Monitoring Vegetation Dynamics at a Tidal Marsh Restoration Site: Integrating Field Methods, Remote Sensing and Modeling

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Abstract

Sea level rise threatens coastal wetlands worldwide, and restoration projects are implementing strategies that decrease vulnerability to this threat. Vegetation monitoring at sites employing new restoration strategies and determination of appropriate monitoring techniques improve understanding of factors leading to restoration success. In Central California, soil addition raised a degraded marsh plain to a high elevation expected to be resilient to sea level rise over the next century. We monitored plant survival and recruitment using area searches, transect surveys, and unoccupied aircraft systems (UAS) imagery. We used random forest modeling to examine the influence of nine environmental variables on vegetation colonization and conducted targeted soil sampling to examine additional factors contributing to vegetation patterns. Limited pre-construction vegetation survived soil addition, likely due to the sediment thickness (mean = 69 cm) and placement method. After 1 year, about 10% of the initially bare area saw vegetation reestablishment. Elevation and inundation frequency were particularly critical to understanding restoration success, with greatest vegetation cover in high-elevation areas tidally inundated < 0.85% of the time. Soil analysis suggested greater salinity stress and ammonium levels in poorly-vegetated compared to well-vegetated areas at the same elevation. We found that both transect and UAS methods were suitable for monitoring vegetation colonization. Field transects may provide the best approach for tracking early vegetation colonization at moderate-sized sites under resource limitations, but UAS provide a complementary landscape perspective. Beyond elucidating patterns and drivers of marsh dynamics at a newly restored site, our investigation informs monitoring of marsh restoration projects globally.

Keywords Salt marsh · Salicornia · Elevation · Salinity · Unoccupied aircraft systems

Communicated by Charles T. Roman

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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 and Megonigal 2013; Weston 2014; Watson et al. 2017; 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 (Callaway et al. 2011; Li et al. 2018).

Marshes occupy a narrow vertical range in the intertidal zone, between mean sea level and the king tide line, with most plant species occurring above mean high water (Larson 2001). Reduced riverine sediment supplies and subsidence due to groundwater overdraft or diking have resulted in marsh plain 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 and Megonigal 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 applications of sediment that allow for survival and vertical growth of marsh vegetation through the added sediment, with natural seedling recruitment supplementing growth of surviving vegetation to restore marsh cover (Raposa et al. 2020). Thick sediment applications on highly degraded and subsided marshes, which likely rely more on colonization by tidally dispersed seeds than on vegetation survival (Mendelssohn and Kuhn 2003), require further study to better understand redevelopment of vegetation cover.

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 at least one metric for monitoring restoration progress, as this represents establishment of the foundation species that other marsh species depend on. Innovative methods, such as using imagery collected by unoccupied aircraft systems (UAS), are also being examined to help researchers keep up with an increasing scale and frequency of restoration projects with limited monitoring budgets and staff (Shuman and Ambrose 2003). Remote sensing methods like UAS may be advantageous over traditional field survey methods, like transect sampling, because they can cover large areas in a short period of time while minimizing trampling of newly established vegetation and disturbance to wildlife (Shuman and Ambrose 2003; Tuxen et al. 2008; Chabot and Bird 2015). While UAS monitoring of revegetation associated with restoration projects is an emerging trend (Knoth et al. 2013; Buters et al. 2019; Haskins et al. 2021), its utility in monitoring and understanding early vegetation colonization at restoration sites requires further study. UAS methods have not been extensively applied to mapping and modeling very early vegetation colonization in wetlands, likely because the ultra-high-resolution imagery necessary to identify small patches of plants has only recently become widely available (Anderson and Gaston 2013; Gray et al. 2018).

Many factors can influence marsh vegetation distribution by influencing (1) tidally dispersed seed delivery and (2) seed germination and seedling 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; Armitage et al. 2006; Morzaria-Luna and Zedler 2007). Tidal inundation also influences abiotic conditions that can promote or inhibit germination and growth, including moisture and salinity (Mahall and Park 1976c; Shumway and Bertness 1992; Noe and Zedler 2000, 2001; Woo and Takekawa 2012). Tidal creeks influence marsh species distributions (Zedler et al. 1999; Sanderson et al. 2001) and vegetation height and biomass (Schile et al. 2011), with possible mechanisms including improved drainage near creeks and flushing of salts and other toxins. Additional factors related to soil addition, such as the properties (Reimold et al. 1978; Wigand et al. 2016) and thickness (Stagg and Mendelssohn 2010; Walters and Kirwan 2016) of added soil, can also affect marsh plant survival and colonization.

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 soil addition to create a high-elevation marsh plain. Limited marsh vegetation (less than 20% cover) was present before construction of the restoration site, and one area of interest was whether some of it would survive soil 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 quickly would the site be colonized by new plants? Would any species other than the marsh dominant, *Salicornia pacifica* (perennial pickleweed), colonize the site? What factors are associated with natural colonization? 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 soil 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 soil addition process, and soil properties. Overall, improving understanding of the vegetation colonization process will inform managers about the most important factors to consider when designing high marsh restoration projects, and comparing field- and UAS-based monitoring methods will reveal relative benefits of different strategies to inform future monitoring and analysis.

Methods

Site Description

We conducted this research at a recently restored 25-ha marsh in Elkhorn Slough, located in Monterey Bay in Central

California (Fig. 1). 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 (Wasson et al. 2012). The threat of sea level rise is exacerbated by other stressors including high erosion rates associated with engineering of the estuary mouth, low sediment supply due to river diversion, and eutrophication (Wasson et al. 2017).

Elkhorn Slough is a heavily marine-influenced estuary, with strong tidal currents and most of its waters near marine salinity (Caffrey et al. 2002). Marsh vegetation in this region typically grows through the spring and summer (Mahall and Park 1976a), with natural dieback in the fall and winter. Seeds of the most common marsh plants in Elkhorn Slough are dispersed in the winter and typically begin germinating in the early spring (Mayer 1987).

