too much overlap between classes with the larger sample sizes tested. We also conducted accuracy assessment at locations independent from the training sample locations to verify the classification method. To select segmentation parameters for the object-based classification, we used an iterative approach in ArcGIS Pro’s *Image Classification Wizard* (v. 2.3, ESRI 2019). We began with default settings and altered spectral detail by 0.5, spatial detail by 1, and minimum segment size by 1 to ensure that vegetation was distinguished from mud, individual plants or mud patches were not divided into too many different segments, and small plants were included (final segmentation parameters: spectral detail = 17.5, spatial detail = 14, minimum segment size = 12).

We assessed accuracy of the classified images in ArcGIS Pro (56 vegetated and 43 unvegetated points, “ground truthing” by visual assessment of the high-resolution imagery) and calculated the true skill statistic (TSS) using the accuracy assessment confusion matrix, a measure of model performance based on true-positives and true-negative rates for each class (Allouche et al. 2006). After selecting the final classified image, we categorized the cells within the main seed dispersal area (as identified by inundation data, excluding tidal creek interiors and actively planted areas) as “high” or “low” cover using the Jenks natural breaks classification method (Jenks 1967). We evaluated different sample sizes for randomly sampling cells in the high-cover class, in intervals of 50 samples between 150 and 300, and calculated the Nearest Neighbor Index (NNI) to find the largest sample size that did not have significant autocorrelation between sampled cells. We only calculated NNI for the high-cover cells because they appeared more susceptible to autocorrelation, and we applied the same sample size to the low-cover cells. Based on this method, we randomly sampled 150 cells in each of the two cover classes (NNI = 0.95, z = -1.12).

Several UAS DEMs and DEM-derived products were used as potential predictors of vegetation development in site-wide vegetation cover analysis, in addition to other GIS-derived predictors (Table 1). We modeled salinity across the site based on September 2019 field measurements of conductivity at 349 points using a machine learning approach with elevation, amount of sediment addition/removal, and tidal creek distance as predictors using *Forest-Based Regression* in ArcGIS Pro (number of trees = 1500, replicates = 15, data withheld for validation per replicate = 25%). We evaluated the influence of these factors on vegetation cover using random forest modeling with the *randomForest* package in R. We used the same parameters and technique for variable selection and performance assessment that we used for modeling the transect data.

SEDIMENT COMPARISON AT WELL- AND POORLY-VEGETATED SITES

We collected sediment samples at 10 well-vegetated and 10 poorly-vegetated sites of similar elevation and distance to tidal creek to examine additional factors that might be leading to low colonization and growth in some areas, but are not represented in transect or UAS sampling. We chose to hold elevation and creek distance relatively constant because other marsh restoration research suggests these are two important factors (Mayer 1987; Chapple and Dronova 2017), but they may not explain all of the patterns emerging at Hester Marsh during the first year of restoration. We used GIS layers to select sampling sites, first by limiting the elevation range to 1.88 m to 1.95 m (using an August

2019 DEM, pixel size = 2.6 cm) and then by selecting representative well-vegetated and poorly-vegetated areas through visual inspection of high-resolution true color drone imagery from August 2019 (pixel size = 1.3 cm). Well-vegetated areas were those with relatively high cover and large plants, while poorly-vegetated areas were those with low cover and small plants. After selecting a general representative area within the elevation range, we created a point approximately 10 m from a tidal creek, which we navigated to in the field with a GPS.

We located these sites in the field with a handheld GPS (Trimble Juno 3B, Trimble Inc., Sunnyvale, CA) and collected two samples at each site under clear conditions on October 2, 2019. We analyzed one set of samples for six sediment properties, and sent another set of samples to a third-party soil testing facility for analysis of additional properties (Control Laboratories, Watsonville, CA). We collected all samples at least 20 cm from plants. We also measured the height of the tallest five plants within a 1-m radius of the GPS point (or all plants, if there were fewer than five present).

We collected samples for sediment property analysis with a push corer to an average depth of 18 cm (SD 3.6) and examined them for mean grain size (bulk and digested), moisture content, carbon content, and Atterberg liquid and plastic limits using standard procedures. We conducted grain size analysis of both bulk (including organic material) and digested sediment (dissolved with acetic acid and hydrogen peroxide to remove organic material) using a laser particle size analyzer (Clarke et al. 2014). We calculated moisture content by calculating the difference of the sample weight obtained directly from the core and the weight of the same sample after cooking for 24 hours in a convection oven at 60 degrees Celsius. We measured organic carbon content using a muffle furnace according to methods described by the National Lacustrine Core Facility (2013). We heated sediment at temperatures of 60 degrees Celsius for 24 hours to remove moisture, 550 degrees Celsius for four hours to remove organic carbon content, and 1100 degrees Celsius for two hours to remove carbonates. We examined Atterberg liquid limits (the moisture content at the boundary between liquid and plastic states) using a mechanical liquid limit device and plastic limits (the moisture content and the boundary between plastic and semisolid states) by rolling out samples according to New York Department of Transportation, Geotechnical Engineering Bureau methods (2015).

We collected samples for third-party sediment analysis with a hand trowel and stored them overnight in a cooler before delivering them to the laboratory for analysis. At each of the 20 total sampling locations, we collected three separate samples and combined them in a gallon-size zip-top bag into one 500-cm^3 sample, as recommended by the laboratory. We collected the three samples approximately 30 cm apart, each to a depth of 8-10 cm. Parameters measured by the laboratory include nitrate nitrogen (NO_3-N; ppm), ammonia nitrogen (NH_3-N; ppm), phosphorus (P; ppm), saturation (%), pH, conductivity (ECe; dS/m), sodium (Na; ppm), chloride (Cl; meq/L), sulfate (SO_4-S; meq/L), calcium (Ca; ppm), potassium (K; ppm), magnesium (Mg; ppm), and cation exchange capacity (CEC; meq/100 g).

We conducted a suite of related non-metric multi-dimensional scaling analyses using Primer v. 7.0 (Clarke et al. 2014). Data were normalized to enable comparison between variables with different scales. We created a Euclidean similarity matrix and visualized differences among well- vs. poorly-vegetated sites using a two-dimensional ordination plot and carried out an analysis of similarity (ANOSIM) to test for differences among the categories. We used Similarity Percentages (SIMPER) to further examine groupings and the variables that best distinguished them. We also conducted t-tests to compare categories for the variables that emerged as important in the SIMPER.

CHAPTER 3 – RESULTS

ESTIMATING HISTORICAL VEGETATED AREA

Historical vegetated area within the restoration project footprint was approximately 18.5 ha in 1931 (Fig. 2, 3A). Vegetated area declined to 4.6 ha by 2015, which is representative of the state of the marsh prior to restoration (Fig. 2, 3B). When the Hester Marsh plain is fully vegetated, there will be more marsh area than there was in 1931 (Fig. 2).

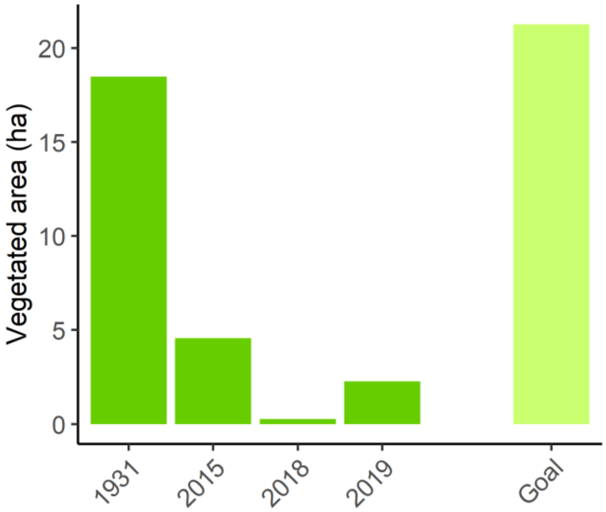

Figure 2. Vegetated marsh area within Hester Marsh project footprint, 1931 – present, and future expected vegetated area. Data sources summarized in Table B2.

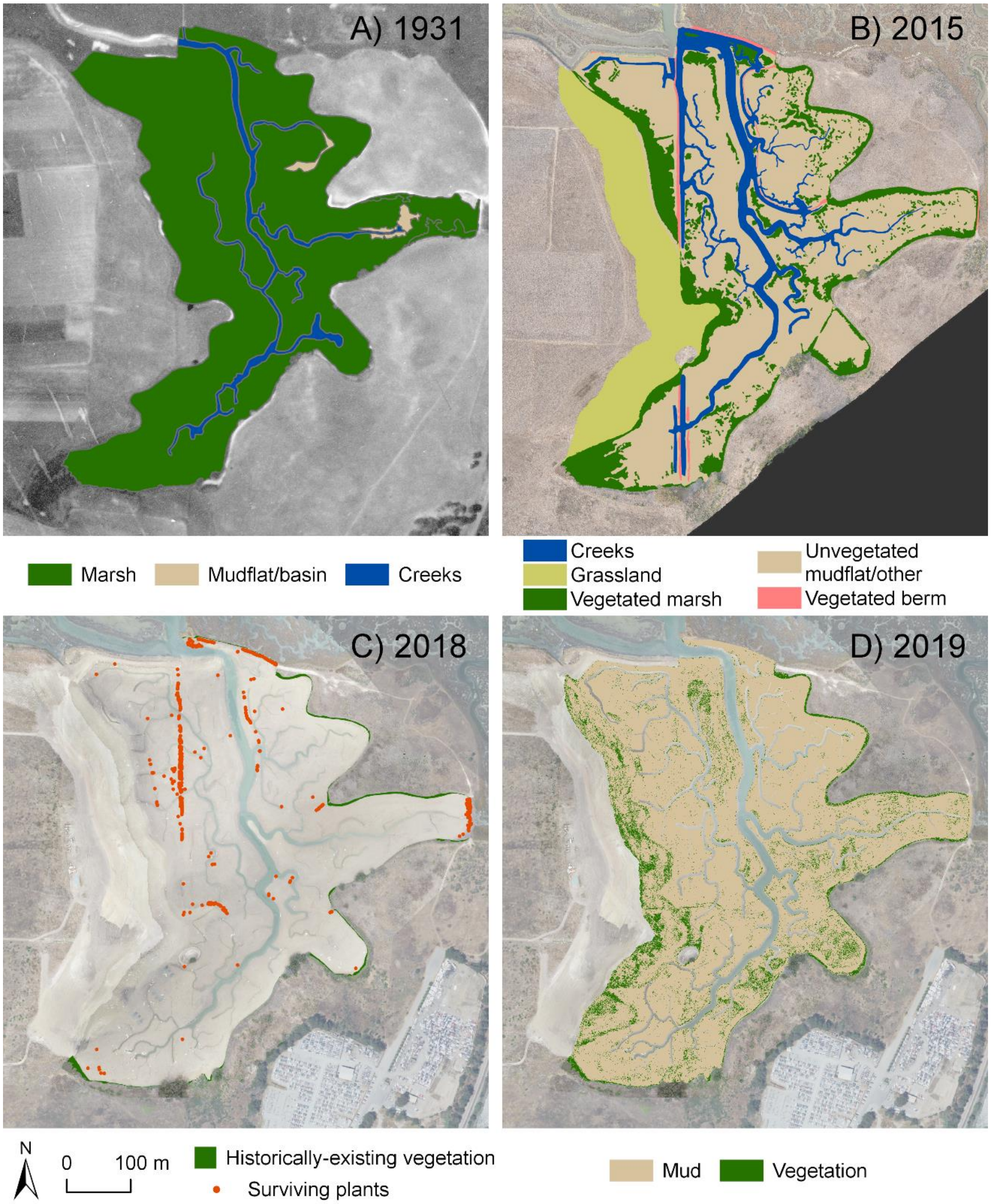

Figure 3. Maps of vegetated areas within Hester Marsh, 1931 – present. (A) Digitized 1931 aerial imagery of the historically well-vegetated marsh. (B) Digitized 2015 UAS imagery of the marsh, which had degraded to mostly unvegetated mudflat before construction of the restoration site. (C) The relatively bare landscape at the end of construction in August 2018, with locations of surviving plants logged during GPS surveys and digitized historically-existing vegetation. Points are enlarged to be visible, and cover of surviving vegetation was much less than implied by size of points. (D) Classified October 2019 UAS imagery showing patchiness of natural vegetation colonization.

INITIAL AREA SEARCHES OF SURVIVING MARSH VEGETATION

During area searches in Fall 2018, two to three months after construction ended, we recorded a total of 520 points that had plants within a 1-m diameter area, for a total estimate of 4142 plants (Fig. 3C). These were mostly native marsh species (*Distichlis spicata*, *Frankenia salina*, *Salicornia, Jaumea carnosa,* and *Spergularia* sp.), though they also included a few upland weeds. We assumed these upland weeds (7 points, representing 12 individuals) were opportunistic new colonists and not survivors because the species found were unlikely to occur on the marsh plain prior to restoration.

Based on estimates of plant numbers and assumed sizes of individuals of each species, initial plant cover was 30.5 m^2 within the sediment addition/removal area. An additional 2542.4 m^2 of marsh vegetation was present within the overall project footprint in Fall 2018, corresponding to a relatively narrow strip of historically-existing vegetation on site edges that was not scraped or buried during construction (Fig. 3C). The initial vegetated area within the entire project footprint in 2018 was 0.26 ha (Fig. 2).

The surviving plants were mostly located on former berms or other vegetated areas that had been scraped down to the target elevation of the marsh (2887 plants; 69.7% of initial plants) or in areas of sediment addition within five meters of former berms (426 plants; 10.3% of initial plants). These near-berm plants were assumed to have originated from berm material that was pushed off to the side as the berm was levelled. An additional 445 plants (10.7% of initial plants) were in areas of sediment addition that were formerly vegetated marsh. On average, the level of sediment addition this third group of plants experienced was 29.7 cm (SD 16.2). However, this category includes some overlap with vegetation that may have originated from berms, which may explain the high levels of sediment addition that some plants appeared to survive. Only 387 plants (not including weeds) did not fall into one of these categories of survival; they may have originated from other sources, or may actually belong to one of the survival categories but have been excluded from them due to digitizing or GPS error.

TRANSECT MONITORING OF VEGETATION COLONIZATION

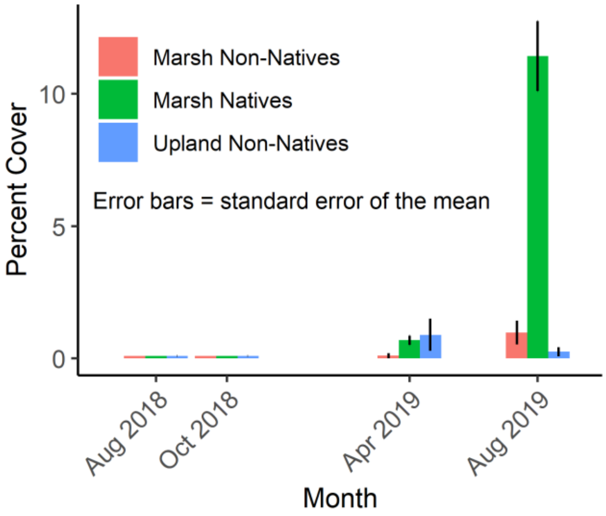

Figure 4. Marsh native, marsh non-native, and upland non-native cover from quarterly transect surveys, August 2018 – August 2019. Data from 2018 was collected only in long-term quadrats (n = 94), while data from 2019 included long-term and short-term quadrats (n = 269). Quadrats in historically-existing vegetation were excluded.

During the first transect vegetation surveys in August and October 2018, no live vegetation was found in the long-term monitoring quadrats in the initially-bare sediment addition area; historically-existing vegetation at the tops of eastern and southern transects persisted, with over 100% plant cover due to canopy layering (consisting of mostly *Distichlis*, *Salicornia*, *Frankenia*, and *Jaumea*). In April 2019, average cover of all plants combined was still low (2.1%) in the initially-bare sediment addition area. By August 2019, average cover reached 13.6% in the sediment addition area (Fig. 4). New vegetation was dominated by native species, with 11.4% average native marsh cover (99% of which was *Salicornia*, with minimal *Frankenia* and *Spergularia* cover). We also found 1.0% cover of marsh non-natives (*Atriplex prostrata* and *Parapholis incurva*) and 0.3% cover of upland non-natives. We found 0.9% cover of non-native *Erigeron bonariensis* and native *E. canadensis*, but could not distinguish between the native and non-native during field surveys.

