



Habitat Conversion by Native *Spartina* Highlights the Importance of Wetland Restoration Design Relative to Site-Specific Vertical Range of Vegetation

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Received: 5 November 2024 / Revised: 12 May 2025 / Accepted: 18 June 2025 / Published online: 1 July 2025
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Abstract

Native vegetation is planted in wetland restoration projects to supplement natural recruitment and achieve a habitat mix that supports ecological functioning. The native cordgrass *Spartina foliosa*—an ecosystem engineer with a wide elevation range—is frequently planted in wetland restorations in Southern California to jumpstart low marsh development. Although plantings can increase vegetation cover, planted *S. foliosa* can also convert areas designed as tidal creeks or mudflat to salt marsh, hindering progress towards restoration objectives. At the restored San Dieguito Wetlands (SDW) in Southern California, *S. foliosa* was planted during (2008–2009) and after wetland construction (2011–2018). In 2023, *S. foliosa* occupied 10.8 ha at SDW, but had converted 42% of built tidal creek and mudflat habitat to salt marsh. Genetic testing ruled out potential hybridization with non-native *Spartina*. Tidal creek elevations were higher at SDW than at other California wetlands, overlapping with the design elevation of low marsh for the site. *Spartina foliosa* extended to lower elevations at SDW than other California wetlands, overlapping with the design elevation of mudflat for the site. Thus, habitat conversion at SDW was likely due to insufficient excavation of built tidal creeks and the lower than expected elevation range of *S. foliosa* at the site. Much of the existing tidal creek and mudflat habitat at SDW is likely susceptible to habitat conversion to salt marsh. Our results emphasize the need to consider the design elevation of restored habitats relative to site-specific elevation ranges of target wetland species.

Keywords Coastal wetlands · Habitat conversion · Mudflat · Salt marsh · *Spartina* · Tidal creeks · Vegetation cover

Introduction

Coastal wetlands provide disproportionate ecosystem services relative to their small global footprint (Duarte, 2017; Zedler & Kercher, 2005). They support biodiversity, create essential habitat for rare species, improve water quality, protect shorelines, and store carbon (Barbier et al., 2011; Himes-Cornell et al., 2018). However, coastal wetlands have declined by at least 50% globally due to human activities (Davidson, 2014; Zedler & Kercher, 2005), including coastal development, hydrological alterations, eutrophication, and

the spread of invasive species (Lotze et al., 2006; Zedler & Kercher, 2005). On the U.S. West Coast, up to 85% of vegetated tidal wetlands have been lost (Brophy et al., 2019; Endris et al., 2024; Stein et al., 2014) and the remaining wetlands are highly vulnerable to future sea-level rise, particularly in the Southern California Bight (Thorne et al., 2018).

Wetland restoration promises to counter these declines. Substantial global investments and policy initiatives aim to assist wetland recovery from degradation (Bayraktarov et al., 2016; Society for Ecological Restoration International Science & Policy Working Group, 2004; Waltham et al., 2020). Restoration projects are designed to meet site-specific goals and can include passive approaches that aim to remove stressors that inhibit natural recovery (e.g., reducing storm-water run-off) and active approaches that directly change the environment (e.g., restoring tidal inundation, planting native vegetation; Society for Ecological Restoration International

Communicated by John C. Callaway

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Science & Policy Working Group, 2004; Sullivan, 2001; Zedler & Kercher, 2005).

Healthy coastal wetlands include a mosaic of habitat types. Connectivity among river channels, tidal creeks, mudflat, and the marsh plain support biological and physical wetland functions (Kearney & Fagherazzi, 2016; Vivian-Smith, 2001; Wallace et al., 2005). Wetland restoration often aims to recreate a mix of habitats to support this exchange of organisms and materials (Vivian-Smith, 2001; Weinstein et al., 2005; Williams, 2001). Indeed, some species may use multiple habitat types within the same restored wetland; for example, shorebirds may feed on mudflats, but rest or breed on the marsh plain (Vivian-Smith, 2001). Prioritizing habitat heterogeneity in wetland restoration is also a bet-hedging strategy that can support diversity by providing suitable conditions for a suite of native species (Vivian-Smith, 2001). Restoration design must consider how best to support the desired mix of habitats (Weinstein et al., 2005; Zedler, 2000).