An ecosystem-based management initiative launched by the Elkhorn Slough National Estuarine Research Reserve (ESNERR) resulted in 25 ha of restored marsh area, known as Hester Marsh, in 2018. This area included 19 ha of degraded marsh that had been diked and drained, then subsided and degraded to mudflat once the dikes failed. The restoration area also included 6 ha of former agricultural land that was graded to facilitate upland migration in response to anticipated sea level rise. Between December 2017 and August 2018, 176,000 m^3 of soil and sediment were used to restore the degraded marsh plain, raising it by an average of 69 cm to a target elevation of 1.89 m NAVD88 (inundated 1–2% of the time), an elevation expected to be resilient to sea level rise for at least 100 years. Tidal creeks were excavated following soil and sediment addition to resemble the historical creek network. The material added to the degraded marsh was primarily upland soil from former farmland on an adjacent hillside combined with some dredge material from the Pajaro River Bench Excavation Project (Fountain et al. 2019). We will refer to the combined upland and dredge material as "soil" throughout this paper. Because of variation in elevation across the landscape prior to restoration (e.g., high berms, low mudflats, and basins) the amount of soil addition varied across the site, and some high areas had soil removed ("scraped"), rather than added, to meet the target marsh elevation. Placement of soil from these sources resulted in a new high intertidal plain that was virtually bare and lacked halophyte seeds when it was opened to tidal exchange in August 2018. Six blocks were actively planted on the western side of the site, and were excluded from analyses of natural colonization (Fig. 1).

We considered the Hester Marsh restoration project footprint (Fig. 1) to be the area below an elevation of 2.3 m NAVD88 in August 2018 according to a UAS-derived digital surface model (DSM). This includes the construction zone where soil addition or removal occurred, in addition to a very narrow band of existing marsh vegetation on the eastern and southern restoration site edges that was neither buried nor scraped. While DSMs measure the elevation of the surface and any features on it, we primarily relied on DSMs collected when the site was mostly bare so the models would
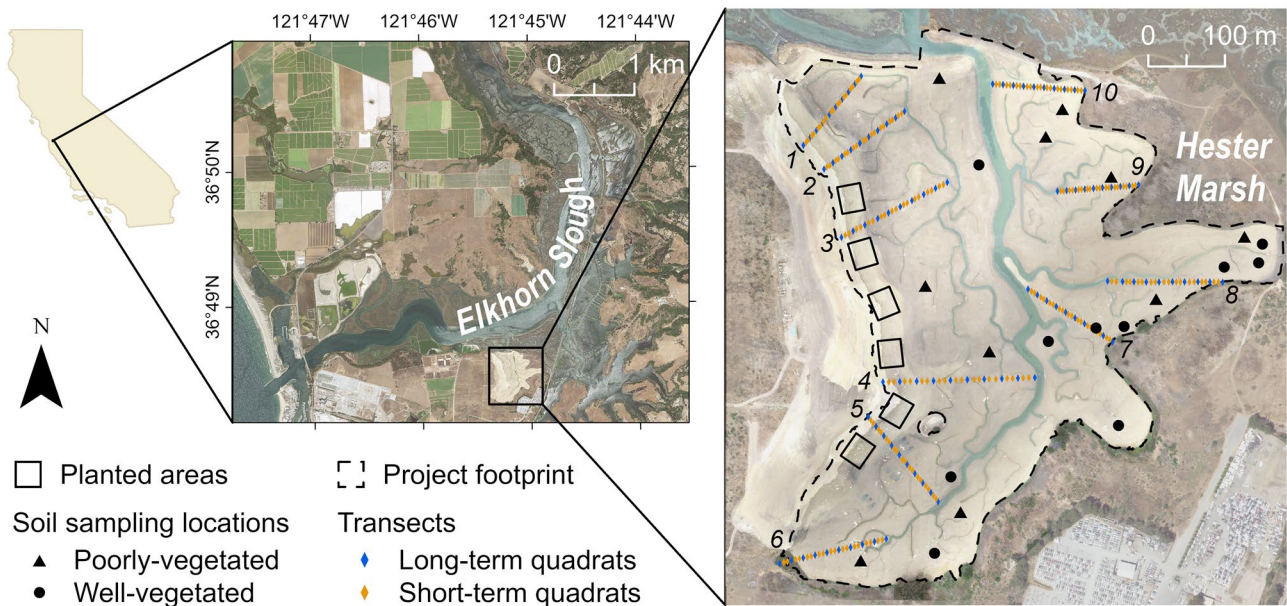

Fig. 1 Geographic location and site map of Hester Marsh, located on the southern side of Elkhorn Slough in Central California, USA

better approximate bare earth. However, we recognize that elevations in areas of our DSMs with larger, well-established plants may not be accurate.

Estimating Vegetated Area Before Degradation and Before Restoration

To quantify baseline conditions at the focal marsh prior to anthropogenic activities that led to marsh degradation (primarily through diking and draining), we digitized historical vegetated area using earliest available aerial imagery from 1931. To quantify vegetated area under degraded conditions shortly prior to initiation of the restoration project, we used 2015 UAS imagery (Electronic Supplement 1).

Area Searches for Marsh Vegetation Surviving Construction

To examine plant survival following the construction phase of restoration, we conducted area searches of the construction zone in Fall 2018. This method involved walking the entire construction zone where soil was added or removed in an attempt to find every plant that survived construction. We logged the locations and approximate numbers of plants we encountered using a handheld GPS (Trimble Juno 3B, Trimble Inc., Sunnyvale, CA). We quantified the area covered by surviving plants based on the number of plants of each species logged with the GPS and an approximate size of an individual of each species. To better understand the spatial patterns of vegetation survival, we examined the GPS points in relation to digitized 2015 UAS imagery (Electronic Supplement 1). To quantify the existing marsh vegetation outside the construction area that remained on the restoration site edge, we digitized this area from UAS imagery collected in August 2018. We estimated the total vegetated marsh area in 2018 as the sum of surviving vegetation cover and the digitized existing vegetation.

Transect Monitoring of Vegetation Colonization

We monitored vegetation, elevation, and associated parameters over time along 10 permanent transects established by ESNERR (Fig. 1). Using a systematic approach, 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. Transect length ranged from 117 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

(transects 6–10 in Fig. 1) started in existing marsh vegetation that was not scraped or buried during construction. Quadrats in existing vegetation were excluded from summary graphs.

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 at all quadrats. For the long-term quadrats, we also measured maximum canopy height of *Salicornia* (the dominant vegetation).

We measured vegetation cover at each quadrat using the point-intercept method within a 50 cm by 50 cm PVC frame. At each of the 16 intercepts on a string grid within the frame, we dropped a metal rod and recorded the presence of each plant species that touched the rod (or "bare" if no live plants were encountered). We used the intercept data to calculate percent cover for each species within the quadrat (Electronic Supplement 1). We collected maximum 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 relative *Salicornia* biomass for each quadrat by multiplying the average of the three canopy heights by percent cover of *Salicornia*.