Average canopy height for newly colonized *Salicornia* was 6.9 cm (SD 4.6), while it was 35.2 cm (SD 5.2) in the quadrats with historically-existing vegetation. Biomass estimates calculated from *Salicornia* height and cover were 300.2 cm^3 (SD 485.8) in quadrats with new colonization and 3091.7 cm^3 (SD 837.7) in quadrats with historically-existing vegetation. The following analyses focused on vegetation in the sediment addition area in August 2019 to better understand natural colonization that occurred in the first year post-construction.

Percent cover of native marsh vegetation in the sediment addition area varied among transects, with the lowest cover on transects 3, 6, 9, and 10 (Fig. 5). On average, quadrats at or above the median elevation of 1.93 m had significantly greater cover (mean = 16.1%, n = 134) than quadrats below median elevation (mean = 6.9%, n = 133; one-tailed t-test, $p < 0.001$; Fig. 6). Mean elevation at the quadrats was 1.95 m in August 2019 (range 1.71 m to 2.30 m).

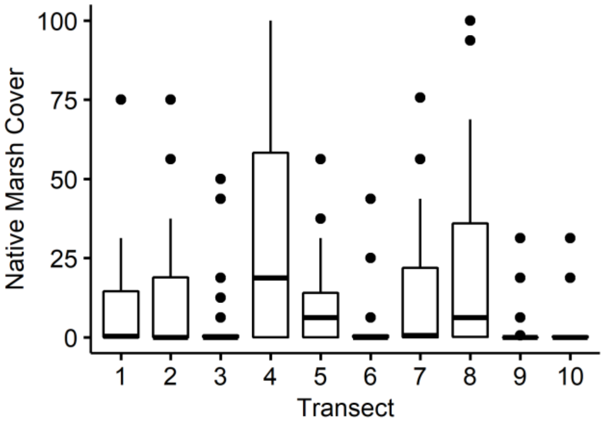

Figure 5. Native marsh cover on 10 transects, August 2019. Quadrats in historically-existing vegetation were excluded.

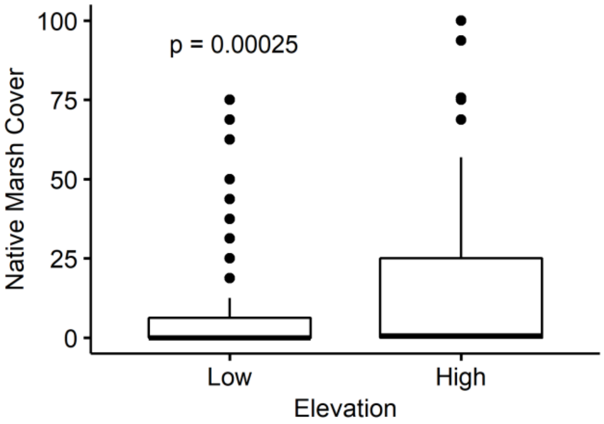

Figure 6. Native marsh cover at high and low elevation quadrats on 10 transects, August 2019. Native marsh cover was significantly greater in high-elevation quadrats at or above median elevation of 1.93 m, compared with low-elevation quadrats below median elevation (one-tailed t-test, $p < 0.001$). Quadrats in historically-existing vegetation were excluded.

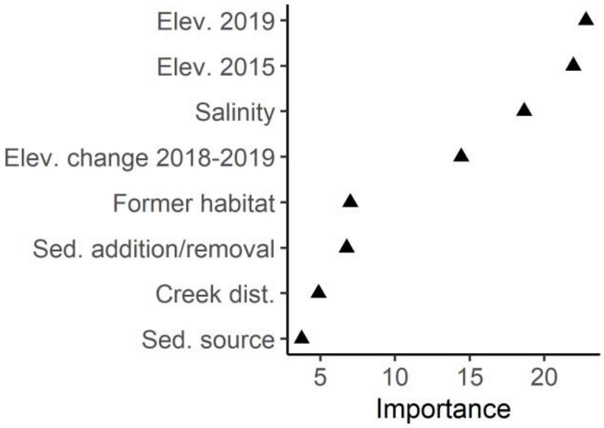

Figure 7. Variable importance for random forest model of transect-surveyed native marsh cover. Importance is the percentage increase in MSE when the variable is randomly permuted.

Modeling of native marsh cover based on August 2019 transect data revealed the following important predictors: post-restoration elevation (2019), pre-restoration elevation (2015), salinity, elevation change over the first year of restoration (2018 to 2019), habitat type prior to restoration, sediment addition or removal during construction, distance to nearest tidal creek, and sediment source (Fig. 7). The model with these variables explained 18.5% of variance in the data.

Post-restoration elevation (2019) was the most important predictor of native marsh vegetation cover (importance = 22.8), with predicted cover increasing sharply between 1.9 m and 2.0 m (Fig. 8A). Pre-restoration elevation (2015) was the next most important predictor (importance = 22.0), with greater vegetation cover predicted in formerly high-elevation areas corresponding to the hillside that was scraped during construction (above 2.8 m), and lower cover predicted in areas on the former marsh plain (1.2 m to 2.7 m; Fig. 8B, Fig. 15B). Very low areas prior to construction, such as low basins (below 1.1 m), were also modeled to have relatively high cover post-construction. Salinity was the next most important predictor (importance = 18.7), with lowest cover predicted between 37 ppt and 42 ppt (Fig. 8C). Elevation change over the first year of restoration (August 2018 to May 2019) was also important (importance = 14.4), with more vegetation cover predicted in areas that experienced elevation loss over that time period (though the initial portion of the drastic decline in predicted cover was driven by relatively few data points; Fig. 8D, 15F). Areas that experienced slight elevation loss over the first year of restoration tended to be more frequently inundated, more saline, and closer to tidal creeks. Raw data by former habitat type show greatest cover on former grassland (G), followed by former mudflat (M), but the model predicted only slightly greater cover in these areas (importance = 7.0; Fig. 8E, A8). Raw data also show greater cover on areas of sediment removal, which correspond to the former grassland and berms, but the model predicted only marginally greater cover on those sediment removal areas (importance = 6.7; Fig. 8F, A9). The modeled relationship with creek distance predicted a decrease in cover from creek edges (0 m) to 10 m distance (importance = 4.9; Fig. 8G, A7). There was also a large predicted increase in cover in the farthest areas from creeks (45 m to 60 m), driven by few data points. Vegetation cover was predicted to be marginally greater on sediment sourced from the local hillside compared with Pajaro River sediment (importance = 3.7; Fig. 8H, 15E).

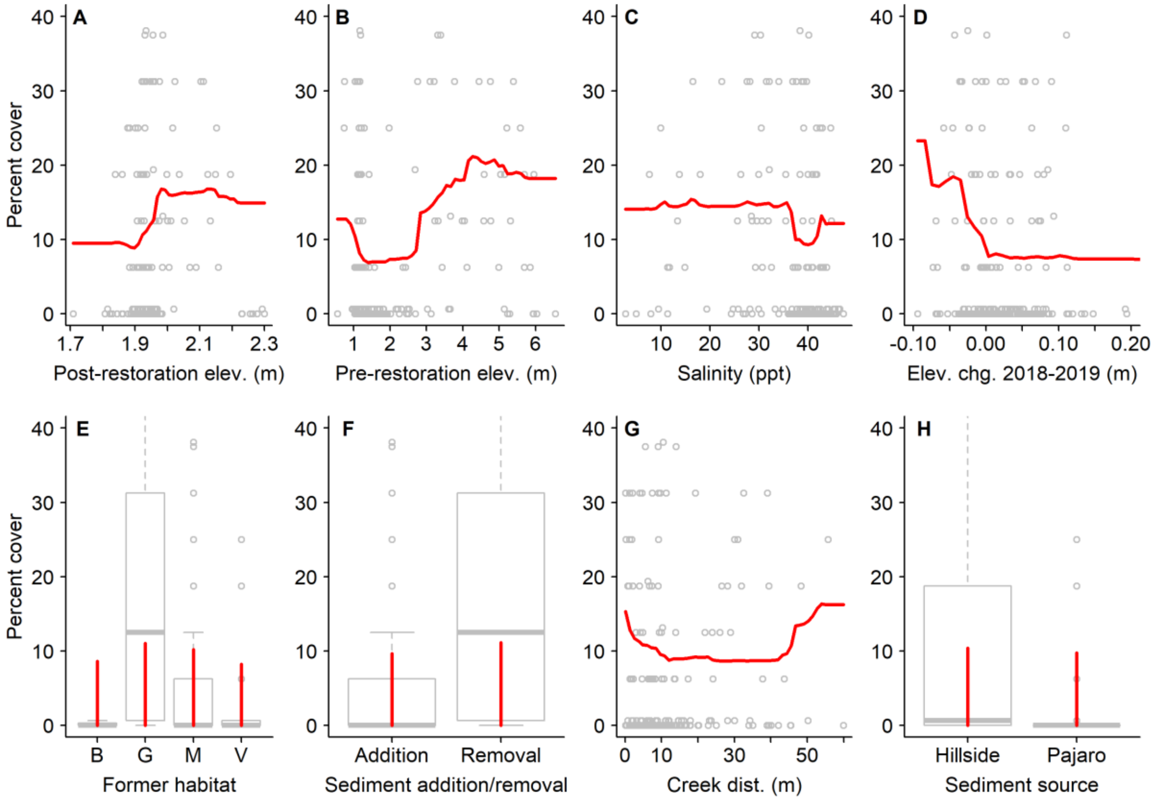

Figure 8. Partial dependence of transect-surveyed native marsh cover on (A) post-restoration elevation, (B) pre-restoration elevation, (C) salinity, (D) elevation change over the first year of restoration, (E) former habitat type (B = vegetated berms, G = grassland, M = mudflats/unvegetated areas, V = vegetated marsh), (F) sediment addition or removal, (G) creek distance, and (H) sediment source based on random forest modeling. Red lines show model predictions, holding all variables in the model constant except the one plotted. Raw data shown as gray points (continuous) or boxplots (categorical). Upper y-axis limit set at 40% cover for ease of viewing the majority of data (25 high-cover data points not shown).

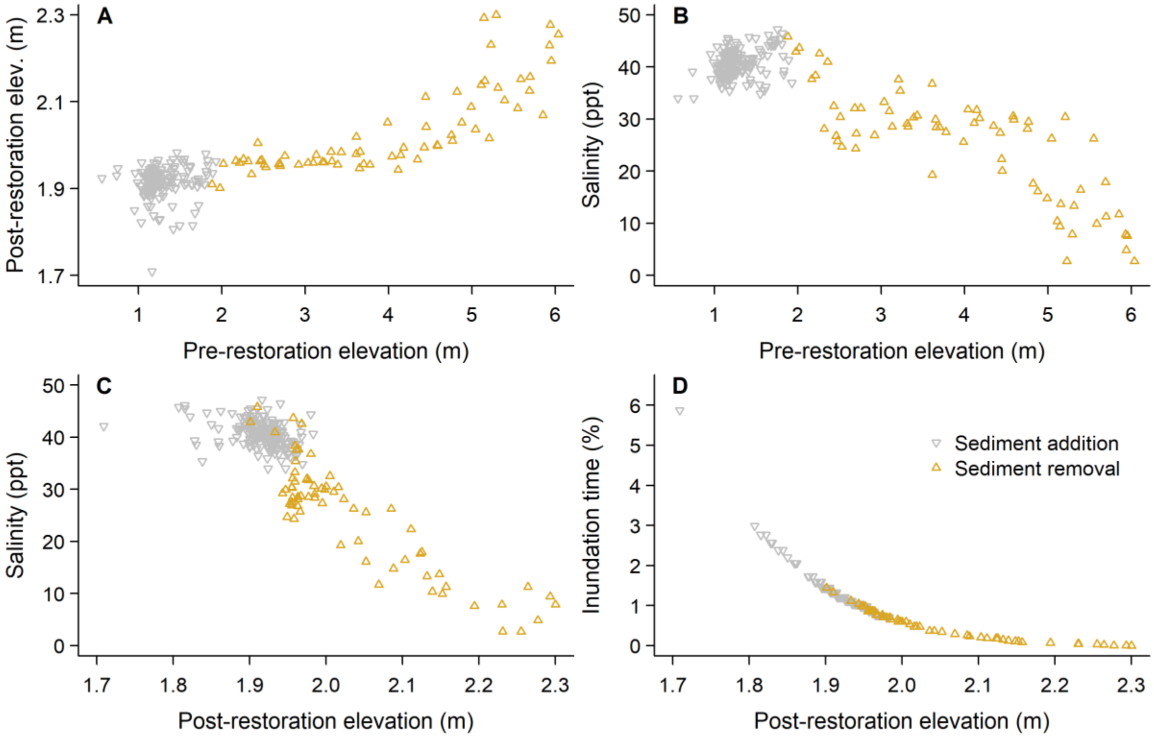

Figure 9. Relationships between (A) post- and pre-restoration elevation, (B) salinity and pre-restoration elevation, (C) salinity and post-restoration elevation, and (D) inundation time and post-restoration elevation. Data from transect quadrats (n = 252).

Several of the variables examined in modeling were correlated with each other, though not linearly. Areas that were high in elevation prior to restoration remained at higher elevations post-restoration (Fig. 9A). Sediment removal lowered these areas from upland to marsh elevations, but because they are in the transition zone between the marsh plain and upland, they remained relatively high. Salinity was also lowest in these formerly high-elevation, sediment removal areas (Fig. 9B). Salinity and post-restoration elevation were negatively related, with lower salinity at higher elevations (Fig. 9C). This trend was mostly driven by the sediment removal areas, which tended to have lower salinity for a given elevation (e.g. 1.95 m) than sediment addition areas. Salinity in the sediment addition areas had a weakly negative relationship with elevation, decreasing slightly at elevations above 1.90 m (Fig. 9C). Inundation time followed a downward sloping curve in relation to post-restoration elevation, as measured by Vierra Marsh tide data (Fig. 9D).

CHARACTERIZATION OF INUNDATION ACROSS ELEVATIONS

The elevation range of Hester Marsh (approximately 1.7 m to 2.3 m) was inundated between 0.0% and 6.2% of the time from August 2018 to May 2019 (Fig. 9D). The highest tide during this period was 2.29 m on August 10, 2018, according to Vierra Marsh tide data. Elevations over 1.95 m were inundated 1.0% of the time. The highest tide during the main seed dispersal period, between October 2018 and March 2019, was 2.14 m.

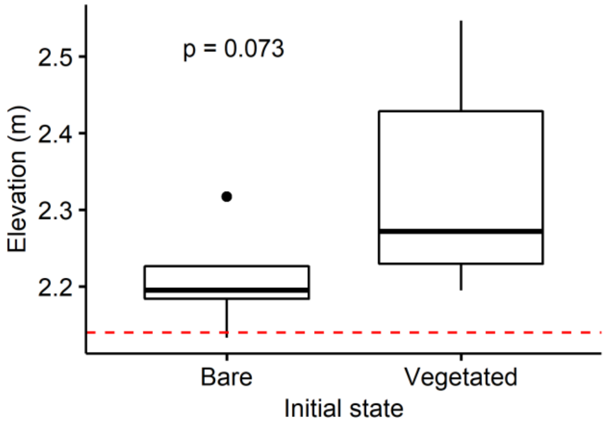

Figure 10. Upper elevational boundary of *Salicornia* on initially-bare western transects compared with initially-vegetated eastern and southern transects (n = 5 per group) and highest tide during high seed dispersal period (2.14 m, red dashed line). The elevation of the highest newly-colonized *Salicornia* plant was marginally significantly lower than the elevation of the highest *Salicornia* plant on initially-vegetated transects (one-tailed t-test, p = 0.073), but was not significantly lower than the 2.14 m tide line.