Even with appropriate project planning, multiple abiotic and biotic factors can contribute to slow vegetation development in areas designed to be salt marsh (Beheshti et al., 2023; Lindig-Cisneros et al., 2003; O'Brien & Zedler, 2006; Pennings & Callaway, 1992; Pennings et al., 2005). Elevation is a dominant driver of habitat development that is critical to restoration design (Davy et al., 2011; Sullivan et al., 2018; Wolters et al., 2008). Design elevations vary by intended habitat type; grading and/or filling to appropriate elevations enables development of desired habitats (Williams, 2001). Indeed, plant zonation along elevation gradients is an iconic feature of natural tidal wetlands (Bertness & Ellison, 1987; Pennings & Callaway, 1992; Silvestri et al., 2005). Elevation is highly correlated with many of the abiotic conditions that affect wetland plants, including the frequency and duration of tidal inundation, soil salinity, soil saturation, and soil redox (Cooper, 1982; Snow & Vince, 1984). Tolerances to the abiotic conditions that vary along these elevation gradients are species-specific (Cain & Harvey, 1983; Gallego-Tévar et al., 2020; Lee et al., 2016; Richards et al., 2005). Thus, restoration plans often target specific elevations for desired plant communities that reflect these tolerances (e.g., low, mid, and high marsh plant communities; SCE, 2005). Grading for restoration projects must create the vertical elevation range needed to support planned vegetation development.

Once an appropriate vertical elevation range has been established for the desired habitat, planting programs can address slow vegetation development related to biotic factors such as interspecific competition and recruitment limitation. Plant species richness is often lower in restored versus natural wetlands (Chang et al., 2016; Diggory & Parker, 2011). To address this discrepancy, a mix of wetland species—often with a focus on rare or dispersal-limited species that will

not recruit naturally—can be planted across the elevation gradient according to individual species' tolerances. Planting can also be combined with other actions, such as soil amendments, decompaction, or irrigation, to encourage vegetation recovery (Beheshti et al., 2023; O'Brien & Zedler, 2006; Pausch, 2024).

In the Southern California Bight, the native marsh cordgrass, *Spartina foliosa*, is commonly used in planting programs to restore low marsh plant communities (Beheshti et al., 2024; Boyer et al., 2000; Zedler, 1993). *Spartina foliosa* is a C4 perennial grass that dominates the natural low marsh community in the region (Boyer & Zedler, 1999), and the species is valued because its tall, dense stems create suitable nesting habitat for the endangered Ridgway's Rail (Boyer & Zedler, 1998; Massey et al., 1984; Zedler, 1993). Restoration projects may explicitly include tidal creek networks to enhance cordgrass growth along creek edges and thereby support bird nesting (Haltiner et al., 1996). *Spartina foliosa* grows best at lower marsh elevations along tidal creeks where there are no competitors; it is unlikely to grow tall at mid- and high marsh elevations, where *Salicornia* and other plants occur (Boyer & Zedler, 1999). Because *S. foliosa* is generally dispersal-limited in Southern California (Callaway & Josselyn, 1992; Morzaria-Luna & Zedler, 2007), planting programs often include the species early in the restoration process to allow time for vegetation cover to meet project benchmarks (Haltiner et al., 1996).

Spartina foliosa is an ecosystem engineer that is known for its rapid clonal growth post-establishment (Ward et al., 2003); these attributes make *S. foliosa* ideal for revegetating low marsh restoration sites. However, this trait is also associated with the invasive behavior of *Spartina* spp. in areas outside of their native range. For example, *Spartina alterniflora* invasion of coastal wetlands along the U.S. West Coast has displaced native species, altered associated communities, converted mudflats to salt marshes, and changed tidal creek geomorphology (Callaway, 2005; Callaway & Josselyn, 1992; Levin et al., 2006). That said, even *S. foliosa* planted in its native range has the potential to drive habitat conversion, encroaching into tidal creek and mudflat habitats that are not planned as salt marsh (Ward et al., 2003). Therefore, it is important to ensure that project design elevations for tidal creek and mudflat habitat remain below the zone of *S. foliosa* occupancy.