To monitor elevation, we established baseline conditions in August 2018 at the 100 long-term quadrats using RTK GPS (EOS Arrow 200 with ArcGIS Collector) and monitored elevation in August 2019 at all 280 long-term and temporary quadrats using a Sprinter 150 laser level. 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 (a subset of the points shown in Electronic Supplement 1, Fig. S5; 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 UAS surveys, including DSMs and imagery. To include inundation time as a predictor, we calculated percent time inundated over the first year of restoration using data from a nearby water quality monitoring sonde located at Vierra Marsh (Electronic Supplement 1,

Characterization of Inundation Across Elevations). 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). We systematically removed one variable at a time to determine which factors to include in the final model (Electronic Supplement 1). 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).

Site-Wide UAS Monitoring of Vegetation Colonization

We monitored vegetation development and elevation changes for the first year of restoration approximately monthly using UAS imagery. We analyzed factors influencing vegetation presence based on high-resolution imagery collected in October 2019 (pixel size = 0.79 cm; Electronic Supplement 1), at the end of the first growing season. We created a classified image of vegetated and unvegetated areas using the October 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. Initially, we created two classified images using a pixel-based and an object-based approach, and selected the more accurate of the two classified images based on qualitative and quantitative assessment. We used stratified random sampling to sample 150 low-cover and 150 high-cover cells for site-wide modeling of factors influencing vegetation cover (Electronic Supplement 1, Site-Wide UAS Monitoring of Vegetation Colonization). We used tide data from a nearby sonde to limit our analysis to the extent of expected marsh plant seed dispersal, in order to exclude most upland plant cover (Electronic Supplement 1, Characterization of Inundation Across Elevations).

Several UAS DSMs and DSM-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). In order to include salinity as one of the nine predictors, 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 soil 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 the nine potential predictors on vegetation cover using random forest modeling with the *randomForest* package (v. 4.6–14; Liaw and Wiener 2002) in R software (v. 3.5.1; R Core Team 2018). We used the same parameters and technique for variable selection and performance assessment that we used for modeling the transect data.

Soil Comparison at Well-Vegetated and Poorly-Vegetated Sites

We collected soil samples at 10 well-vegetated and 10 poorly-vegetated sites of similar elevation and distance to tidal creeks to examine additional factors that might be leading to low colonization and growth in some areas but were

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 laser leveling in August 2019	August 2018 DSM (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 DSM (pixel size = 3.3 cm)
Elevation change over first year of restoration (m)	Calculated by subtracting August 2018 DSM from May 2019 DSM (pixel size = 3.3 cm)	Calculated by subtracting August 2018 DSM from May 2019 DSM (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)
Soil source (categorical)	Digitized from mid-construction UAS imagery (Feb 2018)	Digitized from mid-construction UAS imagery (Feb 2018)
Soil addition/removal (categorical)	Categorical elevation change raster (Oct 2015 DSM subtracted from Aug 2018 DSM; pixel size = 6 cm)	Categorical elevation change raster (Oct 2015 DSM subtracted from Aug 2018 DSM; pixel size = 6 cm)
Elevation pre-restoration (m)	Oct 2015 DSM (pixel size = 6 cm)	Oct 2015 DSM (pixel size = 6 cm)
Former habitat type (categorical)	Digitized 2015 habitat map	Digitized 2015 habitat map

not represented in transect or UAS surveys (Fig. 1). Well-vegetated areas were those with relatively high cover and large plants, while poorly-vegetated areas were those with low cover and small plants. We identified sampling locations using UAS imagery and a DSM (Electronic Supplement 1).

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 soil 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 20 samples for soil 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 (Clarke et al. 2014a; National Lacustrine Core Facility 2013; NYDOT 2015). We analyzed 20 additional soil samples (0–10 cm) by homogenizing three triplicate samples collected 0.3 m apart for nitrate, ammonium, phosphorus, saturation (%), pH, conductivity, sodium, chloride, sulfate, calcium, potassium, magnesium, and cation exchange capacity (Electronic Supplement 1).

We conducted a suite of related non-metric multi-dimensional scaling analyses using Primer v. 7.0 to determine whether soil properties differed between well- and poorly-vegetated sites, and which parameters contributed to those differences (Clarke et al. 2014b). 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.

Results

Estimating Vegetated Area Before Degradation and Before Restoration

Historical vegetated area within the restoration project footprint was approximately 18.5 ha in 1931 (Figs. 2 and 3a). Vegetated area declined to 4.6 ha by 2015, which is representative of the state of the marsh prior to restoration (Figs. 2 and 3b). Assuming the target restoration goal of a

fully vegetated marsh plain is achieved (the entire project footprint excluding creeks is vegetated), there will be more marsh area than there was in 1931 (Fig. 2).

Area Searches for Marsh Vegetation Surviving Construction

During area searches in Fall 2018, 2 to 3 months after construction ended, we recorded a total estimate of 4142 plants (Fig. 3c). Surviving plants were mostly found on or near berms that had been scraped during restoration site construction (Electronic Supplement 1). These plants were mostly native marsh species (*Distichlis spicata*, *Frankenia salina*, *Salicornia*, *Jaumea carnosa*, and *Spergularia* sp.) but included 0.3% upland non-native species. Based on estimates of plant numbers and assumed sizes of individuals of each species, surviving plant cover was 31 m^2 within the construction zone. An additional 2542 m^2 of marsh vegetation was present within the project footprint in Fall 2018, corresponding to a relatively narrow strip of existing vegetation on site edges that was not scraped or buried during construction (Fig. 3c). The total vegetated area within the project footprint in 2018 was 0.26 ha (Fig. 2).