The highest elevation of newly-colonized *Salicornia* on western, initially-bare transects was marginally significantly lower than the highest elevation of historically-existing *Salicornia* on eastern and southern transects (Fig. 10, Table B2; one-tailed t-test, p = 0.073). Contrary to our expectation, the upper limit of newly-colonized *Salicornia* on initially-bare transects was not significantly lower than 2.14 m, the highest tide during the main seed dispersal period (Fig. 10). However, only 3% of all new marsh cover was found in quadrats above 2.14 m, and mean cover of new marsh and upland vegetation in these quadrats did not differ significantly (t-test, p = 0.65). Because of this equal dominance of marsh and upland cover above 2.14 m, and the vast majority (97%) of new marsh vegetation occurring below 2.14 m, we used this “main seed dispersal area” boundary to limit the UAS analysis to examine drivers of marsh, rather than upland, vegetation colonization.

Site-Wide UAS Monitoring of Vegetation Colonization

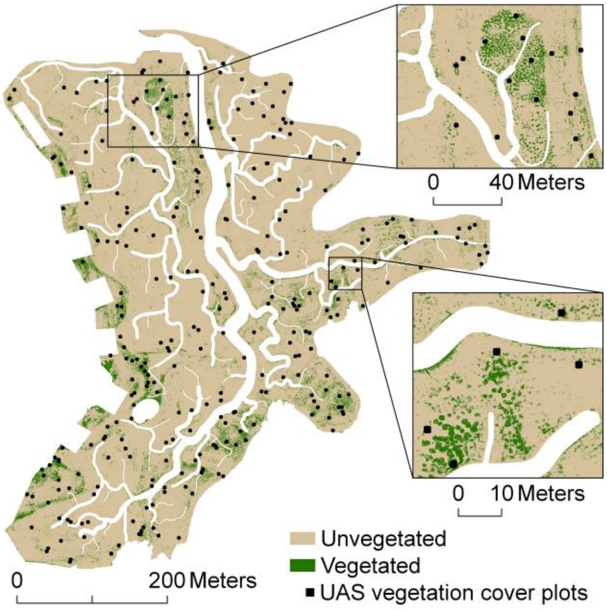

Figure 11. Classified October 2019 UAS imagery of vegetated and unvegetated areas and plots for modeling vegetation cover within the main seed dispersal area, excluding actively planted areas and tidal creek interiors. Some example areas are shown to highlight patchiness of natural colonization. Classification was performed in ArcGIS software using a pixel-based maximum likelihood approach (TSS = 0.82). We modeled percent cover of classified vegetation in 1-m^2 plots, created using stratified random sampling in high- and low-cover areas (n = 300).

Image classification of a high-resolution October 2019 UAS imagery (pixel size = 0.79 cm) produced estimates of 2.3 hectares of vegetated cover in the overall project footprint (Fig. 2, 3D), including 1.4 hectares of naturally-colonized vegetated cover in the main seed dispersal area (Fig. 11). We calculated vegetation cover estimates and performed modeling of vegetation points using the pixel-based classification, because both images had good overall accuracy (TSS = 0.82 and 0.85 for pixel-based and object-based, respectively) but the object-based image had a few relatively large areas that were incorrectly classified. Both methods of classification had additional minor limitations, including difficulty distinguishing sunken footprints and dark mud from vegetation and inability to distinguish different species from each other. These were relatively minor issues in our case, as most vegetation in the main seed dispersal area was *Salicornia* and problem areas like footprints and dark mud were small relative to the entire area.

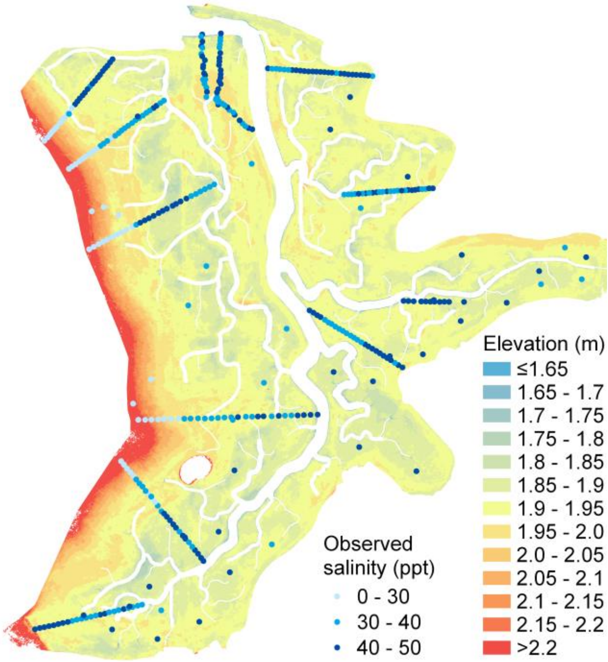

Figure 12. UAS-derived digital elevation model (DEM) of Hester Marsh in May 2019 and salinity data points collected in September 2019 (n = 349). Site-wide salinity was modeled based on these data points using elevation, sediment addition/removal amount, and tidal creek distance as predictors (out-of-bag RMSE = 3.08).

Salinity modeling included the following predictors in order of variable importance percentage based on Gini coefficients: amount of sediment addition or removal during construction (importance = 41%), elevation (importance = 36%; Fig. 12), and tidal creek distance (importance = 23%). Model validation indicated fairly good performance (out-of-bag RMSE = 3.08 ppt). Salinity was predicted to be lowest at high elevations that were inundated infrequently, and salinity was particularly low in the former grassland on the western side of the site that had upper layers of sediment removed during the construction process, and which remained at higher elevation than the marsh plain to the east (Fig. 9A-C, 15D).

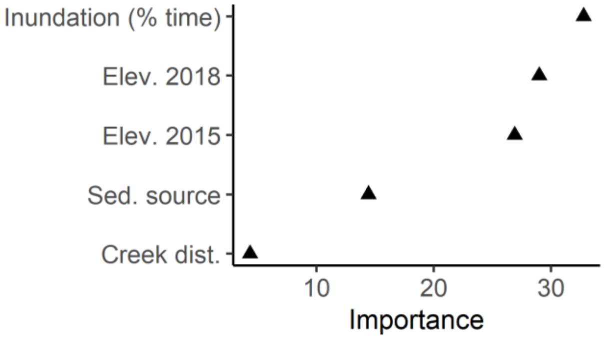

Figure 13. Variable importance for random forest model of UAS-derived classified vegetation cover. Importance is the percentage increase in MSE when the variable is randomly permuted.

Site-wide modeling of classified vegetation cover revealed that inundation (% time), post-restoration elevation (2018), pre-restoration elevation (2015), sediment source, and tidal creek distance (m) were important factors explaining vegetation cover during the first year of restoration at Hester Marsh (Fig. 13). The model with these five variables explained 25.4% of variance in the data. The site-wide vegetation cover model performed better without the remaining predictors: modeled salinity (Fig. 15D), sediment addition or removal (Fig. A9), habitat type prior to construction (Fig. A8), and elevation change over the first year of restoration (Fig. 15F).

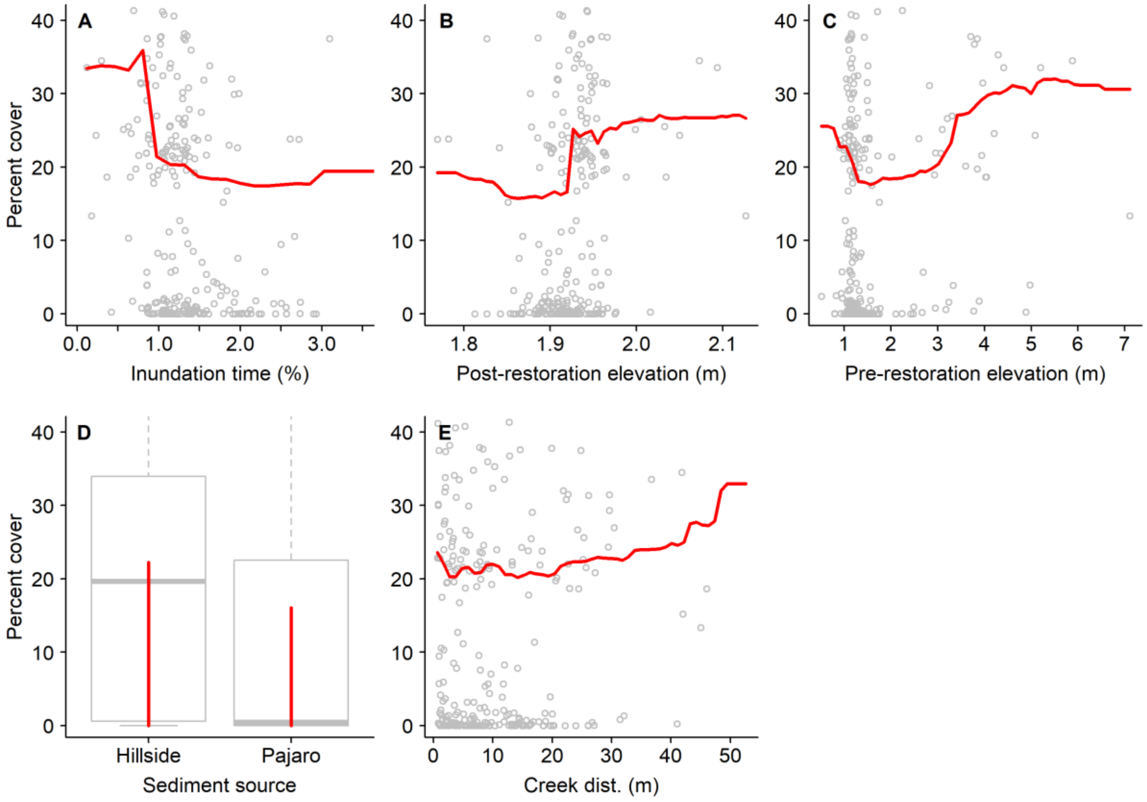

Figure 14. Partial dependence of UAS-derived vegetation cover on (A) percent time inundated, (B) post-restoration elevation, (C) pre-restoration elevation, (D) sediment source, and (E) creek distance based on random forest modeling. Red lines show model predictions, holding all variables in the model constant except the one plotted. Raw data shown as gray points (continuous) or boxplots (categorical). Upper y-axis limit set at 40% cover for ease of viewing the majority of data (55 high-cover data points not shown).

Inundation (% time over the first 10 months of restoration), post-restoration elevation (2018), and pre-restoration elevation (2015) were the most important predictors of vegetation cover. Vegetation cover was predicted to be greatest in areas inundated approximately 0.85% of the time or less (importance = 32.8; Fig. 14A, 15C). Post-restoration elevation predicted a sharp increase in vegetation cover around 1.92 m (importance = 29.0; Fig. 14B, 15A). Cover was predicted to be lowest on former marsh plain elevations (1.2 m to 3.0 m) and greatest on scraped hillside areas that were above

3.3 m in elevation prior to construction of the restoration site (importance = 26.9; Fig. 14C, 15B). Vegetation cover was also predicted to be high in formerly low areas (below 1.2 m; Fig. 14C, 15B). Sediment source was moderately important (importance = 14.4), with more vegetation predicted on areas that received hillside sediment rather than Pajaro River sediment (Fig. 14D, 15E). Tidal creek distance was only marginally important (importance = 4.3), with vegetation cover predicted to be greatest in areas farthest from creeks, though this was driven by only a few data points (Fig. 14E, A7).

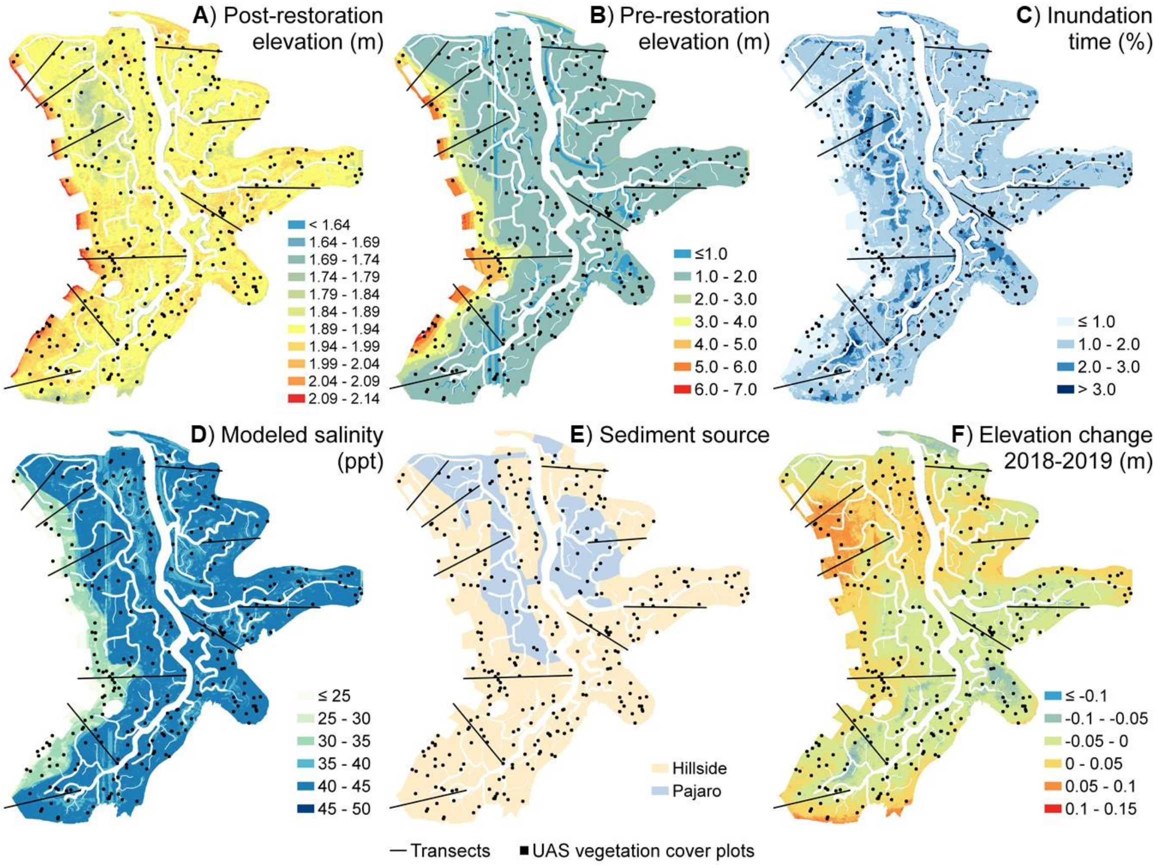

Figure 15. Maps of (A) post-restoration elevation, (B) pre-restoration elevation, (C) percent time inundated, (D) modeled salinity, (E) sediment source, and (F) elevation change over the first year of restoration across the main seed dispersal area at Hester Marsh, excluding tidal creeks and actively planted areas. Modeling was conducted on UAS-derived vegetation cover in 300 plots, and on field-surveyed native vegetation cover along 10 transects. Data sources for maps are summarized in Table 1. Full-size maps in Appendix A.

While tidal creek distance did not clearly show greater vegetation cover in close proximity to creeks as a predictor in the site-wide UAS analysis, the pattern of high cover adjacent to creeks was visibly notable in the field and may be important on a smaller scale. Sloped creek banks also had very high cover, but were not included in the analysis. We also observed some relatively bare strips within four to 10 meters of historically-existing vegetation on some site edges. Field observations indicated that many of these areas adjacent to historically-existing vegetation were slightly sunken, leading to poor drainage and water pooling. Drone imagery and DEMs supported field observations of little new colonization and lower elevation in these areas near the edges (Fig. 16A-B).