Here, we characterize *Spartina* encroachment into areas that were originally planned as tidal creek or mudflat habitat at a restored coastal wetland in Southern California, the San Dieguito Wetlands (SDW). To assess the potential presence of—or hybridization with—the invasive *S. alterniflora* that has invaded other coastal wetlands along the U.S. West Coast (Ayres et al., 2004; Cívile et al., 2005), we genotyped the *Spartina* spp. at the restored wetland and nearby natural wetlands to confirm the identity of the native *S. foliosa*. To

examine mechanisms of *Spartina* encroachment, we used real-time kinematic GPS (RTK-GPS) elevation surveys to compare the distribution of vegetated and unvegetated areas within designed tidal creek and mudflat habitat at SDW relative to other nearby natural and restored wetlands without *Spartina* encroachment. Together, these findings illuminate mechanisms of habitat conversion that can inform the design of other coastal wetland restoration projects.

Methods

Study Sites

The San Dieguito Lagoon (32.970° , -117.260°) is an urban estuary in Del Mar, California that is located near the mouth of the San Dieguito River (Fig. 1). The semi-arid region receives seasonal rainfall of ~ 28 cm/year and tides at the lagoon are semi-diurnal (Elwany, 2011). Tidal wetland habitat in the lagoon is highly degraded, with more than 70% of historical wetland area lost to coastal development since the 1920s (Beller et al., 2014; Kent & Mast, 2005).

To counter these losses and also provide out-of-kind compensatory mitigation for impacts to nearshore fish populations in the Southern California Bight due to operations of the San Onofre Nuclear Generating Station, 60.7 ha of

wetland habitat (10.8 ha of mudflat, 37.5 ha of salt marsh) were restored from 2006 to 2011 as part of the San Dieguito Wetlands (SDW) Restoration Project. Restoration involved grading ruderal upland to planned tidal elevations for salt marsh and mudflat habitat, maintaining tidal exchange at the river inlet, and instituting a planting program of high and mid-marsh species to jumpstart vegetation development (Beheshti et al., 2024; SCE, 2005). Contractors planted marsh cordgrass, *S. foliosa*, at lower tidal elevations (1.1–1.3 m NAVD88) to facilitate development of low marsh vegetation during the early stages of the restoration (nearly 25,000 plants added from 2008 to 2012; Table 1). The initial *S. foliosa* transplants suffered substantial mortality immediately after installation (7–22% survival; Tomsovic, 2009) due in part to herbivory by the native scale insect *Haliopsis spartinae* (Rinehart et al., 2017). *Spartina foliosa* recovered from this initial dieback and proliferated throughout the restoration project in the following years, including into areas not designed to support salt marsh habitat (e.g., tidal creeks, mudflat).

We compare vegetation elevation and genetics at SDW to three reference wetlands in Southern California (Fig. 1). These sites included the natural wetlands, Mugu Lagoon (MUL; 34.1021° , -119.0973°) and Tijuana River Estuary (TJE; 32.5696° , -117.1269°), and the restored wetland, San Elijo Lagoon (SEL; 33.0087° , -117.2727°).