Transect Monitoring of Vegetation Colonization

During the initial transect vegetation surveys in August and October 2018, no live vegetation was found in the long-term monitoring quadrats in the initially bare construction zone;
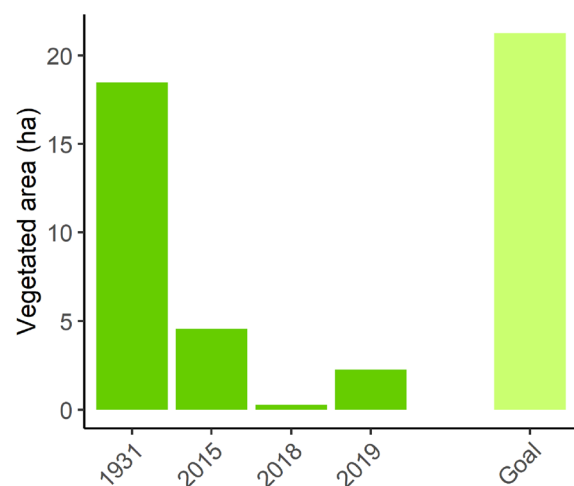

Fig. 2 Vegetated marsh area within Hester Marsh project footprint, 1931–present, and future planned vegetated area. Areas in 1931 and 2015 represent historical and degraded pre-restoration conditions, respectively. Area in 2018 represents vegetation following soil addition, while area in 2019 represents conditions after a growing season of restoration
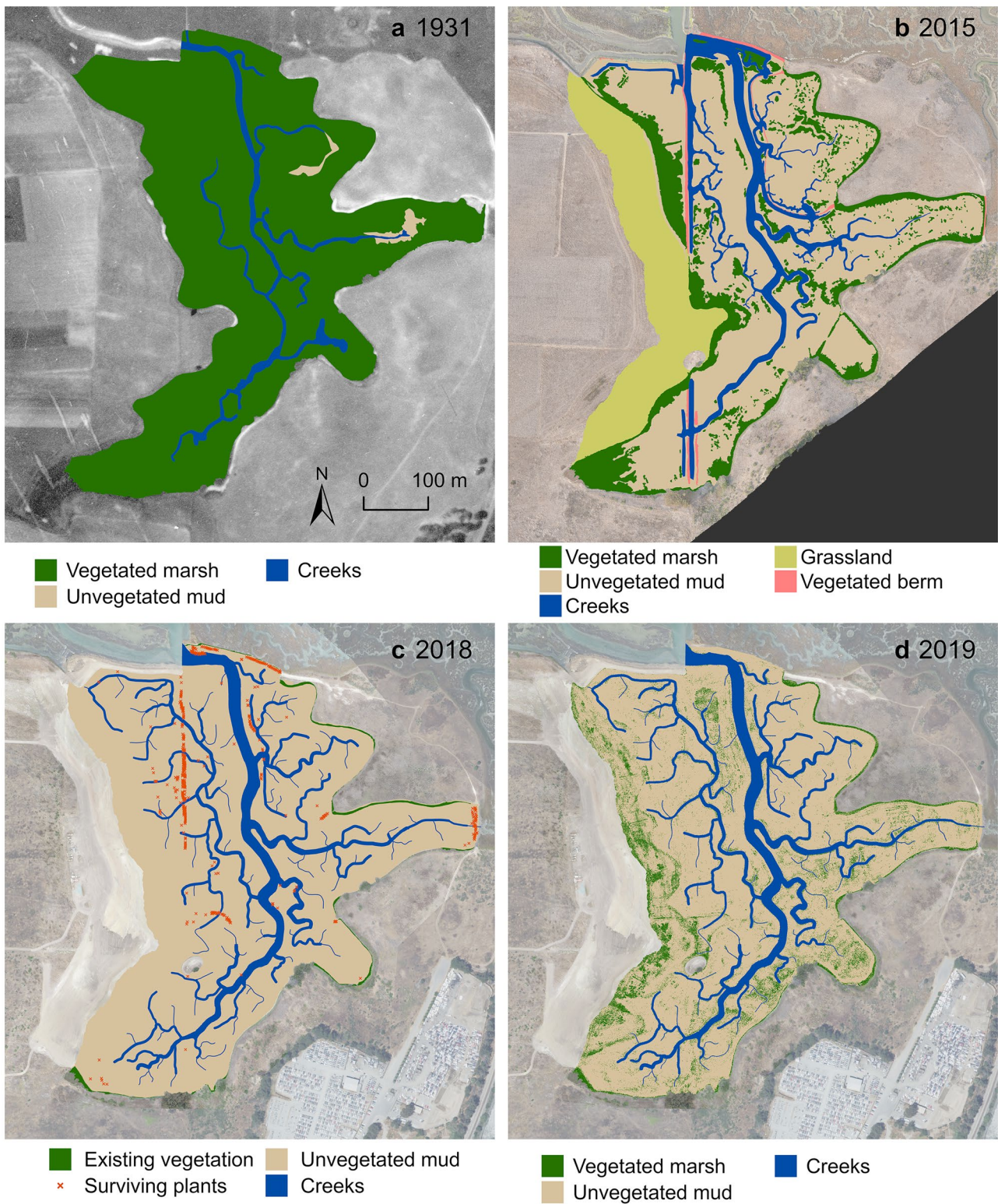
Fig. 3 Maps of vegetated areas within Hester Marsh, 1931–present. **a** Digitized 1931 aerial imagery of the historically well-vegetated marsh. **b** Digitized 2015 UAS imagery of the marsh, which had degraded to mostly unvegetated mudflat before construction of the restoration site. **c** The relatively bare landscape at the end of construction in August 2018, with locations of surviving plants logged during GPS surveys and digitized existing vegetation above the construction area. 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
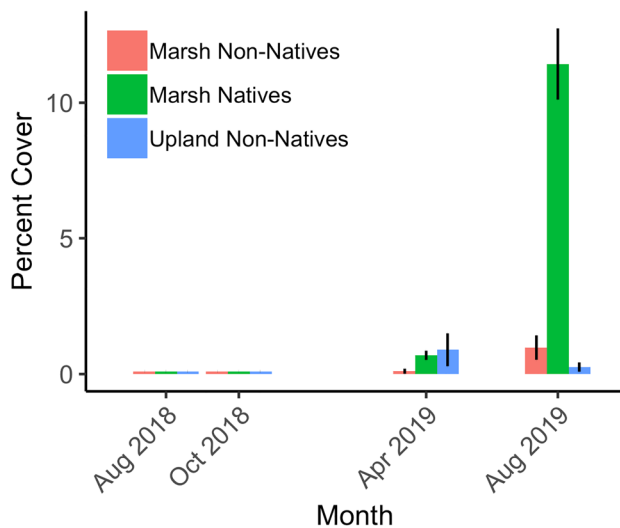
Fig. 4 Marsh native, marsh non-native, and upland non-native cover from quarterly transect surveys, August 2018–August 2019. Data from 2018 were collected only in long-term quadrats ($n=94$), while 2019 data included long-term and short-term quadrats ($n=269$). Error bars represent standard error of the mean