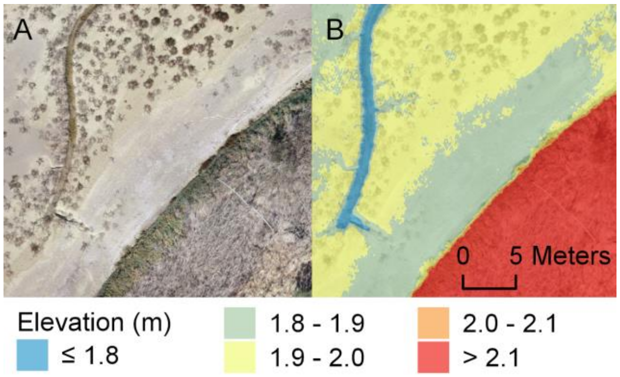

Figure 16. Bare ground between new colonization and historically-existing marsh vegetation in (A) UAS imagery (October 2019) and (B) semi-transparent digital elevation model (May 2019) overlaid on UAS imagery. This bare strip was lower in elevation, supporting field observations of water pooling in edge areas.

SEDIMENT COMPARISON AT WELL- AND POORLY-VEGETATED SITES

Well-vegetated sites had qualitatively greater cover and larger plants (average height = 13 cm), in comparison to poorly-vegetated sites (average height = 5 cm). The 20 sites were at a mean elevation of 1.91 m (SD 0.02) and mean creek distance of 12.3 m (SD 3.65). As intended in the design of these paired comparisons, elevation and creek distance did not differ significantly between well-vegetated and poorly vegetated sites.

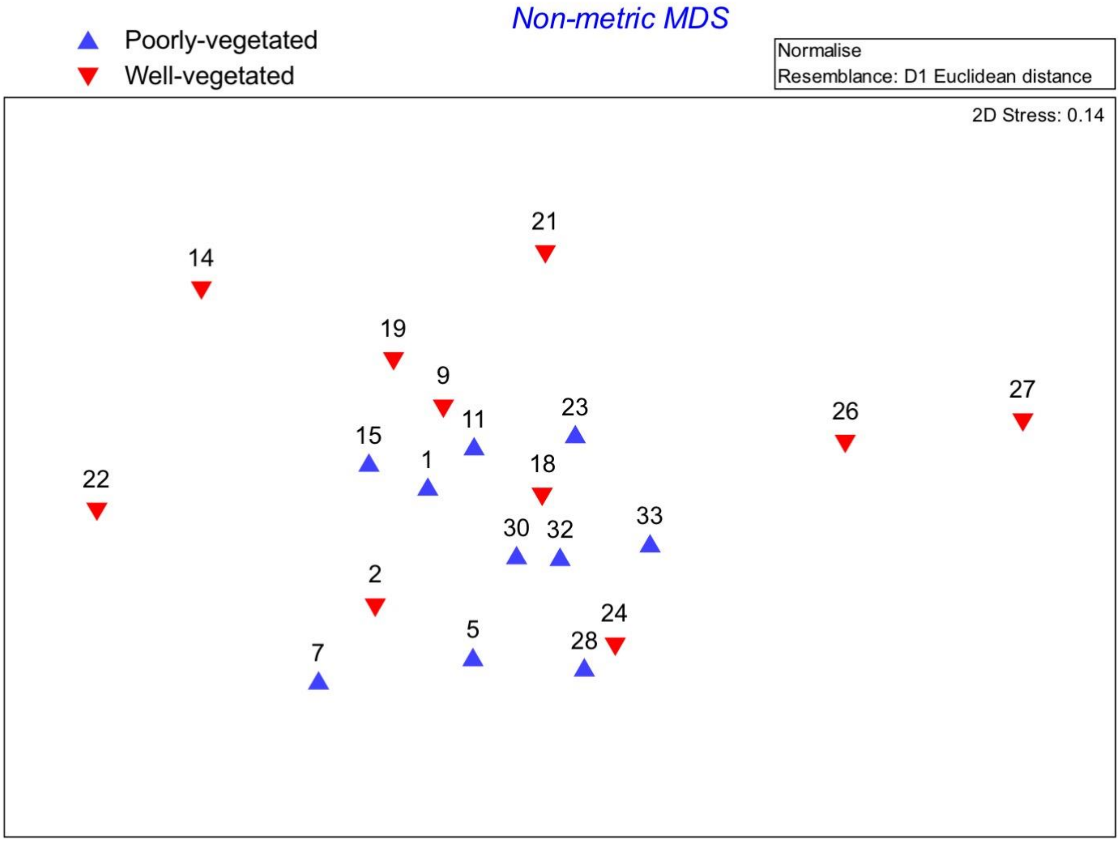

Figure 17. Non-metric multidimensional scaling results for soil samples collected at well- and poorly-vegetated sites in October 2019 (n = 20).

There was significant separation between the 10 well-vegetated and 10 poorly-vegetated sites (R = 0.13, p = 0.02, ANOSIM), driven by a wide range of sediment properties (Table 2). SIMPER analysis revealed that poorly-vegetated sites were more similar to each other than well-vegetated sites (average squared distance = 15 and 30, respectively; Fig. 17). Poorly-vegetated sites had significantly greater ammonia nitrogen, conductivity, and sodium and chloride concentrations compared to well-vegetated sites (Table 2).

Table 2. Comparison of soil properties between well- and poorly-vegetated sites in October 2019 (n = 20). The first column lists the top 14 variables identified as contributing to the separation of the two groups in a SIMPER analysis, and the second column shows the percentage of contribution to this separation. The next four columns show the means and standard deviations for the variables by group. Finally, the p-value is shown for two-tailed t-tests for all variables.

		Poorly-vegetated		**Well-vegetated**		
Variable	**% Contribution**	**Mean**	**SD**	**Mean**	**SD**	**P-value**
NH_3-N (ppm)	4.92	3.05	0.93	2.23	0.34	p = 0.023
Cl (meq/l)	4.86	1611.0	131.6	1374.3	255.5	p = 0.021
Conductivity (dS/m)	4.81	102.6	8.2	91.6	11.1	p = 0.022
Na (ppm)	4.76	14154.0	1577.2	11786.6	2648.6	p = 0.029
Atterberg liquid limit (%)	4.42	20.8	3.8	24.9	5.9	p = 0.084
CEC (meq/100 g)	4.38	91.9	11.2	79.1	19.8	p = 0.098
Moisture content (%)	4.37	15.3	4.6	19.4	5.9	p = 0.099
SO_4-S (meq/l)	4.19	158.5	20.5	142.2	30.3	p = 0.18
pH SMP buffer	4.18	7.61	0.06	7.56	0.08	p = 0.18
Bulk grain size (µm)	4.18	3.28	0.81	3.91	1.22	p = 0.19
K (ppm)	4.10	461.1	44.3	414.9	114.2	p = 0.26
pH sample	4.08	7.10	0.21	6.95	0.37	p = 0.29
Saturation (%)	4.03	38.1	2.6	39.9	5.2	p = 0.34
Mg (ppm)	3.97	2442.0	360.8	2220.3	715.7	p = 0.40

We also used the sediment sample data and field-collected conductivity/salinity data to further investigate the potential differences in Pajaro River dredge material and hillside material, given the moderate importance of sediment source in vegetation modeling. All of the sediment sampling sites that likely represented Pajaro source material were in the poorly-vegetated category, so we compared these samples only with the other samples within the poorly-vegetated category. We examined differences in the variables in Table 2 between the sites representing different sediment sources using two-tailed t-tests. While our sample size was very small for this comparison (n = 3 and 7 for Pajaro and hillside sediment sites, respectively), sites with hillside material had significantly greater moisture content (p = 0.044), larger mean bulk grain size (p = 0.029), and lower lab-measured conductivity (p = 0.028). We also examined salinity in relation to sediment source, modeled from field conductivity measurements along the 10 transects, considering only the sediment addition areas because salinity modeling indicated lower salinity in areas where sediment was scraped. Based on these data, salinity was significantly lower on hillside sediment areas (two-tailed t-test, p = 0.018, df = 71), though the difference in mean salinity was only 1.0 ppt.

CHAPTER 4 – DISCUSSION

Overall, the multi-faceted approach we took, involving field surveys and UAS, and both random and targeted sampling, revealed key patterns and drivers of marsh colonization in the first 12-14 months following restoration. We detected very low initial survival of vegetation following sediment addition, but relatively rapid and extensive colonization of new marsh plants. We found that various physical variables predict patterns of vegetation, particularly elevation and inundation time, and therefore recommend that these are particularly critical considerations for planning and monitoring of marsh restoration projects.

PLANT SURVIVAL FOLLOWING SEDIMENT ADDITION

While several studies of thin-layer sediment placement projects suggest that vegetation can survive sediment placement thicknesses of up to 20-30 cm (Reimold et al. 1978; Mendelssohn and Kuhn 2003; Frame et al. 2006), we observed little survival on formerly vegetated, sediment addition areas (estimated vegetated cover in these areas was 38,925 m^2 pre-construction and 3.7 m^2 post-construction). Poor survival may be partially attributed to the thickness of sediment added at Hester (on average, 69 cm in all sediment addition areas and 37 cm on formerly vegetated areas), but is also likely due to the method of sediment placement, because even areas with low levels of sediment addition had few or no survivors. Thin-layer placement typically involves spraying or piping in sediment slurries (Slocum et al. 2005; Frame et al. 2006), while sediment at Hester was placed by heavy construction equipment that drove over the marsh repeatedly. Future thick-layer sediment addition projects, at least those using a similar method of sediment placement, should expect low survival of vegetation.

Somewhat surprisingly, most of the surviving vegetation at Hester Marsh was on former berms or areas within five meters of those berms, where berm material may have been used for fill, suggesting that they likely grew from roots or other intact plant material that remained in upper layers of sediment. Outside of the actively planted areas, these former berms and adjacent areas have the most native marsh species diversity; *Salicornia* and *Frankenia* both occur in these areas, and *Jaumea* and *Distichlis* on the marsh plain are almost entirely limited to these areas. Some of the initial plants (9.3%)

did not meet one of our survival categories (on former berm or vegetated area that was scraped, filled area adjacent to berm, or former vegetated area that was filled), indicating that there may be additional mechanisms by which plants survived. One possibility is that construction equipment moved sediment from vegetated berms or other areas around farther than five meters, and that some of those plants were found later in areas that were not formerly vegetated or near a former berm.

TEMPORAL TRAJECTORY OF EARLY COLONIZATION

Past studies of bare sediment addition sites have revealed variable rates of colonization, from 0% cover after 1 year (La Peyre et al. 2009) on the slow end of the spectrum to 77% after 2.5 years on the rapid end (Mendelssohn and Kuhn 2003). We observed no new colonization by marsh species during the first eight months of the project (August 2018 - April 2019). New seedlings began to emerge in early April 2019, and germination appeared to continue through June and July. This timing suggests that winter rains may be crucial for seed germination, possibly through reducing salinity and/or increasing moisture (Noe and Zedler 2001b). Elevation of the landward marsh boundary of newly colonized vegetation supports earlier research that seed transport is also seasonal (Mayer 1987), because new marsh vegetation was rarely found above the highest winter king tide line (2.14 m); earlier, higher king tides may not have brought as many seeds as winter tides. However, the occasional new colonization in areas higher than we expected, above the highest tide line between October and March, suggests that some seed dispersal may occur outside of this temporal window. Instead of being set by the highest tide during this period, the upper marsh boundary may instead be set by a threshold inundation frequency.

Overall vegetation cover was still relatively low in the initially-bare area at the end of the first growing season: estimated vegetated cover was 13.6% according to August 2019 transect surveys, and 7.6% according to October 2019 drone image classification. The discrepancy in estimates between the datasets may be due to the classified image underestimating cover (failing to capture small, sparse plants), as well as the transect dataset overestimating cover (possibly oversampling the high-elevation, scraped area with high vegetation cover). There was substantial variability in cover across the site (standard deviation of vegetated cover in initially-bare quadrats = 24.3). Native marsh species colonization captured during August 2019 transect surveys was dominated by *Salicornia* (99% of native marsh cover), with some representation of *Spergularia* sp. and *Frankenia*. Patchy colonization should be expected at future high marsh restoration sites, but results from vegetation monitoring and analysis at this site can inform the design of future sites to increase early colonization.

PREDICTORS OF PLANT COLONIZATION

Typically, salt marsh distribution and community structure is closely related to tidal inundation, which in turn is affected by elevation (Johnson and York 1915; Callaway et al. 1990; Janousek et al. 2019). In our study, the best predictors of vegetation cover overall were pre- and post-restoration elevation, salinity, and inundation. While the overall predictive power of models was low, possibly due to high stochasticity in seed deposition, both pre- and post-restoration elevation were important predictors in models of both transect and UAS vegetation cover data. Marsh vegetation cover was predicted to be greater at high elevation (above 1.92 m to 1.95 m) and low inundation frequency (below 0.85% time inundated). Salinity was lowest in these high-elevation, infrequently inundated areas, indicating more favorable conditions for plant germination (Callaway et al. 1990; Shumway and Bertness 1992). This trend suggests that moisture was not limiting in high elevation areas, at least under non-drought conditions.

High vegetation cover was also predicted on the former hillside, which was grassland habitat above marsh elevation before sediment was removed during construction. Sediment "scraping" was favorable to marsh vegetation colonization, likely in part because these areas remained at higher elevation post-construction (Fig. 9A). Lower salinity in scraped compared with sediment addition areas at the same elevation may also indicate favorable drainage, groundwater, or other sediment conditions in scraped areas (Fig. 9C).

Other factors indicated greater vegetation colonization near tidal creeks. Creeks are commonly understood to influence marsh vegetation community structure (Sanderson et al. 2001), but while other studies suggest better flushing of salts drives greater vegetation growth near creeks (Schile et al. 2011; Chapple and Dronova 2017), areas near creeks at Hester Marsh do not appear to have lower salinity (Krause 2020). There are several possible explanations for greater vegetation cover in these areas, despite their greater salinity, relating to either pre- or post-settlement processes. These include greater seed deposition (Hopkins and Parker 1984), increased moisture ameliorating salinity stress (Noe and Zedler 2000), lower sulfide toxin concentrations (King et al. 1982), and nutrient subsidies from fish and invertebrates (Allen et al. 2013). Frequently-inundated areas near tidal creeks may also have faster development of the soil microbial community, which can be a precursor to vegetation development (Lynum et al. 2020).

Sediment properties are widely considered to be important in marsh restoration (Broome 1989), with potential effects on pore water nutrients and toxins (Wigand et al. 2016). Better understanding of these factors can inform selection of source material for sediment addition projects and adaptive management to mitigate plant stressors. Sediment analysis at Hester Marsh indicated greater salinity and ammonia levels at poorly-vegetated compared to well-vegetated sites. Future studies should examine strategies to mitigate salinity stress at sediment addition sites, particularly in areas away from tidal creeks. Differential colonization relating to sediment source at Hester Marsh suggests variability in sediment properties between the two source materials, though we did not have sufficient data to conclusively determine the properties or stressors that varied between sediment source areas. Additional sediment analyses can examine this question further in order to inform sediment sourcing for future projects.

Detailed spatial monitoring such as our transect and UAS analyses are valuable for informing adaptive management of restoration projects. By identifying areas where recruitment may be limited due to seed deposition or abiotic stress, managers can develop targeted strategies such as seeding or planting, increasing microtopography to enhance seed retention, soil amendments, and irrigation or shading to reduce salinity stress. Our findings can also inform planning and expectations for future projects.

Future restoration projects created using a similar approach, by adding thick layers of sediment on degraded marsh and mudflat to create a high marsh plain, should expect low cover in mid-elevation areas (inundated one to six percent of the time). However, the low explanatory power of salinity on its own suggests that vegetation colonization may be influenced by seed deposition and germination limitations other than salinity stress. Sediment sampling can examine additional potential abiotic and biotic limitations of vegetation colonization, such as sediment compaction (as an indicator of porosity/permeability) or development of the soil microbial community. Variability in seed deposition should also be examined through further studies; seed-trapping experiments could inform whether seeds are limited in some types of areas, which can in turn inform whether seed retention interventions are necessary.