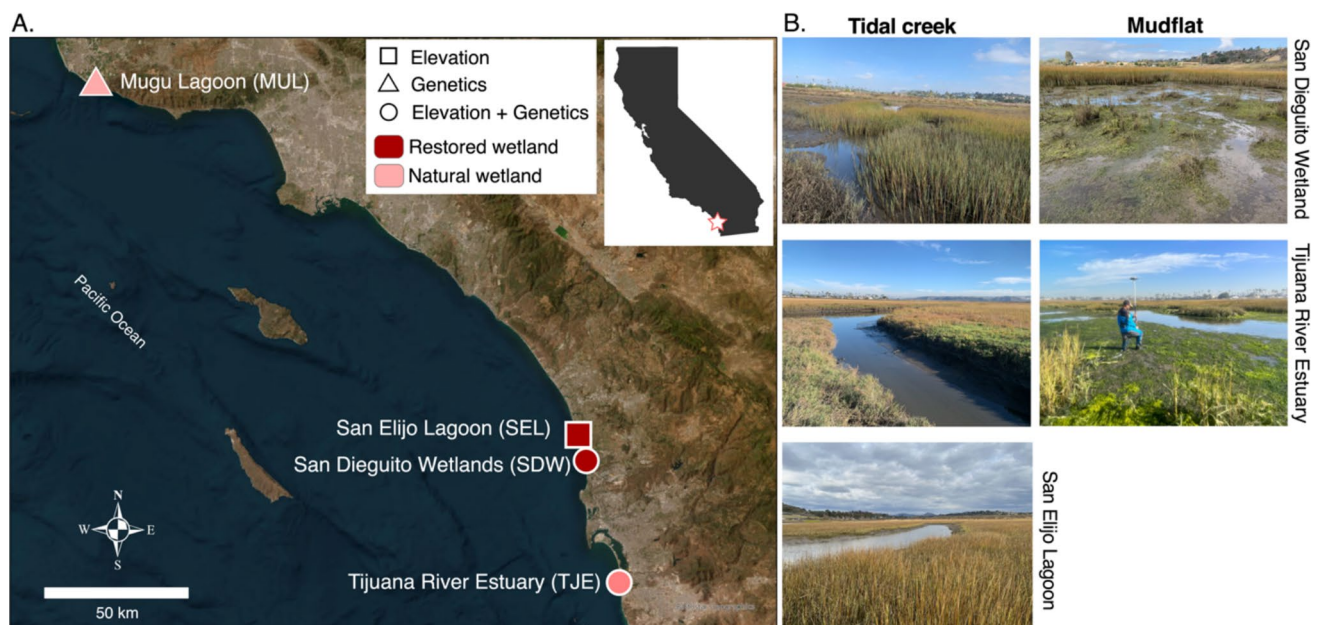


Fig. 1 **A** Map with locations of elevation and genetics surveys at restored and natural wetlands in Southern California. From north to south, survey sites included Mugu Lagoon (MUL), San Elijo Lagoon (SEL), San Dieguito Wetlands (SDW), and Tijuana River Estuary (TJE). Symbols indicate the type of survey(s) performed at each site (square = elevation survey, circle = genetics survey, circle = elevation and genetics surveys) and colors indicate wetland type (dark pink = restored wetland, light pink = natural wetland). There was no evidence of the invasive *Spartina alterniflora* or hybrids at any of the tested sites. **B** Photos of tidal creek and mudflat habitats at SDW, TJE, and SEL, as observed in the elevation surveys. No elevation surveys were conducted at MUL

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Table 1 Timeline of *Spartina foliosa* plantings at the restored San Dieguito Wetlands. Plantings occurred during wetland construction (2008–2009) and in the following years (2011–2018) to accelerate increases in vegetation cover. Dashes indicate data gaps

Year	<i>Spartina foliosa</i> planting (#)	<i>Spartina foliosa</i> source location	Latitude	Longitude
2008	200	—	—	—
2009	999	Tijuana River Estuary	32.569639°	– 117.126927°
2011	19450	Batiquitos Lagoon	33.089290°	– 117.292593°
2012	3900	—	—	—
2018	9700	San Elijo Lagoon	33.008745°	– 117.272726