existing vegetation at the landward end 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 construction zone. By August 2019, average cover reached 13.6% in the construction zone (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). Cover of marsh non-natives (*Atriplex prostrata* and *Parapholis incurva*) and upland non-natives was 1.0% and 0.3%, respectively.
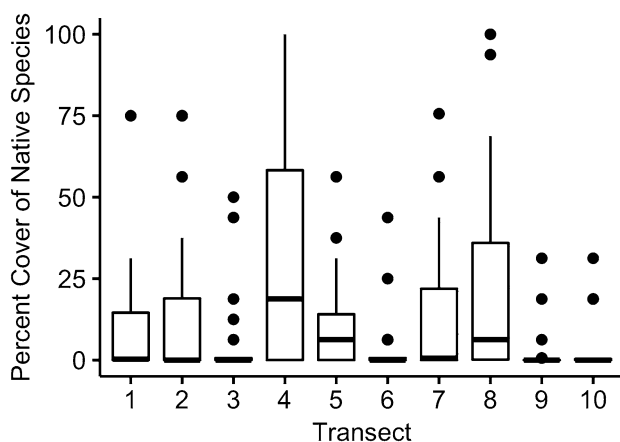
Fig. 5 Percent cover of native marsh plants on 10 transects, August 2019

Additionally, cover of non-native *Erigeron bonariensis* and native *E. canadensis* combined was 0.9%, but we could not distinguish between the native and non-native during field surveys.

Average maximum canopy height for newly colonized *Salicornia* in August 2019 was 6.9 ± 4.6 cm, while it was 35.2 ± 5.2 cm in the quadrats with existing vegetation that was present before restoration. Relative biomass calculated from *Salicornia* height and cover was 300 ± 486 cm³ in quadrats with new colonization and 3092 ± 838 cm³ in quadrats with existing vegetation.

Percent cover of native marsh vegetation in the construction zone in August 2019 varied among transects (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, $p < 0.001$; Electronic Supplement 1, Fig. S1). Quadrat elevation ranged from 1.71 to 2.30 m.

Modeling of native marsh cover based on August 2019 transect data revealed the following important predictors (importance in parentheses, measured as percentage increase in MSE when the variable is randomly permuted; Electronic Supplement 1, Fig. S2): post-restoration elevation (22.8), pre-restoration elevation (22.0), salinity (18.7), elevation change over the first year of restoration (14.4), habitat type prior to restoration (7.0), soil addition or removal during construction (6.7), distance to nearest tidal creek (4.9), and soil source (3.7). 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, with predicted cover increasing sharply between 1.9 and 2.0 m (Fig. 6a). Pre-restoration elevation (2015) was the next most important predictor, 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 to 2.7 m; Fig. 6b; Electronic Supplement 1, Fig. S9). 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, with lowest cover predicted between 37 and 42 ppt (Fig. 6c). Elevation change over the first year of restoration (August 2018 to May 2019) was also important, 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. 6d; Electronic Supplement 1, Fig. S13). 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
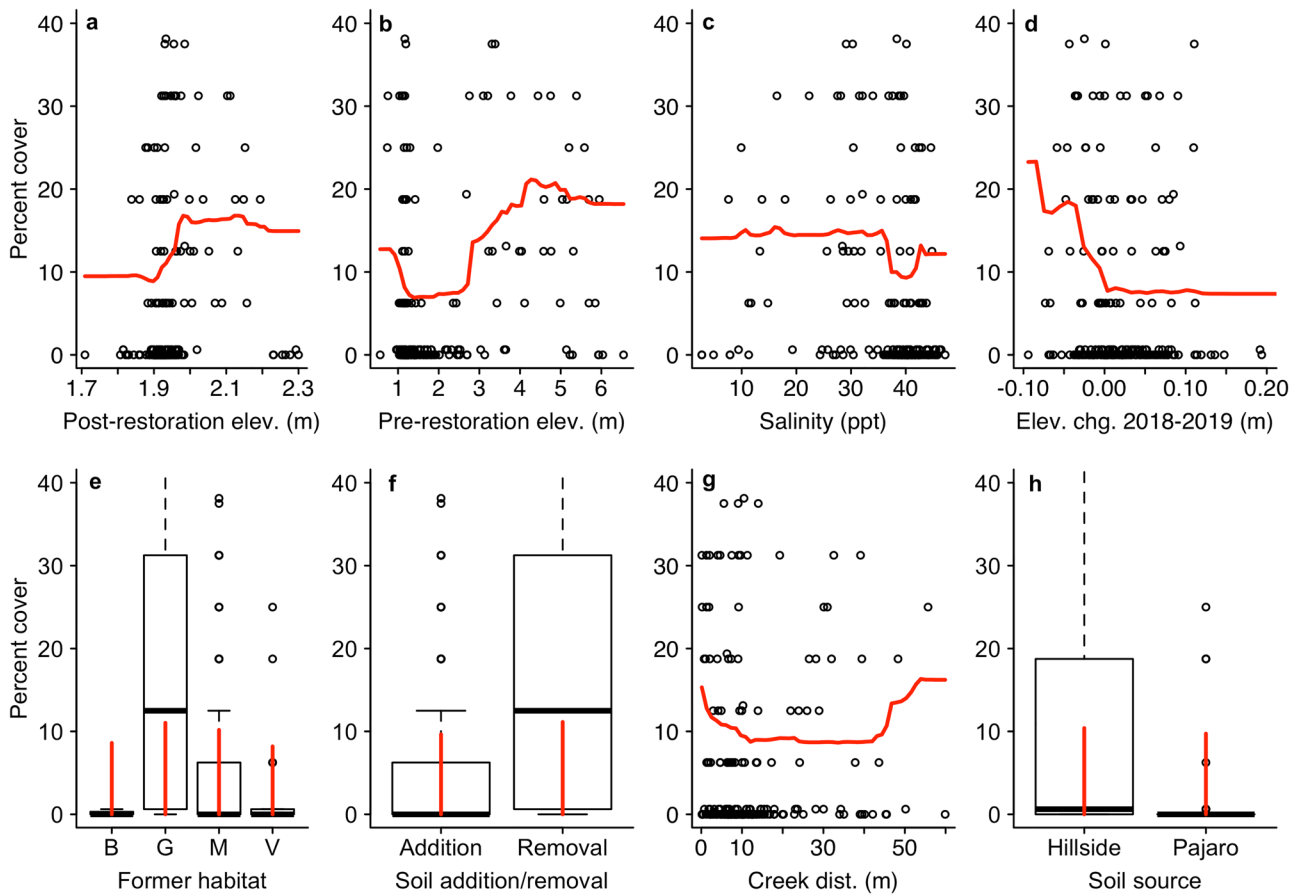
Fig. 6 Partial dependence of transect-surveyed native marsh cover on **a** post-restoration elevation, **b** pre-restoration elevation, **c** salinity, **d** elevation change over the first year of restoration, **e** former habitat type (B = vegetated berms, G = grassland, M = mudflats/unvegetated areas, V = vegetated marsh), **f** soil addition or removal, **g** creek dis- tance, and **h** soil source based on random forest modeling. Red lines show model predictions, holding all variables in the model constant except the one plotted. Open circles and boxplots show raw data. Upper *y*-axis limit set at 40% cover for ease of viewing the majority of data (25 high-cover data points not shown)