COMPARISON OF MONITORING METHODOLOGIES

Monitoring of vegetation development is critical to marsh restoration projects (Zedler 2000; Williams and Faber 2001), particularly for understanding and evaluating relatively novel approaches like sediment addition (Mendelssohn and Kuhn 2003). With recently introduced technologies like high-resolution remote sensing by UAS in marsh restoration (Chabot and Bird 2013), there is not yet consensus on the most effective approach for tracking vegetation cover, monitoring physical variables related to vegetation, and modeling the drivers of vegetation patterns. We have some recommendations based on our comparison of multiple approaches.

For monitoring plant colonization, field- and UAS-based approaches yielded similar estimates of overall vegetation cover at the end of year 1. We found field methods more advantageous for distinguishing between species in cover assessments, enabling us to evaluate the upper marsh boundary in relation to tide data. While other studies find UAS more efficient in time and effort spent compared with field methods (Chabot and Bird 2013), this advantage was not as apparent at this moderately-sized site, where four people could survey 280 quadrats in one day. Another general advantage of UAS monitoring is the ability to cover an entire site, while field methods are limited by walking access. Similarities in transect and UAS modeling results indicate that limitations in transect survey coverage did not impact our understanding of the predictors of vegetation cover, though transect monitoring may have slightly oversampled the high-elevation, scraped area with high vegetation cover.

To quantify critical explanatory variables, we recommend focusing on elevation, given its high importance in both modeling approaches. Field measurements with laser leveling from benchmarks as well as DEMs created from UAS linked to ground control points both yielded accurate elevation profiles. Inundation frequency was also a useful explanatory variable, which we calculated fairly easily using water level data from a nearby sonde of known elevation. Inundation frequency predicted more variation than salinity estimates in our UAS analysis, and elevation outperformed salinity in both transect and UAS analyses, suggesting that salinity data modeled across the entire site were not sufficiently accurate to predict vegetation. Given the relative difficulty of obtaining salinity data, and lower explanatory power of this variable, we recommend focusing on elevation and inundation frequency, at least in very marine-influenced marshes such as this one.

While field-collected data on vegetation and explanatory variables were somewhat more advantageous than UAS data at our site, UAS was still a very useful complement; drone imagery and DEMs provided many of the predictors used for modeling of both UAS and transect vegetation data (Table 1). UAS methods also have the benefit of enabling estimates of vegetation cover in any area of the site (including those not easily accessible by foot) and examining vegetation in these areas in relation to new predictors that may not be adequately sampled on established transects. Ideally, managers can use both approaches to monitor vegetation, but under budget constraints, transect monitoring may be ideal for sites this size or smaller.

Large-scale restoration projects provide a remarkable opportunity for learning about mechanisms, and investing in rigorous monitoring informs future projects and enhances their success (Zedler 2000). Our investigation serves as a model for other salt marsh restoration projects, by integrating data on elevation, inundation, sediment properties and vegetation from both field sampling and remote sensing, and incorporating all of these into predictive models. The multi-faceted monitoring and modeling approach we implemented proved powerful in characterizing patterns of colonization as well as elucidating the potential mechanisms behind the observed patterns, and will inform future marsh restoration in California and beyond.

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APPENDIX A

FULL-SIZE MAPS OF PREDICTORS

Figure A1. Map of elevation at Hester Marsh following sediment addition (Aug 2018 DEM).

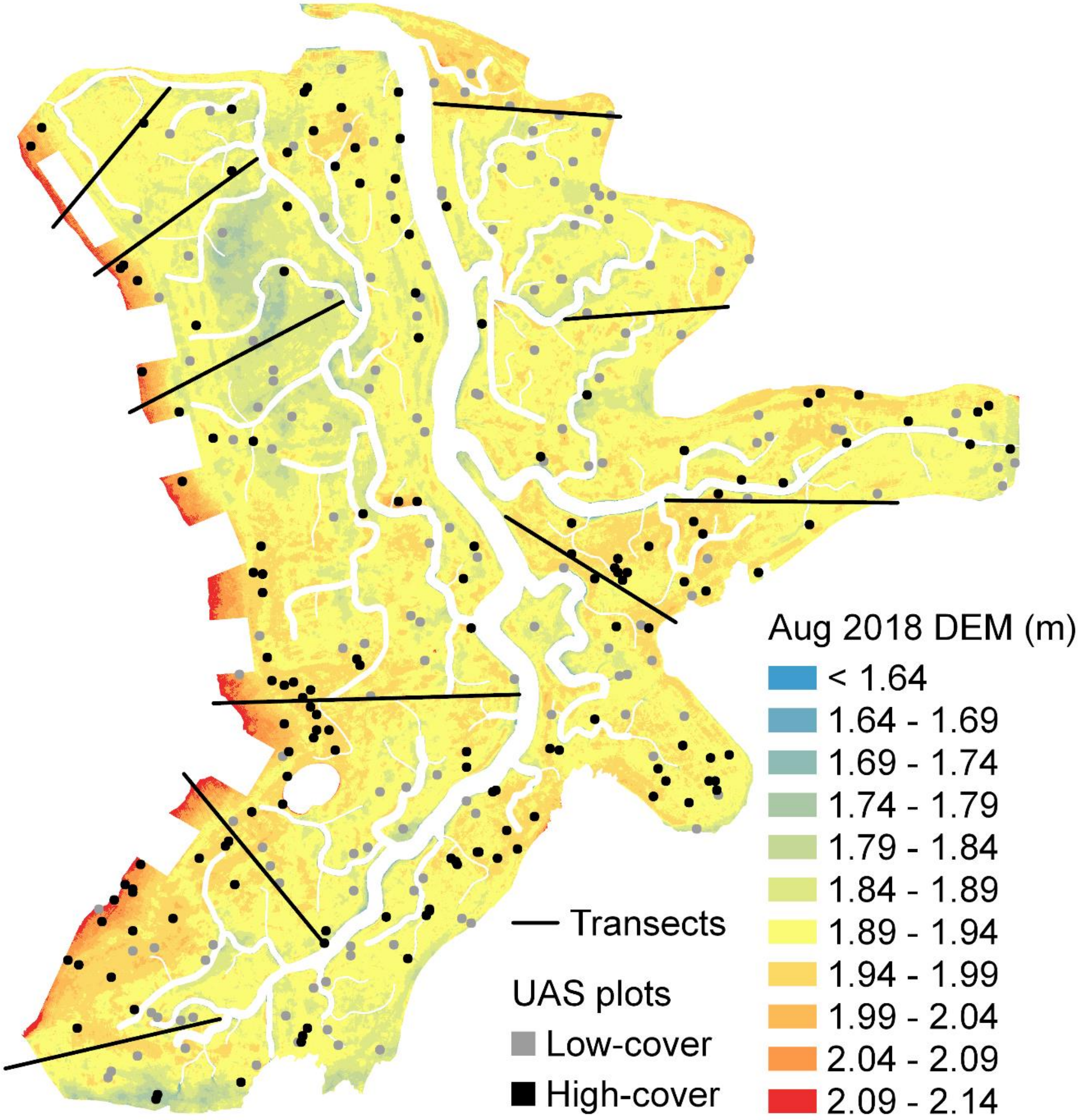


Figure A2. Map of elevation at Hester Marsh prior to restoration (Oct 2015 DEM).

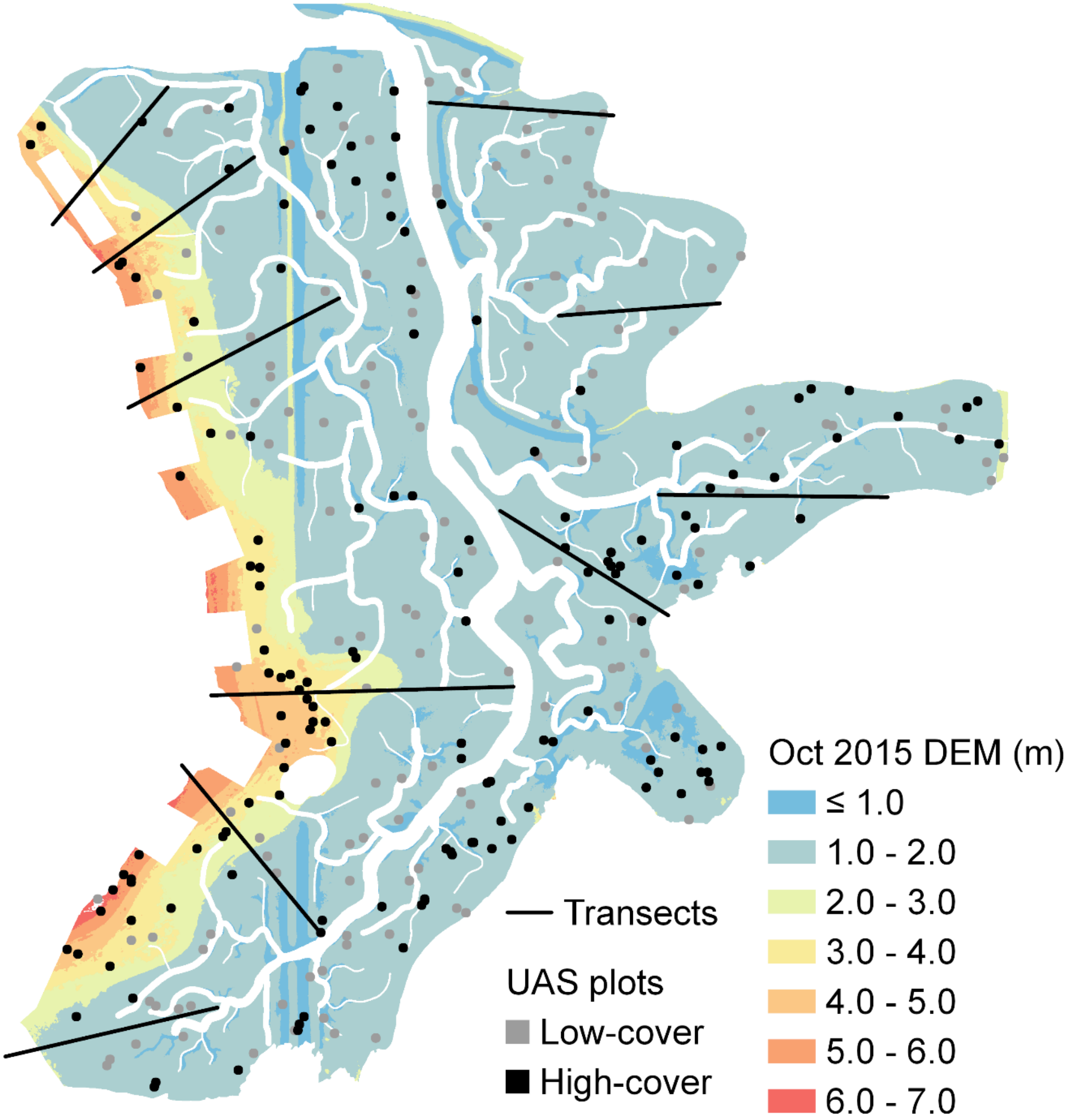


Figure A3. Map of inundation time (%) at Hester Marsh (tide data from Aug 2018 – May 2019, calculated based on elevations from May 2019 DEM).

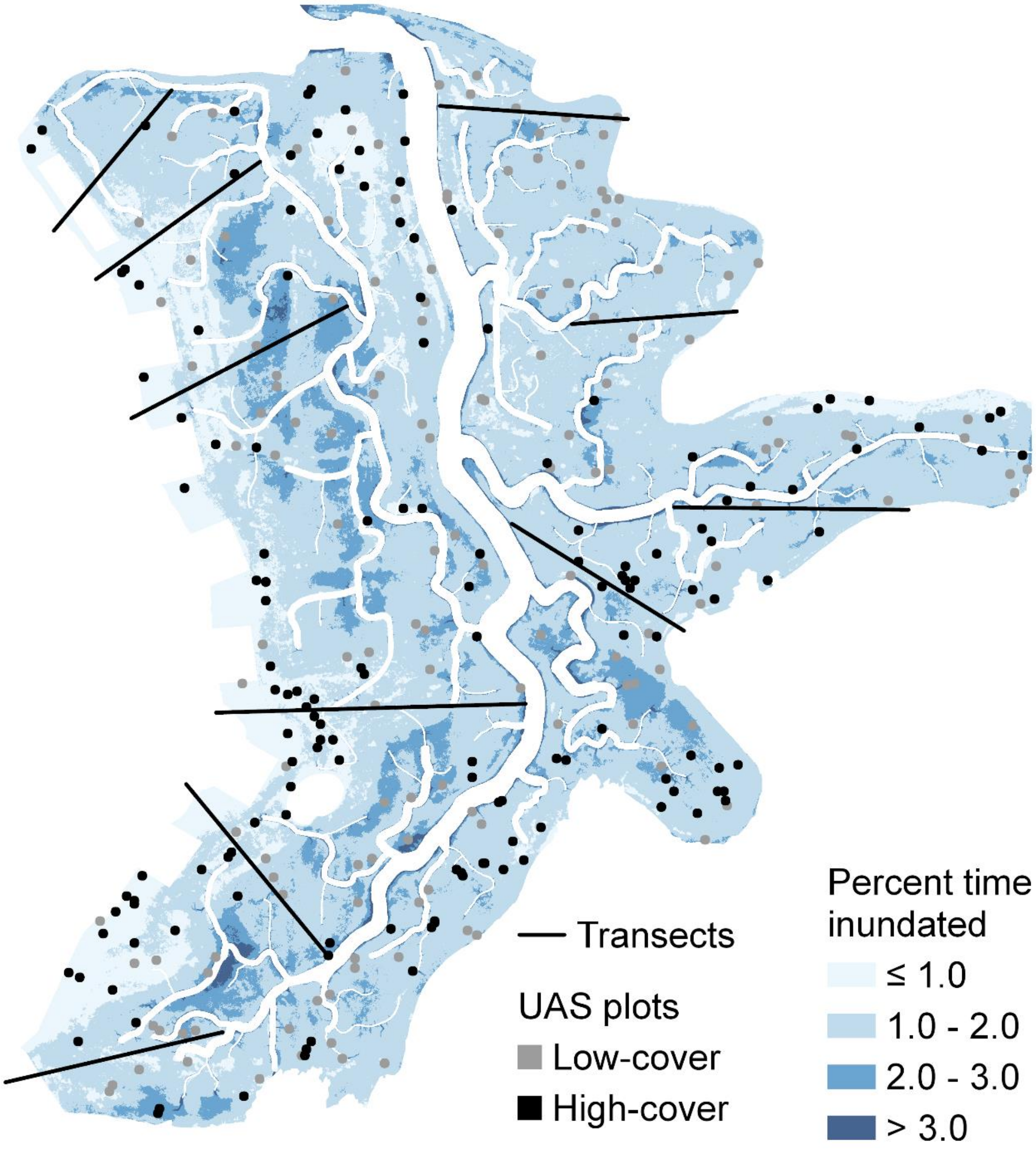


Figure A4. Map of modeled salinity at Hester Marsh. ArcGIS Pro forest-based regression model trained using 349 salinity data points collected in the field using a conductivity meter with elevation (May 2019 DEM), tidal creek distance (m; Fig. A7), and amount of sediment addition or removal during construction (m; Fig. A9) as predictors (out-of-bag RMSE = 3.08 ppt).