Characterizing Habitat Conversion at SDW with Multispectral Imagery

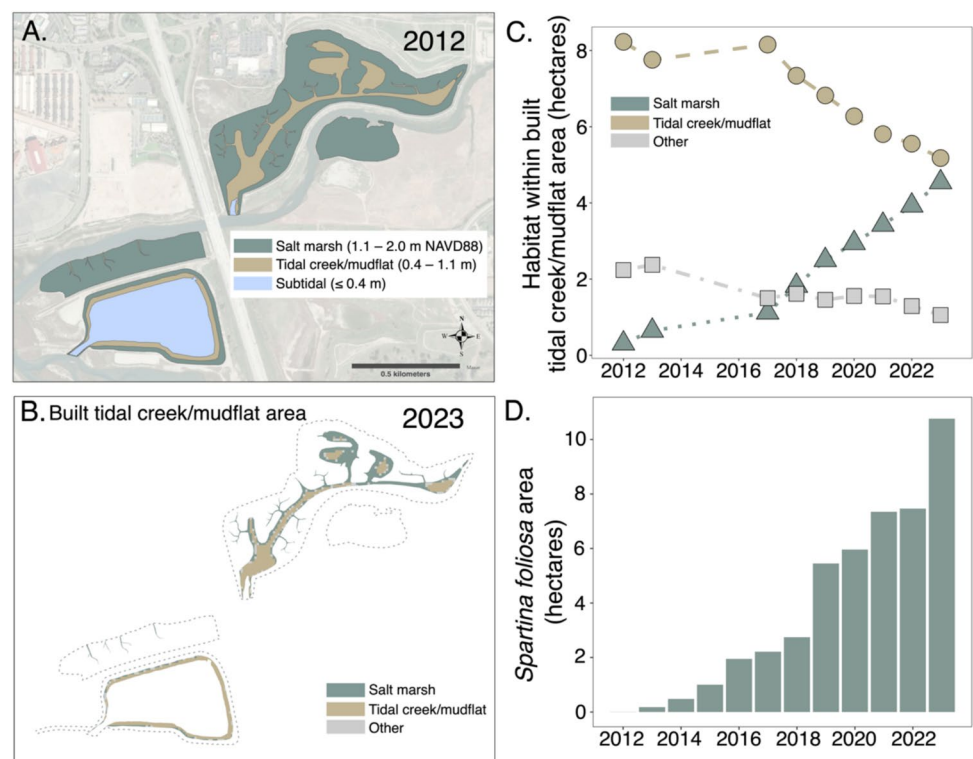
The restoration plan for the SDW Restoration Project included a mix of subtidal (≤ 0.4 m North American Vertical Datum of 1988, NAVD88), tidal creek/mudflat (0.4–1.1 m), and salt marsh (1.1–2.0 m) habitats delineated by elevation boundaries (SCE, 2005). The restored wetland was built to those design specifications (Fig. 2A). The restoration plan grouped tidal creek habitat in the same vertical elevation range as mudflat (0.4–1.1 m NAVD88; Fig. 2A). Within this common elevation range, tidal creeks were built with a steeper geomorphology that was expected to narrow and deepen over time to be similar to natural tidal creeks, whereas mudflat habitat was built with flatter slopes that were expected to persist over time.

To monitor changes in vegetation cover and habitat area over time, we assessed tidal creek/mudflat and salt marsh

areas annually using multispectral aerial imagery. Flights occurred in the spring-early summer during the period of maximum growth of salt marsh plants and targeted neap tidal sequences when intertidal areas were exposed. We collected red green blue (RGB) and near-infrared (NIR) spectrum images stored as georeferenced mosaics (pixel size: 20 cm $\times$ 20 cm). We assigned each pixel an elevation based on RTK-GPS elevation contour surveys corresponding to the restoration design boundaries (0.4, 1.1, and 2.0 m NAVD88 contours) and classified each pixel as vegetated or non-vegetated; the unique spectral signature of *Spartina* also allowed us to classify this species at the pixel level.

We superimposed 10 m $\times$ 10 m grid cells over the restored wetland and determined the percent vegetation cover of each grid cell by summing the number of vegetated pixels and dividing by the total number of pixels per cell. We classified each grid cell as tidal creek/mudflat or salt marsh habitat based on the elevation contours (tidal creek/mudflat: 0.4–1.1 m

Fig. 2 **A** Map of built areas and elevations of salt marsh, tidal creek/mudflat, and subtidal habitat at the restored San Dieguito Wetlands (SDW) in 2012. **B** Map of salt marsh, tidal creek/mudflat, and other habitat within the built tidal creek/mudflat area (0.4–1.1 m NAVD88) of SDW in 2023. **C** Within the built tidal creek/mudflat area, tidal creek/mudflat hectares have decreased and salt marsh hectares have increased since 2017. **D** *Spartina foliosa* area increased at SDW from 2012 to 2023



NAVD88, salt marsh: 0.4–2.0 m) and the following vegetation cover categories: tidal creek/mudflat was sparsely vegetated (<5% vegetation cover), whereas salt marsh had $\geq 30\%$ vegetation cover. All values not assigned to mudflat or salt marsh habitat were classified as “other” habitat (vegetation cover 5–30%, 0.4–2.0 m NAVD88). See Page et al. (2022) for more detailed methods.