these areas (Fig. 6e; Electronic Supplement 1, Fig. S15). Raw data also show greater cover on areas of soil removal, which correspond to the former grassland and berms, but the model predicted only marginally greater cover on those soil removal areas (Fig. 6f; Electronic Supplement 1, Fig. S16). Vegeta- tion cover was found to be greatest both adjacent to (0–10 m) and far (< 45 m) from tidal creeks (Electronic Supplement 1, Fig. S14), though the latter trend was driven by few data points (Fig. 6g). Vegetation cover was marginally greater on soil sourced from the local hillside compared with Pajaro River sediment (Fig. 6h; Electronic Supplement 1, Fig. S12).

Several of the variables examined in modeling were cor- related with each other. Areas that were high in elevation prior to restoration remained at higher elevations post- restoration (Fig. 7a). Soil 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, soil removal areas (Fig. 7b).

Salinity and post-restoration elevation were negatively related, with lower salinity in higher-elevation (Fig. 7c), infrequently inundated areas (Electronic Supplement 1, Fig. S3). This trend was mostly driven by the soil removal areas, which tended to have lower salinity for a given eleva- tion (e.g., 1.95 m) than soil addition areas. Salinity in the soil addition areas had a weakly negative relationship with elevation, decreasing slightly at elevations above 1.90 m (Fig. 7c). Inundation time at Hester Marsh ranged from 0.0 to 6.2% and followed a downward sloping curve in relation to post-restoration elevation, as measured by Vierra Marsh tide data (Fig. 7d).

Site-Wide UAS Monitoring of Vegetation Colonization

Image classification of high-resolution October 2019 UAS imagery (pixel size = 0.79 cm) produced estimates of 2.3 ha of total vegetated cover in the project footprint (the entire

Fig. 7 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)
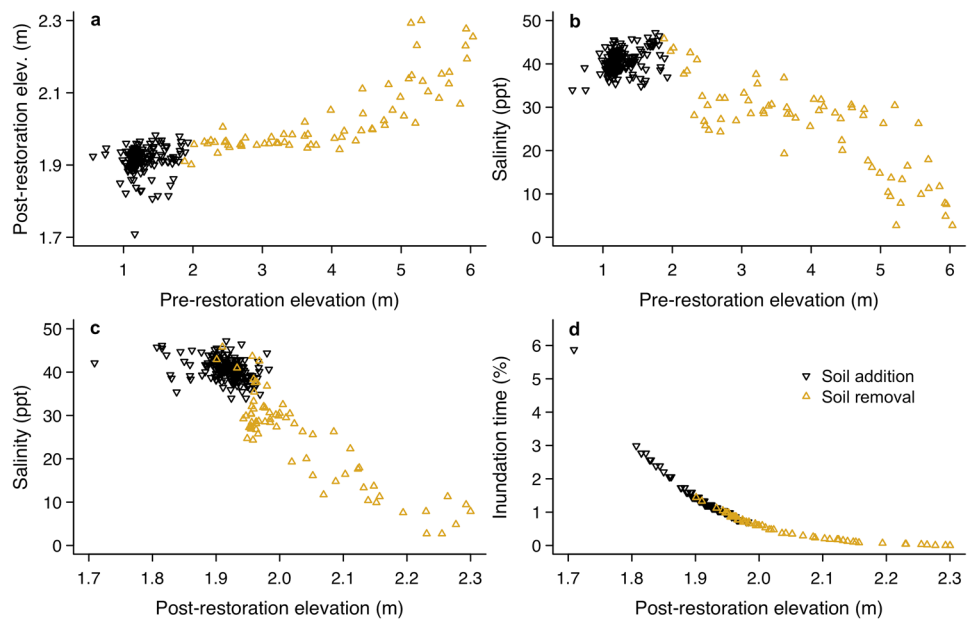
area up to 2.3 m NAVD88, including soil addition and removal areas as well as existing vegetation that remained above the construction zone; Figs. 2 and 3d). This included 1.4 ha of naturally colonized vegetated cover in the main seed dispersal area (Fig. 8), which we determined was the
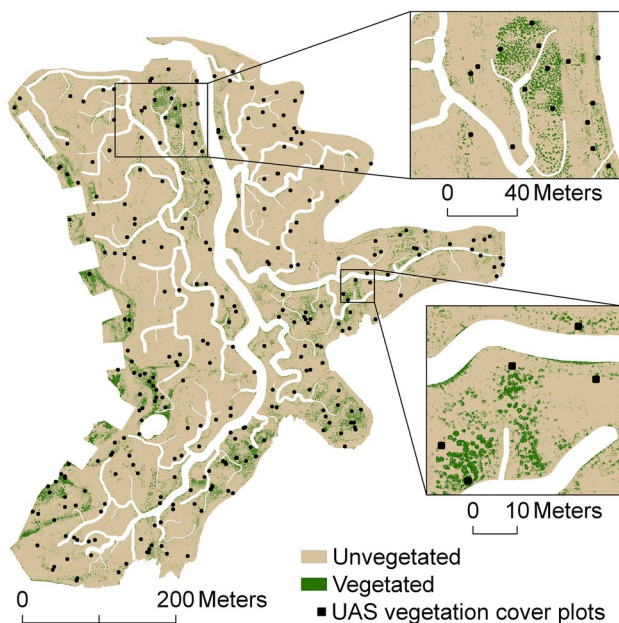
Fig. 8 Classified October 2019 UAS imagery showing vegetated and unvegetated areas and plots for modeling vegetation cover within the main seed dispersal area, excluding actively planted areas and tidal creek interiors. Some example areas are shown to highlight patchiness of natural colonization. We modeled percent cover of classified vegetation in 1-m² plots, created using stratified random sampling in high- and low-cover areas (*n* = 300)

area below 2.14 m (Electronic Supplement 1, Characterization of Inundation Across Elevations). We calculated vegetation cover estimates and performed modeling of vegetation points using the pixel-based classification, because both classified images had good overall accuracy (true skill statistic = 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.