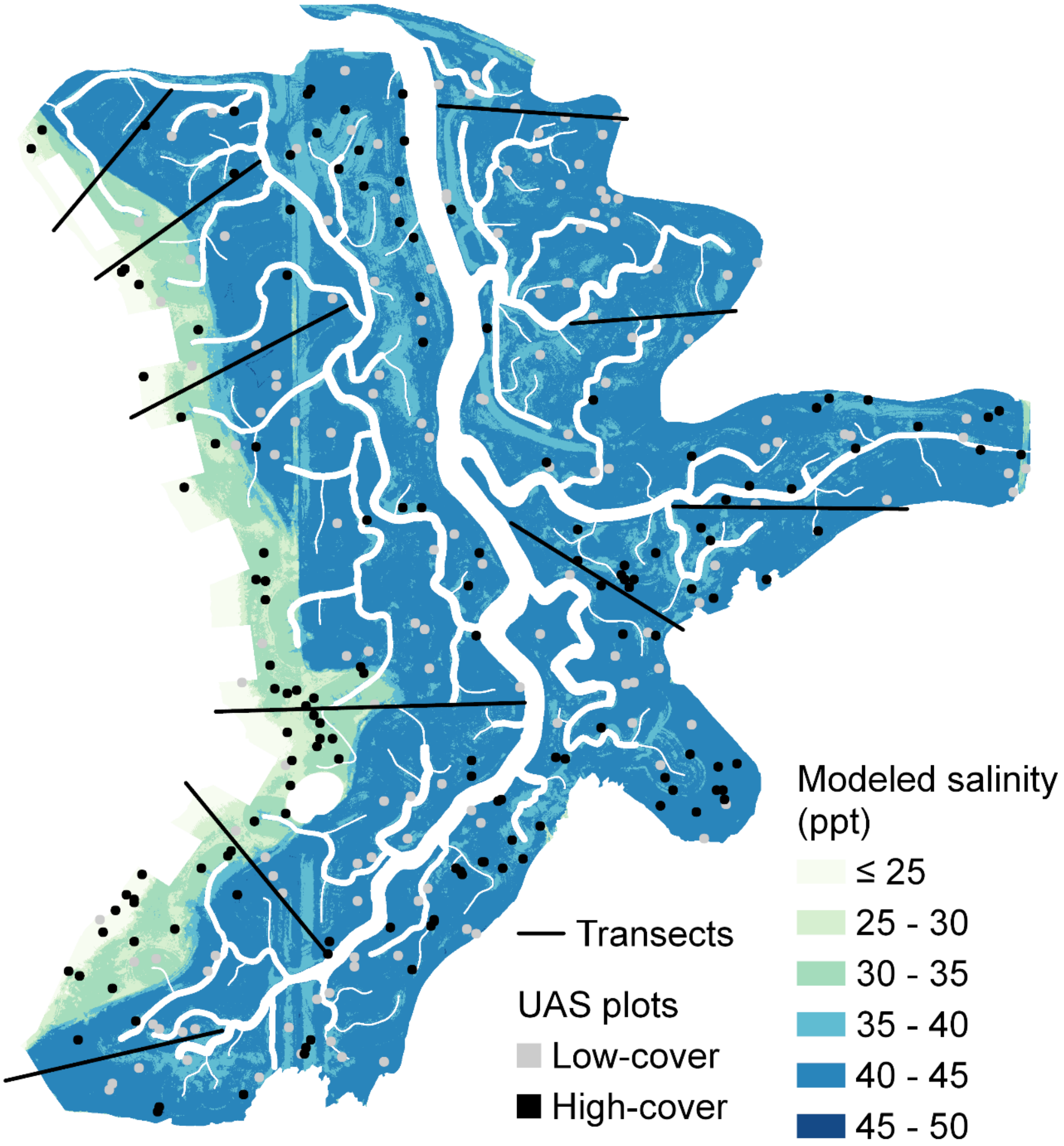


Figure A5. Map of Hester Marsh areas distinguished by sediment source used during site construction.

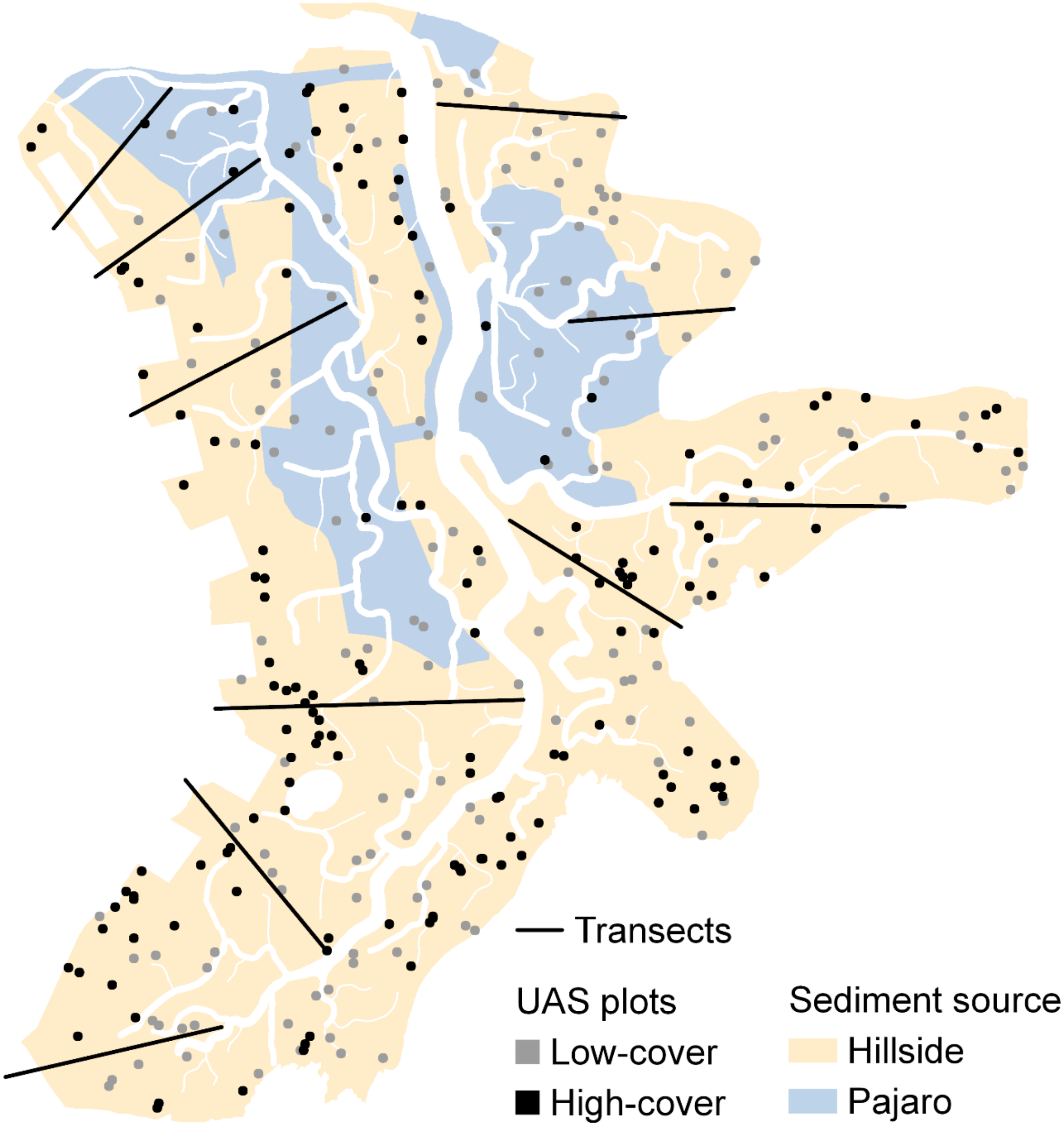


Figure A6. Map of elevation change over first year of restoration at Hester Marsh (August 2018 DEM subtracted from May 2019 DEM).

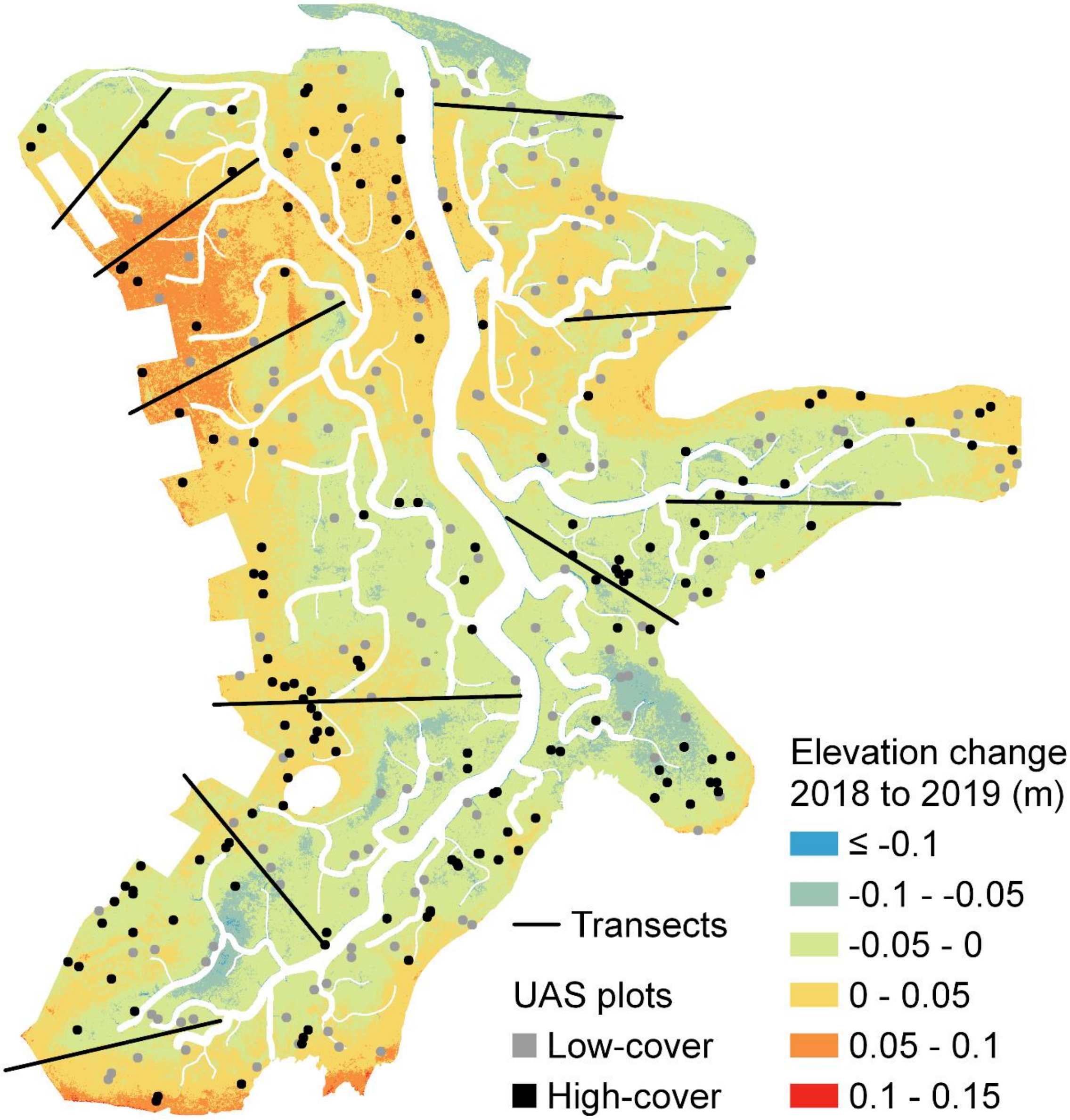


Figure A7. Map of tidal creek distance across Hester Marsh. Calculated using Euclidean distance from tidal creek polygon feature.

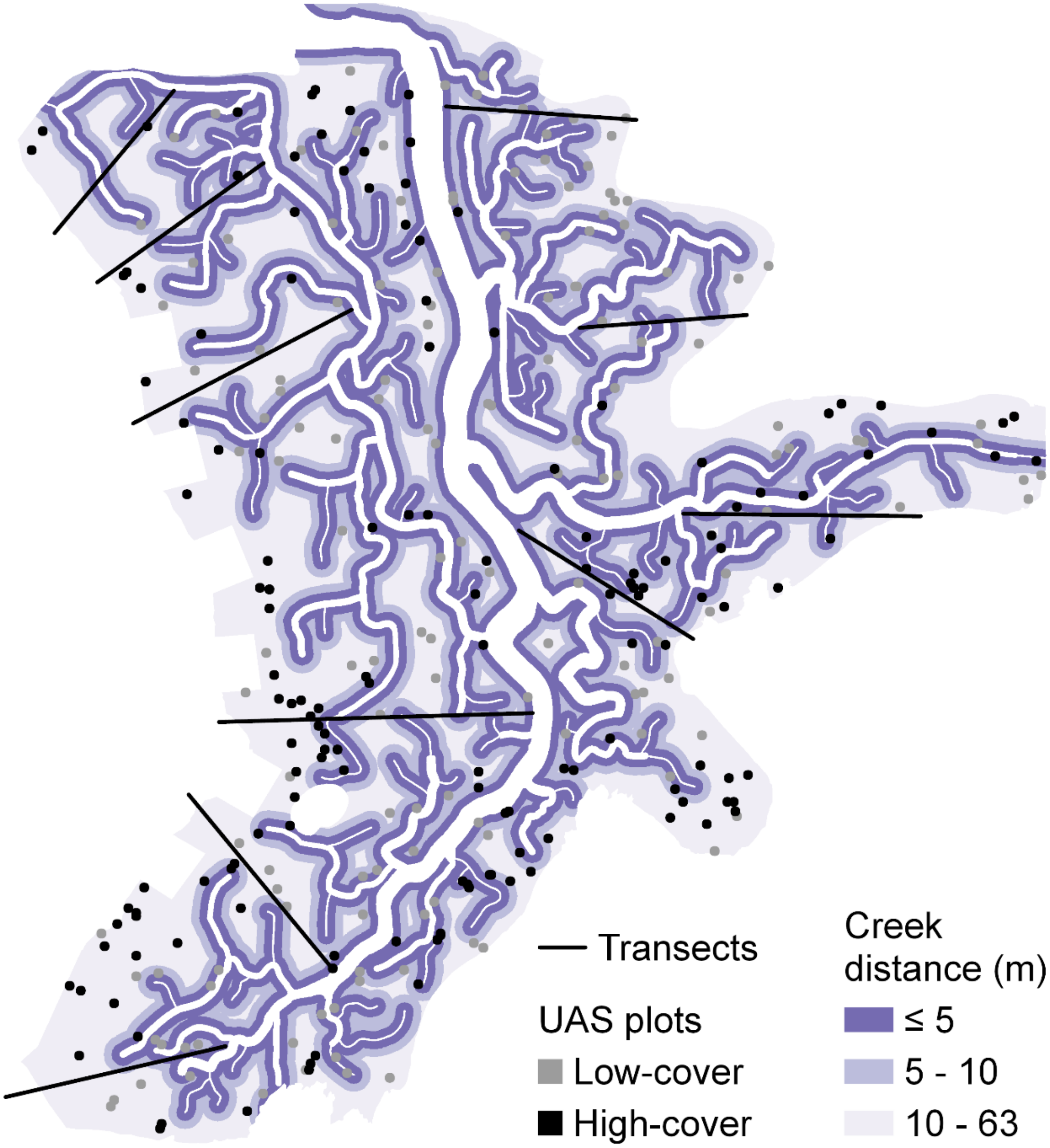


Figure A8. Map of habitat types across Hester Marsh in 2015, prior to restoration. Digitized from 2015 UAS imagery.