We assessed how habitat distribution within the elevation contour designated as tidal creek/mudflat habitat (0.4–1.1 m NAVD88) changed from 2012 to 2023. Within this built area, we summed the total number of hectares assigned to each category (tidal creek/mudflat, salt marsh, other) for each year of monitoring after wetland construction (2012–2023). We also summed the number of pixels classified as *Spartina* to determine the area of *Spartina* at SDW for each year (2012–2023).

***Spartina* Spp. Genetics**

Given the wide vertical elevation range and rapid growth of *Spartina* at SDW, we were concerned about the potential presence of *Spartina alterniflora* or its hybrids (Daehler & Strong, 1996; Strong & Ayres, 2009). *S. alterniflora*, native to the North American Atlantic and Gulf coasts, has a wide vertical elevation range and out-produces *S. foliosa* in terms of above- and below-ground biomass, growth rates, and seed production and germination (Callaway & Josselyn, 1992). To assess the identity of *Spartina* at SDW, we collected *Spartina* leaf tissue samples from tidal creek and mudflat habitats. We took samples from independent clones located throughout the entire restoration project footprint ($n=6$ from tidal creek habitat; $n=9$ from mudflat). We also collected samples from two other natural wetlands in the Southern California Bight for comparison (Fig. 1A; 5 samples from tidal creek and 5 samples from mudflat habitat in TJE; 5 samples from tidal creek and main channel habitat at MUL). We did not collect *Spartina* samples from San Elijo Lagoon (SEL) because prior genetic analysis confirmed that those *Spartina* populations are *S. foliosa* (personal communication, Brian Ort and Doug Gibson). We targeted tall *Spartina* clones located at lower tidal elevations because these characteristics are associated with non-native *S. alterniflora* and its hybrids (Callaway & Josselyn, 1992). We genotyped the collected samples to confirm *S. foliosa* identity and used STRUCTURE (v. 2.3.4) to determine how our samples grouped with the existing genetic database developed by the San Francisco Estuary Invasive *Spartina* Project (Ort & Thornton, 2016; Pritchard et al., 2000).

Comparing Elevations of Tidal Creek and Mudflat Habitat at SDW to Other Natural and Restored Wetlands

We compared elevations of constructed tidal creek and mudflat habitat at SDW to those in two other nearby wetlands

with abundant *S. foliosa* (TJE, SEL). For the elevation surveys, we used an RTK GPS (TopCon Spectra Precision Ranger 3, SP80 GNSS Receiver) calibrated to known ground-control points prior to data collection at each wetland. We surveyed natural tidal creek and mudflat elevations at TJE and constructed tidal creek elevations at SEL (Fig. 1). The area of mudflat habitat was limited at SEL, so we did not survey mudflat habitat at this wetland.

For tidal creek surveys, we measured elevation along a minimum of five transect cross-sections per tidal creek. At each creek, we deployed the first transect at the creek mouth and laid subsequent transects at ~ 10 m intervals moving up creek. We measured elevations at seven points along each transect that included the thalweg, the mid-point between the thalweg and the top of each creekbank, the transition to the marsh plain, and the marsh plain on both sides of the creek (Fig. S1). For mudflat surveys, we measured elevation on five transects per mudflat. We began transects at the edge of each mudflat and took at least six elevation points along each transect at ~ 2 m intervals extending into each mudflat. See supplement for details on survey locations (Figs. S2–4) and sample sizes (Table S1). We also documented the vegetation type present at the location of each elevation measurement (unvegetated, *Spartina*, mixed marsh, *Spartina* with mixed marsh). Mixed marsh included the plants *Salicornia pacifica*, *Jaumea carnosa*, *Frankenia salina*, and *Batis maritima*. Some sites did not have mixed marsh alone, so we excluded this category from the presented analyses at all sites.