Salinity modeling included the following predictors in order of variable importance percentage based on Gini coefficients: amount of soil addition or removal during construction (importance = 41%), elevation (importance = 36%; Electronic Supplement 1, Fig. S5), and tidal creek distance (importance = 23%). Model validation indicated fairly good performance (out-of-bag root mean square error, RMSE = 3.1‰). 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 soil removed during the construction process, and which remained at higher elevation than the marsh plain to the east (Fig. 7a–c; Electronic Supplement 1, Fig. S11).

Site-wide modeling of classified vegetation cover in the main seed dispersal area included the following important predictors explaining vegetation cover during the first year
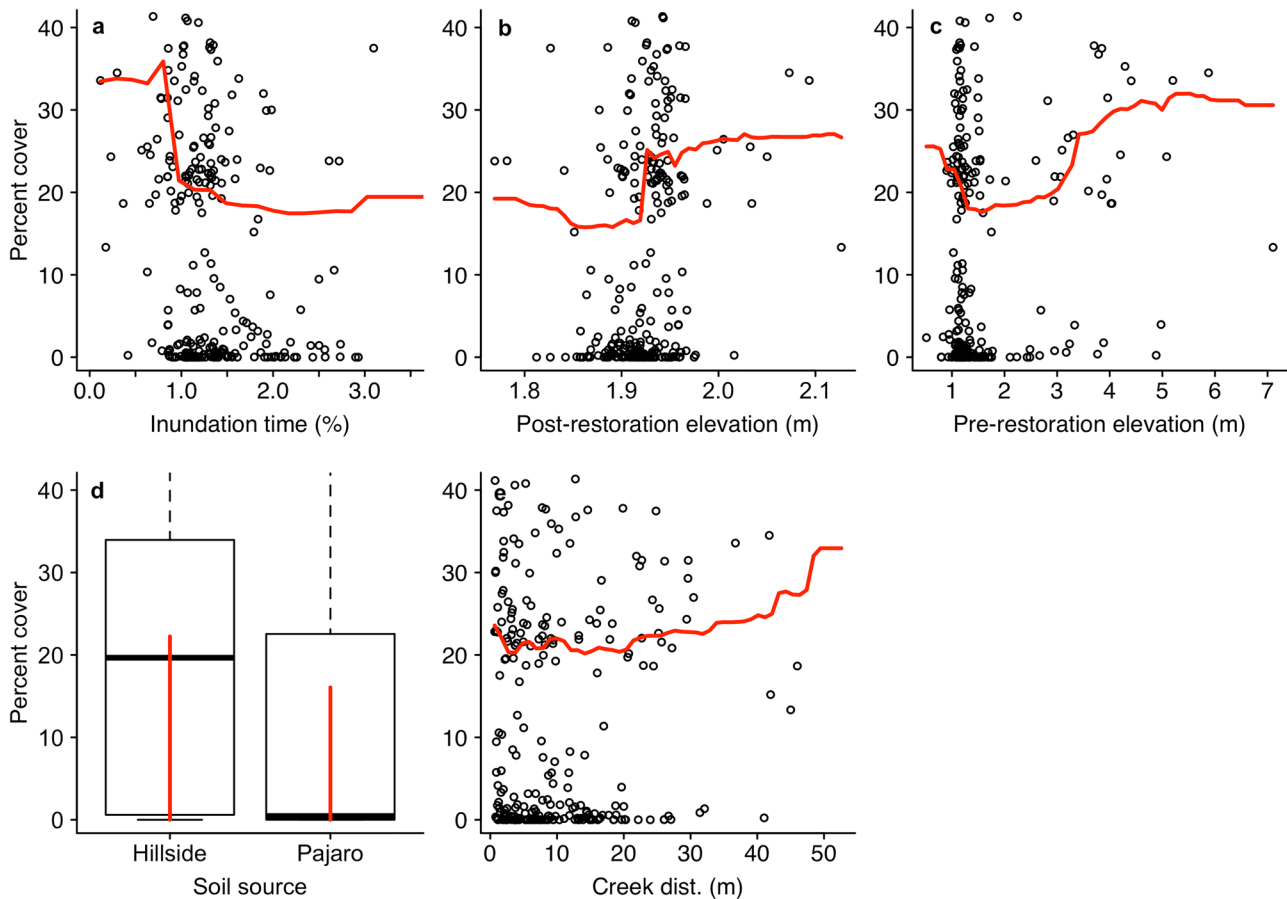
Fig. 9 Partial dependence of UAS-derived vegetation cover on **a** percent time inundated, **b** post-restoration elevation, **c** pre-restoration elevation, **d** soil source, and **e** creek distance based on random forest modeling. Red lines show model predictions, holding all variables in the model constant except the one plotted. Raw data shown as open circles (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)

of restoration at Hester Marsh (importance for each variable in parentheses, measured as percentage increase in MSE when the variable is randomly permuted; Electronic Supplement 1, Fig. S6): percent time inundated (32.8), post-restoration elevation (29.0), pre-restoration elevation (26.9), soil source (14.4), and tidal creek distance (4.3). 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 (Electronic Supplement 1, Fig. S11), soil addition or removal (Electronic Supplement 1, Fig. S16), habitat type prior to construction (Electronic Supplement 1, Fig. S15), and elevation change over the first year of restoration (Electronic Supplement 1, Fig. S13).

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 (Fig. 9a; Electronic Supplement 1, Fig. S10). Post-restoration elevation predicted a sharp increase in vegetation cover around 1.92 m (Fig. 9b; Electronic Supplement 1, Fig. S8). Cover was predicted to be lowest on former marsh plain elevations (1.2 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 (Fig. 9c; Electronic Supplement 1, Fig. S9). Vegetation cover was also predicted to be high in formerly low areas (below 1.2 m). Soil source was moderately important, with more vegetation predicted on areas that received hillside soil rather than Pajaro River sediment (Fig. 9d; Electronic Supplement 1, Fig. S12). Tidal creek distance was only marginally important, with vegetation cover predicted to be greatest in areas farthest from creeks, though this was driven by only a few data points (Fig. 9e; Electronic Supplement 1, Fig. S14).

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 we did not include these areas in the analysis due to an inability to accurately classify vegetation separately from the darker mud and algae present. We also observed some relatively bare swaths of marsh plain within four to 10 m of the existing vegetation that remained above the construction zone on some restoration site edges. Field observations indicated that many of these areas adjacent to existing vegetation were slightly sunken, leading to poor drainage and water pooling. Drone imagery and DSMs supported field observations of little new colonization and lower elevation in these areas near the site edges (Electronic Supplement 1, Fig. S7a-b).