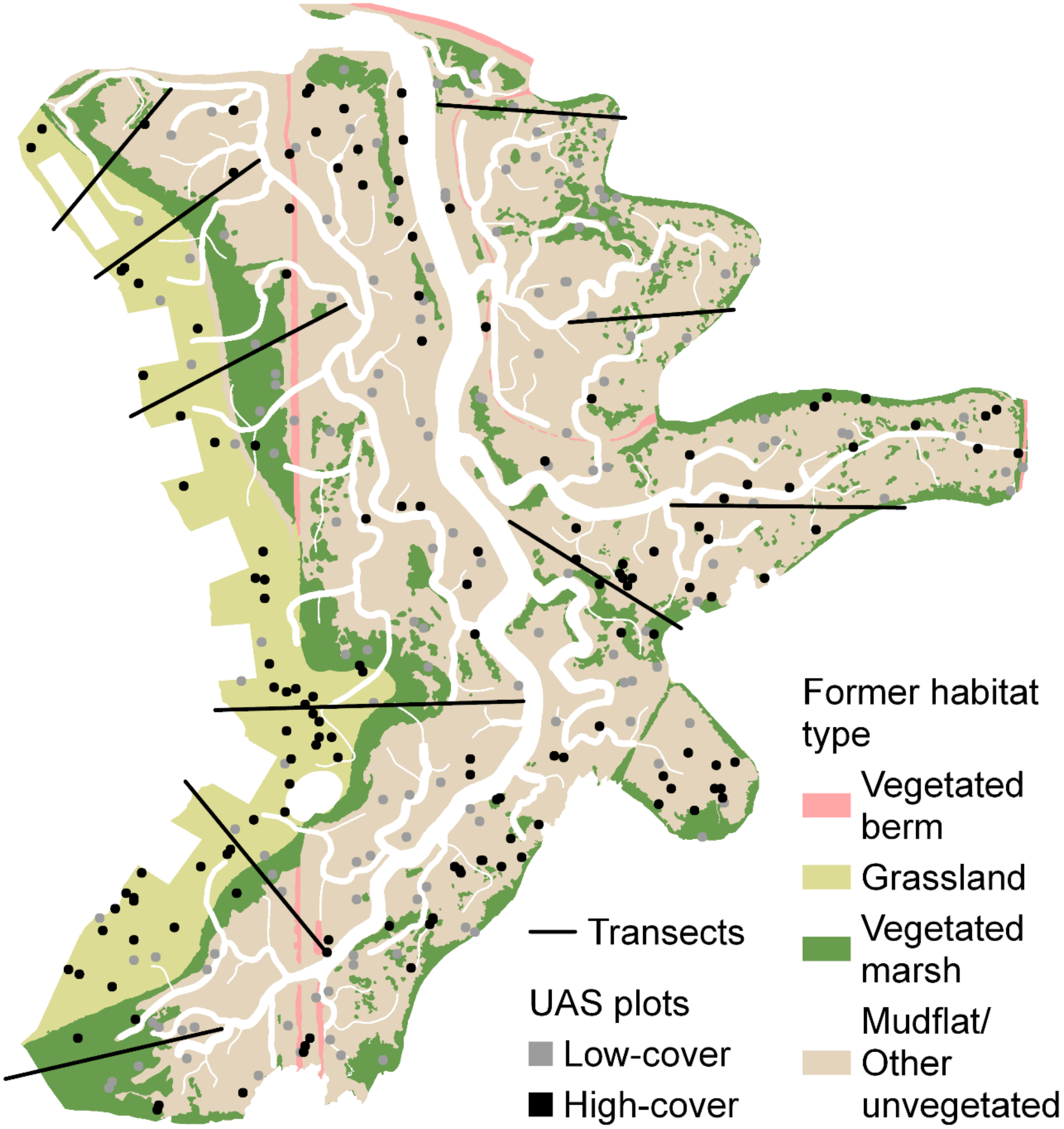
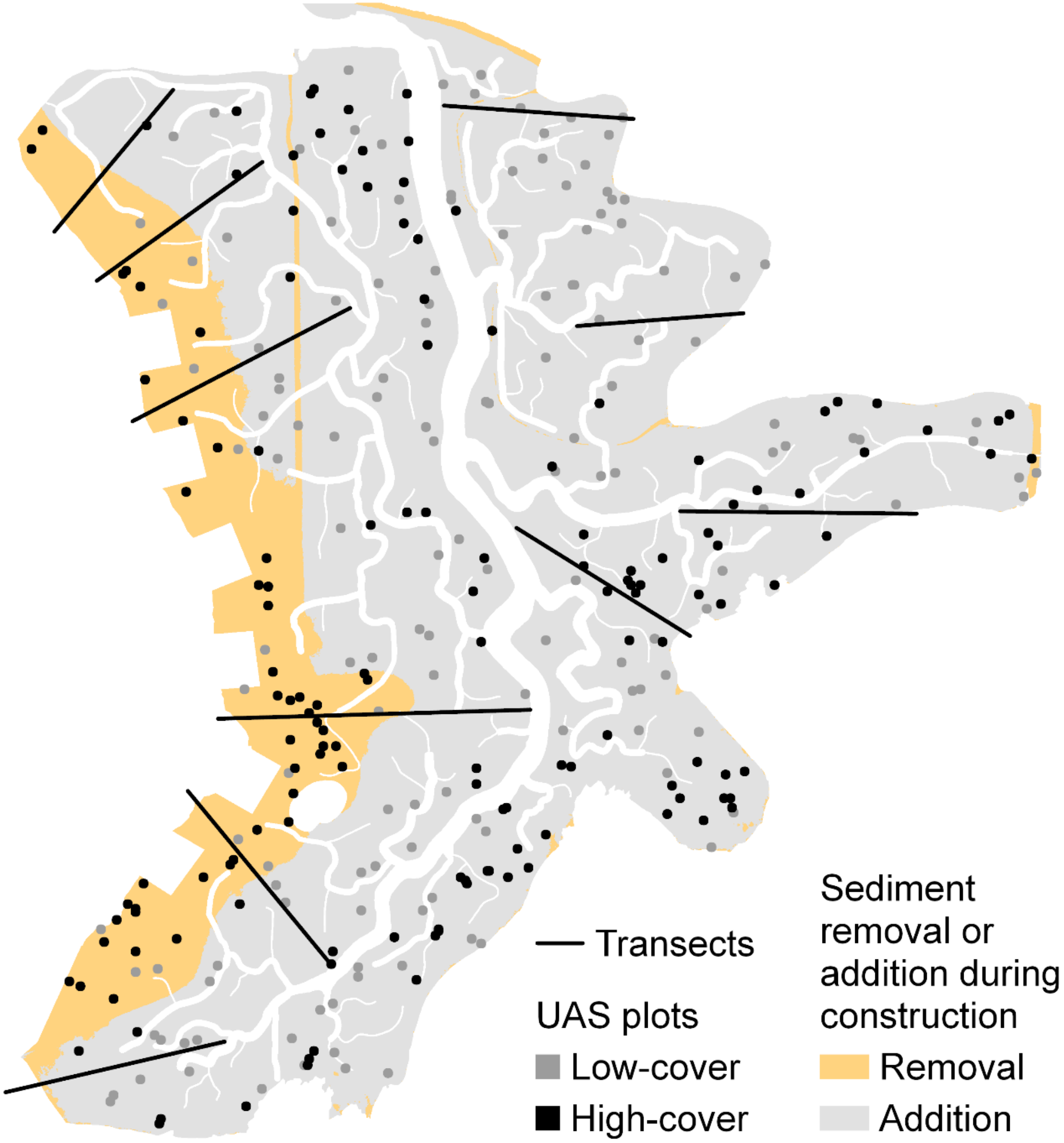


Figure A9. Map of sediment addition versus removal areas at Hester Marsh during construction of the restoration site. Calculated by subtracting October 2015 DEM from August 2018 DEM.



APPENDIX B

SUPPLEMENTARY DATA

Table B1. Vegetated marsh area within the Hester Marsh restoration project footprint, 1931 – present, and future expected vegetated area.

Year	Area (ha)	Source
1931	18.5	Digitized aerial imagery (1931)
2015	4.6	Digitized UAS imagery (Oct 2015)
2018	0.3	Digitized UAS imagery (Aug 2018) and estimates from area searches (Oct – Nov 2018)
2019	2.3	Classified UAS imagery (Oct 2019)
Goal (100% cover)	21.3	Whole project footprint excluding tidal creeks; digitized using UAS imagery and DEM (Aug 2018)

Table B2. Landward boundary of newly colonized *Salicornia* on initially-bare western transects (1-5) and of historically-existing *Salicornia* on southern and eastern transects (6-10).

Transect	Elevation (m; Aug 2019 DEM)
1	2.13
2	2.18
3	2.32
4	2.20
5	2.23
6	2.55
7	2.23
8	2.43
9	2.19
10	2.27

Other datasets too large to include here are available on request in comma-separated values format.

APPENDIX C

EVALUATING BENEFITS OF ACTIVE PLANTING IN MARSH RESTORATION

INTRODUCTION

The ecotone transition zone between the lower-elevation marsh plain and higher-elevation grassland is an important region in salt marshes, providing a unique assemblage of plants that supports diverse animal species and nutrient cycling (Page 1995; Traut 2005). Active planting is a potential method to boost initial ecosystem functioning by vegetation (Callaway et al. 2003), and may be necessary to achieve native species diversity (Lindig-Cisneros and Zedler 2002, Armitage et al. 2006). Early vegetation establishment is valuable in marsh restoration because it can prevent soils from becoming hypersaline and inhospitable to colonization by new plants (Shumway and Bertness 1992, Zedler et al. 2003, Boyer and Thornton 2012), may impede non-native species colonization by limiting open space available to opportunistic invaders (Callaway et al. 2003, Boyer and Thornton 2012), and indicates that the restoration site is beginning to provide ecosystem functions like biomass production and nitrogen retention (Callaway et al. 2003). Biodiversity is often a major goal for restoration projects because different species may provide distinct ecological functions (Zedler et al. 2001, Callaway et al. 2003, Boyer and Thornton 2012) and greater diversity may increase overall ecosystem function (Naeem et al. 1994, 1995, 1996; Zedler et al. 2001, Callaway et al. 2003), provide invasion resistance (Tilman 1997), and increase resiliency (Carvalho et al. 2013).

To examine whether active planting provided benefits in boosting early vegetation establishment and diversity at Hester Marsh, we compared native species richness and various percent cover metrics in areas that were actively planted with five different species in monocultures and similar areas that were left unplanted over the first year of restoration. In Elkhorn Slough, the majority of the marsh plain is dominated by a virtual monoculture of *Salicornia pacifica*, and marsh diversity is concentrated at the landward margin in the marsh-upland transition zone, which is also subject to invasion by upland weeds (Wasson and Woolfolk 2011). This ecotone occurs between Mean Higher High Water and the king tide line, which in most of Elkhorn Slough's marshes spans only a few horizontal meters, making the community there very sensitive to sea level rise (Wasson et al. 2013). At Hester Marsh, the marsh-upland ecotone was strategically designed with a much gentler slope than in most parts of the estuary, to allow for representation of marsh diversity and provide opportunities for marsh migration.

METHODS

While the marsh plain at Hester Marsh was left unplanted with the expectation that tides would bring in seeds of the dominant vegetation species, *Salicornia pacifica*, we actively planted five native marsh species in the most landward portion of the marsh on the western side of the site to examine these questions on early vegetation establishment and diversity. The five planted species were *Frankenia salina, Jaumea carnosa, Spergularia macrotheca, Distichlis spicata,* and *Extriplex californica*. All five species were planted in each of six 30 by 35 meter blocks in the gently sloped ecotone, where the marsh plain transitions to grassland (Fig. 1). In each block, each species was planted in a monoculture column with 60 rows. Plants were spaced 50 cm apart within each row. The number of plants per row alternated between four and five plants for a total of 270 plants per column. Space was left between planted blocks to enable comparison of unplanted and actively planted areas over time. All planted and unplanted areas span an approximate elevation gradient of 1.95 m to 2.25 m NAVD88 from top to bottom of each column.

To assess whether active planting was necessary to achieve early vegetation establishment and diversity, we surveyed vegetation cover and richness in unplanted and actively planted areas in June 2019 using the line intercept method. We surveyed one transect in each monoculture column of each planted area (n = 6 transects per planted species), and three approximately evenly spaced transects in each intervening unplanted area, for a total of 30 planted and 15 unplanted transects. On each 30 m transect, we dropped an intercept rod at 20 cm intervals and recorded the species that touched the rod, or “bare” if no live vegetation was touched. We calculated percent cover for each transect as the number of total “hits” for a species divided by total intercepts on the transect, multiplied by 100. We calculated native cover and total cover as indicators of early vegetation development and ecosystem functioning, *Salicornia* cover and non-native cover as indicators of holding space against the dominant vegetation species and non-natives, and native species richness as an indicator of diversity. Native cover was the sum of percent cover for *Baccharis pilularis*, *Distichlis*, *Extriplex*, *Frankenia*, *Grindelia stricta, Jaumea*, *Spergularia* spp., and *Salicornia*. Non-native cover was the sum of percent cover for all live plants identified as non-native species, and total cover was the sum of percent cover for all live plants.

We conducted broad treatment comparisons of unplanted (n = 15) and planted transects (n = 30) using two-tailed t-tests for percent cover metrics and generalized linear models (GLM) with a Poisson distribution for species richness. We also compared species richness using block rather than transect as the sampling unit (n = 6 planted and n = 5 unplanted blocks) to examine the effects of planting on vegetation diversity over these larger areas. We conducted equivalent comparisons for the unplanted transects compared with transects in each of the five planted area treatments, separated by the species actively planted (n = 6 per species), using two-tailed t-tests with the unplanted transects as the reference group for percent cover and GLM (Poisson distribution) for species richness.

RESULTS

Overall, average cover was high in both unplanted and actively planted areas (31.8% and 39.7%, respectively). Native cover was the dominant type of cover in both of the broad treatment categories (24.1% cover in unplanted and 28.3% cover in planted areas), and non-native cover was lower (7.7% cover in unplanted and 11.4% cover in planted areas). Average total, native, and non-native percent cover did not differ significantly between unplanted and actively planted areas, though all three vegetation cover metrics indicated a trend towards greater cover in planted areas (Table C1). Planted areas also had significantly greater native species richness (2.4 species per transect) compared to unplanted areas (1.1 species per transect; p = 0.003; Table C1). The difference in native species richness at the block level was even more striking, with an average of 6.5 species per planted block and 1.2 species per unplanted block (p < 0.001). *Salicornia* cover was the only metric we assessed that was lower in planted areas compared to unplanted areas (p = 0.002; Table C1).

Comparisons of the five planted area treatments, distinguished by the species actively planted, indicated some species-specific trends when examined against unplanted areas as the reference group. *Frankenia* planted areas were the only actively planted area that had significantly greater total cover compared to unplanted areas ($p = 0.02$), though *Spergularia* planted areas also tended to have relatively high total cover. The native cover trends were similar to those for total cover: *Frankenia* and *Spergularia* planted areas had significantly greater native cover compared to unplanted areas ($p = 0.006$ and $p = 0.04$, respectively; Fig. C1-A). Planted areas of all species tended to have lower *Salicornia* cover compared to unplanted areas (Fig. C1-B). This trend was marginally significant for *Distichlis* and *Extriplex* planted areas ($p = 0.05$ and $p = 0.06$, respectively) and significant for *Jaumea* ($p = 0.04$), *Spergularia* ($p < 0.001$), and *Frankenia* planted areas ($p < 0.001$). There were no significant differences in non-native cover between unplanted and any of the five types of planted areas (Fig. C1-C). Native richness was significantly greater in *Distichlis*, *Extriplex*, and *Jaumea* planted areas ($p < 0.05$) and marginally significantly greater in *Frankenia* and *Spergularia* planted areas ($p < 0.1$) compared to unplanted areas (Fig. C1-D).

Table C1. Overall comparisons of mean vegetation cover metrics and native richness on unplanted and actively planted transects. P-values from two-tailed t-tests.