To understand how the elevational range of *S. foliosa* at SDW compared to other regional wetlands, we compiled eight peer-reviewed publications and technical reports that documented the elevation range of *S. foliosa* in its native range in California (Table S2). We used the VDatum tool (<https://vdatum.noaa.gov/>) to convert reported elevations to the North American Vertical Datum of 1988 (NAVD88) in meters. To compare among publications, we scaled these elevations to the local tidal range, using a unitless metric, z^* , as defined in Janousek et al., 2019: $z^* = (z - \text{MTL}) / (\text{MHHW} - \text{MTL})$. Here, z is the reported elevation, MTL is the mean tide level, and MHHW is the local mean higher high water. Vegetation usually begins at or above local MTL ($z^* = 0$) (Janousek et al., 2019; Swanson et al., 2014). We then compared the ranges for *S. foliosa* documented at SDW relative to those reported in the literature. We also included data collected in this study for the elevation range of *S. foliosa* at SEL and TJE in the comparison.

Data Analysis

We used R (version 4.4.0) for all analyses (R Core Team, 2024). We performed separate analyses for the elevation surveys in tidal creek and mudflat habitat. For each habitat

(tidal creek, mudflat), we fit three linear models, one for each vegetation type (unvegetated, *Spartina*, *Spartina* with mixed marsh). In each model, we examined how elevation varied as a function of the main effect of wetland (SDW, TJE, SEL for tidal creek habitat; SDW, TJE for mudflat habitat). For all models, we used the “DHARMA” package to ensure that models met assumptions of homogeneity of variance and normality of residuals (Hartig, 2019).

Results

Characterizing Habitat Conversion at SDW with Multispectral Imagery

Within the area of built tidal creek/mudflat habitat at SDW (0.4–1.1 m NAVD88), salt marsh habitat increased from 0.3 ha in 2012 to 4.5 ha in 2023 (Fig. 2C). Simultaneously, tidal creek/mudflat habitat within this area declined from 8.2 ha in 2012 to 5.2 ha in 2023 (Fig. 2C). As of 2023, 42% of the total 10.8 ha of built tidal creek/mudflat transitioned to salt marsh. *Spartina* was the primary species contributing to the conversion of tidal creek and mudflat habitat to salt marsh at SDW. Across the entire restoration project, *Spartina* hectares increased from 0 ha in 2012 to 10.8 ha in 2023 (Fig. 2D).

Spartina Spp. Genetics

STRUCTURE grouped all *Spartina* genetics samples from SDW and two other Southern California natural wetlands

(TJE, MUL) into the genetic cluster containing known *S. foliosa* from San Francisco Bay, with P_{fol} scores (proportion of ancestry in the *S. foliosa* cluster) ranging from 0.992 to 0.994 (Ort & Thornton, 2016). Thus, there is no genetic evidence of *S. alterniflora* or hybridization of this species or other non-native *Spartina* species with *S. foliosa* in these wetlands. We therefore assume that all *Spartina* populations in our study wetlands are *S. foliosa*.

Comparing Elevations of Tidal Creek and Mudflat Habitat at SDW to Other Natural and Restored Wetlands

Tidal Creek

On average, elevations of unvegetated areas in the restored tidal creeks at SDW were 0.3–0.4 m higher than in the natural tidal creeks at TJE and restored tidal creeks at SEL (Fig. 3A; $F_{2,265} = 83.3$, $p < 0.0001$). Unvegetated areas in the tidal creeks at SDW also overlapped more with the design elevations for low marsh at SDW (1.1–1.3 m; Fig. 3A).

Although there was no statistical difference in the average elevation of *S. foliosa* among the wetlands ($F_{2,153} = 0.06$, $p = 0.2$), *S. foliosa* extended to lower elevations in the restored tidal creeks at SDW compared to the other wetlands (Fig. 3B). The elevation range of *S. foliosa* was 2.3 times wider at SDW (0.8–1.5 m) compared to TJE (1.1–1.4 m) and SEL (1.0–1.3 m; Fig. 3B). At SDW, the elevation range of *S. foliosa* overlapped with tidal creek design elevations for this site (0.4–1.1 m). *Spartina foliosa* with mixed marsh was