Soil Comparison at Well-Vegetated and Poorly-Vegetated Sites

Well-vegetated sites had greater cover (estimated 10–50% cover) and larger plants (average height = 13 cm), in comparison to poorly-vegetated sites (estimated cover < 10%, average height = 5 cm). The 20 sites were at a mean elevation of 1.91 ± 0.02 m and mean creek distance of 12.3 ± 3.7 m. As intended in the design of these paired comparisons, elevation and creek distance did not differ significantly between well-vegetated and poorly-vegetated sites.

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 soil properties (Electronic Supplement 1, Table S1). SIMPER analysis revealed that poorly-vegetated sites were more similar to each other than well-vegetated sites (average squared distance = 15 and 30, respectively; Electronic Supplement 1, Fig. S17). Poorly-vegetated sites had significantly greater soil ammonium levels, conductivity, and sodium and chloride concentrations compared to well-vegetated sites (Electronic Supplement 1, Table S1). We also used the soil sample data and field-collected conductivity/salinity data to further investigate the potential differences in Pajaro River dredge material and hillside material (Electronic Supplement 1).

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 year following restoration. We detected very low initial survival of pre-construction vegetation following soil 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 Soil 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 of pre-construction vegetation in the construction zone. Poor survival may be partially attributed to the thickness of soil added at Hester Marsh (on average, 69 cm in all soil addition areas and 37 cm on formerly vegetated areas) but is also likely due to the method of soil placement, because even areas with low levels of soil addition had few or no surviving plants. Thin-layer placement typically involves spraying or piping in sediment slurries (Slocum et al. 2005; Frame et al. 2006), while soil at Hester Marsh was placed by heavy construction equipment that drove over the marsh repeatedly. Future soil addition projects using earth-moving machinery should expect low survival of vegetation.

Somewhat surprisingly, most of the surviving vegetation at Hester Marsh was on former berms or areas within 5 m of those berms, where berm material was used for fill, suggesting that it likely grew from roots or other intact plant material that remained in upper layers of soil. Outside of the actively planted areas, these former berms and adjacent areas have the most native marsh species diversity; while *Frankenia*, *Jaumea*, and *Distichlis* survivors were fairly common in these areas, natural colonists of these species were rarely or never found during transect surveys.

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) to 77% after 2.5 years (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.

Overall vegetation cover was still relatively low in the initially bare construction area at the end of the first full growing season sampled: estimated vegetated cover was 13.6% based on August 2019 transect surveys, and 7.6% based on 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), seasonal dieback causing a true decline in green cover from the August field survey to the October UAS survey, or slight overestimation of cover in the transect dataset (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%; Fig. 5). 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*. Low diversity (Seabloom and van der Valk 2003; Armitage et al. 2006) and patchy colonization should be expected at future high marsh restoration sites, but results from vegetation monitoring and analysis at this site, such as environmental conditions associated with greater vegetation cover, can inform the design of future sites to optimize conditions for early colonization.

Predictors of Plant Colonization

Typically, salt marsh distribution and community structure are 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 did not limit vegetation establishment in high elevation areas, although rainfall was higher than average over the first year of restoration (19.6 inches, July 2018-June 2019; annual average of 16.0 inches since 2001; NOAA NERRS 2020). Different results would likely have been found under drought conditions (Chapple and Dronova 2017).

Relatively dense vegetation cover was also observed on the former hillside, which was grassland habitat above marsh elevation before soil was removed during construction. Soil "scraping" was favorable to marsh vegetation colonization, likely in part because these areas remained at higher elevation post-construction (Fig. 7a). Lower salinity in scraped compared with soil addition areas at the same elevation may also indicate favorable drainage, groundwater, or other soil conditions in scraped areas (Fig. 7c).

Other factors indicated greater vegetation colonization on the marsh plain near tidal creeks, which are commonly understood to influence marsh vegetation community structure (Zedler et al. 1999; Sanderson et al. 2001). While some studies have found reduced salinity near creeks (Balling and Resh 1983; Schile et al. 2011) and improved *Salicornia* growth under reduced salinity (height, Schile et al. 2011; shoot growth, Mahall and Park 1976b), areas adjacent to 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 might include greater seed deposition (Hopkins and Parker 1984), improved drainage (Schile et al. 2011; Chapple and Dronova 2017) or increased moisture (Noe and Zedler 2000) ameliorating salinity stress, lower sulfide accumulations (King et al. 1982), or 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).

Soil properties are an important consideration in marsh restoration (Broome 1989), with potential effects on pore water nutrients, salinity, and pH (Wigand et al. 2016). Better understanding of these factors can inform selection of source material for soil and sediment addition projects and adaptive management to mitigate plant stressors. Soil analysis at Hester Marsh indicated greater salinity and ammonium levels at poorly-vegetated compared to well-vegetated sites. Future studies should examine strategies to mitigate salinity stress at soil/sediment addition sites, particularly in areas away from tidal creeks. 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. Soil sampling can examine additional potential abiotic and biotic limitations of vegetation colonization, such as soil compaction (as an indicator of porosity/permeability), hydrogen sulfide concentrations, or development of the soil microbial community. While we do not believe seeds are limited in the tidal waters at this site due to the proximity of healthy pickleweed marshes and strong tidal currents, further studies can also examine variability in seed deposition on the marsh plain.

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 soil/sediment addition (Mendelssohn and Kuhn 2003). With recently introduced technologies

like high-resolution remote sensing by UAS in restoration monitoring (Knoth et al. 2013; Buters et al. 2019; Haskins et al. 2021), 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 one. We found field methods more advantageous for distinguishing between species in cover assessments, which enabled us to evaluate the upper marsh boundary in relation to tide data (Electronic Supplement 1, Characterization of Inundation Across Elevations). 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; we surveyed 280 quadrats in one day with a team of four people, but it is acknowledged that vegetation cover was sparse during this early stage of restoration. 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. Although transect monitoring was suitable at our site, UAS was a very useful complement, and may provide more substantial benefits over field methods at larger or less accessible sites.

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 DSMs created from UAS linked to ground control points both yielded accurate elevation profiles. Inundation frequency was an important factor in controlling plant colonization, 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.

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; Boyer and Thornton 2012). Our investigation serves as a model for other salt marsh restoration projects by integrating data on elevation, inundation, soil 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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