	Unplanted transects (n = 15)	**Planted transects (n = 30)**	**P-value**
Total cover (%)	31.8	39.7	0.13
Native cover (%)	24.1	28.3	0.35
Salicornia cover (%)	24.0	10.3	0.002
Non-native cover (%)	7.7	11.4	0.17
Native richness (species)	1.1	2.4	0.003

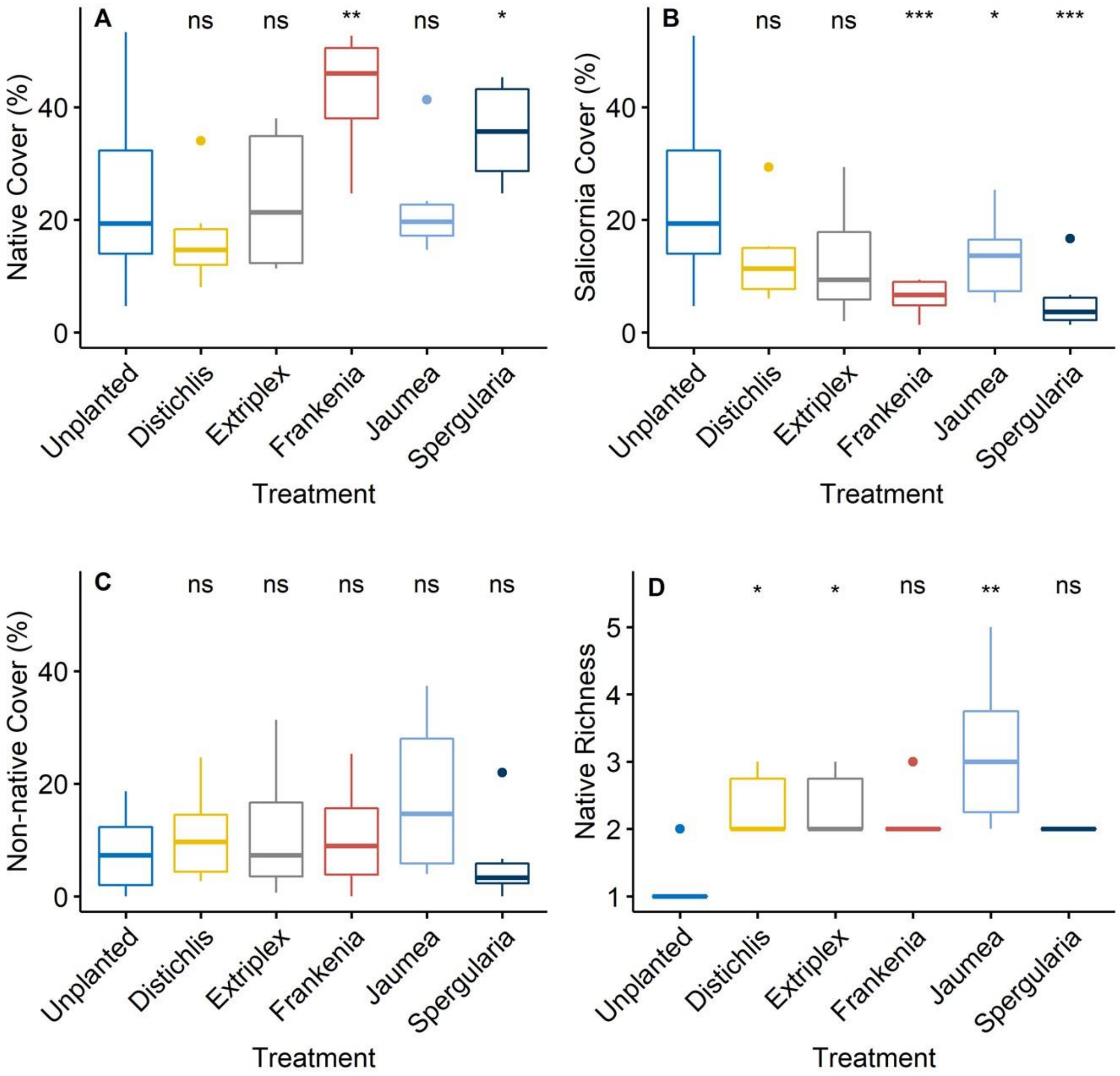


Figure C1. Comparisons of unplanted areas and different monoculture planting treatments by (A) percent cover of native species, (B) percent cover of *Salicornia*, (C) percent cover of non-native species, and (D) native species richness (n = 15 unplanted transects, n = 6 transects for each species actively planted). Data collected in June 2019. Significance values provided for native, *Salicornia*, and non-native percent cover based on t-tests with unplanted treatment as the reference group, and for native species richness based on generalized linear model with Poisson distribution (* indicates $p < 0.001$, ** indicates $p < 0.01$, * indicates $p < 0.05$, 'ns' indicates $p > 0.05$).**

DISCUSSION

Overall, active planting did not result in clear benefits over leaving areas unplanted in terms of boosting early vegetation cover or suppressing colonization by non-native plants (Table C1). Active planting did, however, increase native species richness and limit colonization by *Salicornia*, similar to results of other marsh restoration studies

(Table C1; Armitage et al. 2006). The lower native richness in unplanted areas is a result of *Salicornia* often being the only native colonist; *Salicornia* and the occasional *Spergularia* plants colonized both planted and unplanted areas, while planted area richness was boosted by the one species initially planted in monoculture. Dispersal limitation is widely suspected to limit recruitment in salt marshes (Lindig-Cisneros and Zedler 2002, Morzaria-Luna and Zedler 2007, Diggory and Parker 2011), and low diversity of colonists in the unplanted areas despite the existence of healthy patches of many of the planted species in other parts of the estuary suggests that this is also true of Elkhorn Slough. A longer time series of surveys will be needed to examine whether planted areas retain native richness and actively planted species maintain space against *Salicornia*.

Despite similar total and native cover in broad comparisons of planted and unplanted areas, planting certain species (particularly *Frankenia* and *Spergularia*) boosted overall native cover while limiting *Salicornia* cover because planted individuals of these species grew to a large size and took up space (Fig. C1-A, C1-B). Lower overall *Salicornia* cover in planted areas compared with unplanted areas was driven by trends for these two species. While other planted species did not increase total or native vegetation cover, all species were valuable for increasing native richness and tended to hold space against the dominant colonist, *Salicornia*. These other species may still be valuable to plant, particularly if they provide unique services. For example, *Distichlis* stems may be used by birds for nest construction (Massey et al. 1984), and *Jaumea* may facilitate survival of neighbors by providing structural support, buffering against sedimentation, and lowering sediment salinity (O'Brien and Zedler 2006). Future restoration projects should prioritize planting *Frankenia* and *Spergularia*, the most valuable species for providing early vegetation cover and holding space against the dominant *Salicornia*. Another Spergularia species (*S. marina*) was able to colonize naturally, but because *S. marina* primarily colonized the marsh plain and not the ecotone, planting *S. macrotheca* still appears to benefit vegetation development and diversity in this zone. Planting of other species should be based on the unique benefits they may provide.

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APPENDIX D

R CODE FOR STATISTICAL ANALYSES

```
# Set working directory
setwd("D:/ThesisData")

# Load packages
library(ggpubr)
library(randomForest)

################## Transect data analysis ##################
# Import formatted August 2019 data frame
dat = read.csv("Hester_TransectData_2019Aug_ForAnalysis.csv")
dat = dat[dat$ExistingVeg==0,] # remove quadrats in already-vegetated areas

# Change categorical variable columns to factors
dat$ElChgCat[dat$ElChgCat==0] <- "Removal"
dat$ElChgCat[dat$ElChgCat==1] <- "Addition"
dat$ElChgCat = as.factor(dat$ElChgCat)
dat$SedSrc[dat$SedSrc==0] <- "Hillside"
dat$SedSrc[dat$SedSrc==1] <- "Pajaro"
dat$SedSrc = as.factor(dat$SedSrc)
dat$HabMap4[dat$HabMap4==1] <- "B"
dat$HabMap4[dat$HabMap4==2] <- "G"
dat$HabMap4[dat$HabMap4==3] <- "V"
dat$HabMap4[dat$HabMap4==4] <- "M"
dat$HabMap4 = as.factor(dat$HabMap4)

# Examining differences in salinity by sediment source, excluding scraped areas
t.test(dat$Salinity.Sept[dat$SedSrc=="Hillside"&dat$ElChgCat=="Addition"],
  dat$Salinity.Sept[dat$SedSrc=="Pajaro"&dat$ElChgCat=="Addition"])

# Examining differences by elevation
dat = dat[complete.cases(dat[,"Elev"]),] # remove rows where elevation is NA
dat$ElevGrp[dat$Elev>=median(dat$Elev)] <- "High"
dat$ElevGrp[dat$Elev<median(dat$Elev)] <- "Low"
t.test(dat$NativeMarshSp[dat$ElevGrp=="High"],
  dat$NativeMarshSp[dat$ElevGrp=="Low"], alternative="greater")

# Trim dataset for random forest analysis
vars.t = c("NativeMarshSp", "Salinity.Sept", "SedSrc", "Elev", "ElChgCat",
  "CrkDist", "HabMap4", "Elev2015", "ElChg2019")
dat.t = dat[,vars.t]
dat.t = dat.t[complete.cases(dat.t[,vars.t]),] # remove NA rows

# Random forest model
set.seed(1)
rf1 = randomForest(NativeMarshSp ~ ., data=dat.t,
  importance=T, ntree=1500, corr.bias=T)
rf1
importance(rf1)

################## Marsh boundary analysis ##################
dat = read.csv("Hester_TransectData_2019Aug_ForAnalysis.csv")

# Remove quadrats without elevation data
dat = dat[complete.cases(dat[,"Elev"]),]

##### What % of all new marsh cover is below 2.14 m?
dat$Above214[dat$Elev>2.14] <- "High"
```

```
dat$Above214[dat$Elev<=2.14] <- "Low"
dat$Marsh = rowSums(dat[,c("MarshNonNatives", "NativeMarshSp")])
sum(dat$Marsh[dat$Above214=="Low"&dat$ExistingVeg==0])/
  sum(dat$Marsh[dat$ExistingVeg==0])*100

##### Upland vs marsh vegetation cover above and below 2.14 m
dat$Upland = rowSums(dat[,c("other", "UplandNonNatives")]) # Create upland col

# Paired t-test of upland vs marsh cover for initially-bare quads above 2.14 m
t.test(dat$Upland[dat$ExistingVeg==0&dat$Above214=="High"],
  dat$Marsh[dat$ExistingVeg==0&dat$Above214=="High"], paired=T)

##### Marsh boundary dataset (highest marsh plants on transects)
# Read boundary data sheet
el = read.csv("Hester_MarshBoundary_2019Aug_Elevs.csv", header=T)
el = el[el$Species=="Pickleweed",] # looking at pickleweed only
el$initial[el$Transect%in%1:5] <- "Bare"
el$initial[el$Transect%in%6:10] <- "Vegetated"

# Is pickleweed boundary lower on initially-bare transects
# compared with initially-vegetated transects?
t.test(el$Min190827[el$initial=="Bare"], el$Min190827[el$initial=="Vegetated"],
  alternative="l")

# Is pickleweed boundary on initially-bare transects below 2.14
# (highest winter tide)?
t.test(el$Min190827[el$initial=="Bare"], mu=2.14, alternative="less")

################## UAS cover data analysis ##################
dat.cc = read.csv("CoverCells300_9predictors.csv")

# Make categorical columns factors
dat.cc$ElChgCat[dat.cc$ElChgCat==0] <- "Removal"
dat.cc$ElChgCat[dat.cc$ElChgCat==1] <- "Addition"
dat.cc$ElChgCat = as.factor(dat.cc$ElChgCat)
dat.cc$SedSrc[dat.cc$SedSrc==0] <- "Hillside"
dat.cc$SedSrc[dat.cc$SedSrc==1] <- "Pajaro"
dat.cc$SedSrc = as.factor(dat.cc$SedSrc)
dat.cc$HabMap[dat.cc$HabMap==1] <- "Berm"
dat.cc$HabMap[dat.cc$HabMap==2] <- "Grass"
dat.cc$HabMap[dat.cc$HabMap==3] <- "Marsh"
dat.cc$HabMap[dat.cc$HabMap==4] <- "Mud"
dat.cc$HabMap = as.factor(dat.cc$HabMap)

# Trim dataset for random forest analysis
vars.cc = c("Cover", "CrkDist", "SedSrc", "Inund", "Elev2018", "Elev2015")
dat.cc = dat.cc[,vars.cc]

# Random forest model
set.seed(1)
rf.cc = randomForest(Cover ~ .,
  data = dat.cc, importance=T, ntree=1500, corr.bias=T)
rf.cc
importance(rf.cc)

################## Sediment analysis ##################
dat = read.csv("Hester_SoilSampling_191002_All.csv")

# Check for unintended differences btw healthy & unhealthy
t.test(dat$DEM190827[dat$Vegetated=="Well"],
  dat$DEM190827[dat$Vegetated=="Poorly"])
t.test(dat$CrkDist[dat$Vegetated=="Well"],
  dat$CrkDist[dat$Vegetated=="Poorly"])
```

```
##### Means, SDs, t-test significance for well- vs poorly-vegetated sites
vars = c("NH3.N.ppm", "Cl.meq.l", "ECe", "Na.ppm", "Atterberg_LiquidLimit",
  "CEC.meq.100g", "MoistureContent", "SO4.S.meq.l", "pH.SMP.Buffer",
  "GrainSizeMean_Bulk", "K.ppm", "pH.sample", "Sat...", "Mg.ppm", "Exch..K",
  "Exch..Na", "Exch...Mg")

healthy = dat[dat$Vegetated=="Well",]
for(v in vars){
  print(paste(v, ":",
  "mean =", round(mean(healthy[,v]),2), "/",
  "sd =", round(sd(healthy[,v]),2)))}

unhealthy = dat[dat$Vegetated=="Poorly",]
for(v in vars){
  print(paste(v,":",
  "mean =", round(mean(unhealthy[,v]),2), "/",
  "sd =", round(sd(unhealthy[,v]),2)))}

for(v in vars){
  print(paste(v, ":", "p =",
  round(t.test(healthy[,v],unhealthy[,v])$p.value,3)))}

##### Comparison of properties in hillside vs Pajaro areas
# Examining all variables that were contributors to nMDS
for(v in vars){
  print(paste(v, ":", "p =",
  round(t.test(unhealthy[unhealthy$SedSrc=="Hillside",v],
  unhealthy[unhealthy$SedSrc=="Pajaro",v])$p.value,3)))}

# Examining variables that showed significant differences
t.test(unhealthy$ECe[unhealthy$SedSrc=="Hillside"],
  unhealthy$ECe[unhealthy$SedSrc=="Pajaro"])
t.test(unhealthy$MoistureContent[unhealthy$SedSrc=="Hillside"],
  unhealthy$MoistureContent[unhealthy$SedSrc=="Pajaro"])
t.test(unhealthy$GrainSizeMean_Bulk[unhealthy$SedSrc=="Hillside"],
  unhealthy$GrainSizeMean_Bulk[unhealthy$SedSrc=="Pajaro"])

################## Planted vs. unplanted analysis ##################
dat = read.csv("Hester_PlantedVsUnplanted_Transects_190624.csv")
dat_blocks = read.csv("Hester_PlantedVsUnplanted_Blocks_190624.csv")
dat$Species <- factor(dat$Species, levels=c("Unplanted", "Distichlis",
  "Extriplex", "Frankenia", "Jaumea", "Spergularia"))

##### Native richness: GLMs w/ Poisson distribution
# Native richness ~ treatment (transect as unit)
m.rt = glm(NativeRichness ~ Treatment, data=dat, family=poisson)
summary(m.rt)

# Native richness ~ treatment (block as unit)
m.rt.b = glm(NativeRichness ~ Treatment, data=dat_blocks, family=poisson)
summary(m.rt.b)

# Native richness ~ species (transect as unit)
m.rs = glm(NativeRichness ~ Species, data=dat, family=poisson)
summary(m.rs)

##### Planted vs unplanted t-tests
vars = c("TotalCover", "AllNative", "Pickleweed", "AllExotic")

dat.u = dat[dat$Treatment=="Unplanted",]
for(v in vars){
  print(paste(v, ":", "mean =", round(mean(dat.u[,v]),2)))}
```

```
dat.p = dat[dat$Treatment=="Planted",]
for(v in vars){
  print(paste(v, ":", "mean =", round(mean(dat.p[,v]),2)))}

for(v in vars){
  print(paste(v, ":", "p =", round(t.test(dat.u[,v],dat.p[,v])$p.value,3)))}

##### Species-specific comparisons with unplanted
# Total cover
compare_means(TotalCover ~ Species,  data=dat, ref.group="Unplanted",
  method="t.test")

# Native cover
compare_means(AllNative ~ Species,  data=dat, ref.group="Unplanted",
  method="t.test")

# Pickleweed cover
compare_means(Pickleweed ~ Species,  data=dat, ref.group="Unplanted",
  method="t.test")

# Non-native cover
compare_means(AllExotic ~ Species,  data=dat, ref.group="Unplanted",
  method="t.test")
```