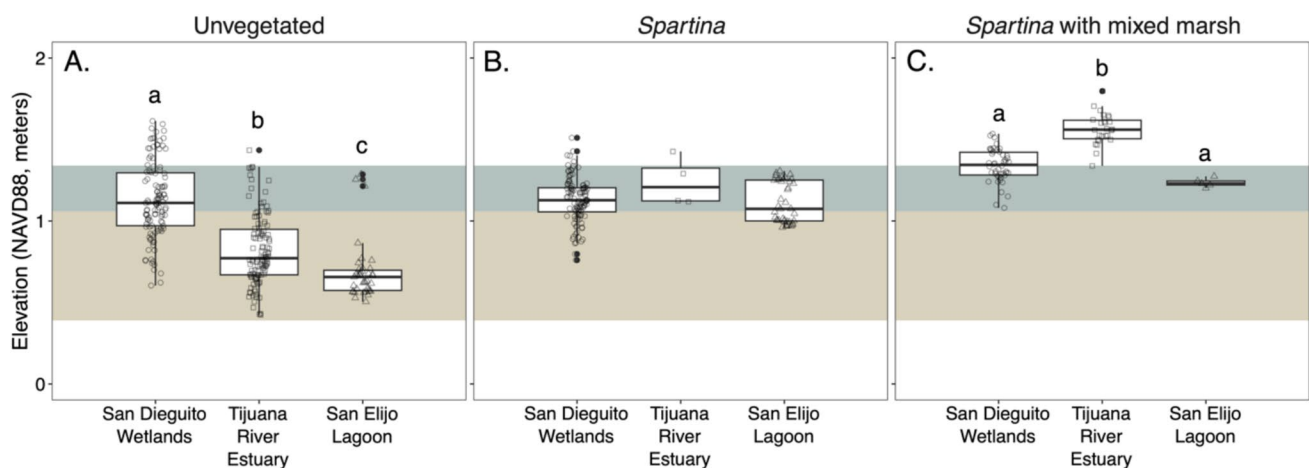


Fig. 3 **A** Unvegetated areas in restored tidal creeks at San Dieguito Wetlands (SDW) occurred at higher tidal elevations that overlapped with the design elevations for low marsh habitat at SDW (green band, 1.1–1.3 m NAVD88) compared to natural tidal creeks at Tijuana River Estuary (TJE) and restored tidal creeks at San Elijo Lagoon (SEL). **B** *Spartina foliosa* colonizing tidal creeks extended to lower

elevations at SDW than the other wetlands, overlapping with the design elevations for tidal creek habitat at SDW (tan band, 0.4–1.1 m NAVD88). **C** *Spartina foliosa* with mixed marsh was present at lower elevations in at SDW compared to TJE. Few examples of this vegetation type were present at SEL. Lowercase letters represent significant differences among wetlands within a panel

present at lower elevations at SDW relative to tidal creeks at TJE (Fig. 3C, F2, $74 = 52.6$, $p < 0.0001$).

Mudflat

Elevations of unvegetated areas in mudflat were comparable between SDW and TJE (TJE: 0.8–1.2 m; Fig. 4A, F1, $202 = 2.4$, $p = 0.1$). On average, *S. foliosa* was present at elevations 0.1 m lower at SDW than at TJE (Fig. 4B, F1, $105 = 28.2$, $p < 0.0001$). The elevation range for *S. foliosa* was also 3 times wider at SDW (0.8–1.4 m) compared to TJE (1.1–1.3 m). *Spartina foliosa* with mixed marsh was present at comparable elevations at both wetlands, although comparison is difficult because there were few examples of this vegetation type at TJE (Fig. 4C, F1, $17 = 0.3$, $p = 0.6$).

At SDW, the distribution of survey points that included *S. foliosa* overlapped for tidal creek and mudflat habitats (Fig. 5A). In contrast, at TJE, the distribution of survey points that included *S. foliosa* was distinct for tidal creek and mudflat habitats, with *S. foliosa* present at lower elevations in mudflats relative to tidal creeks (Fig. 5B).

Spartina foliosa Literature Search

In comparing elevations standardized relative to the local tide for eight wetlands distributed across California, we found that the lower elevation boundary of *S. foliosa* at SDW was lower than that documented at seven out of eight

California wetlands (Fig. 6; Table S2). Only *S. foliosa* in Upper Newport Bay occurred at elevations lower than in SDW.

Discussion

Habitat Conversion of Constructed Tidal Creek and Mudflat Habitat at Restored Wetland

Coastal wetland restoration projects often aim to create and maintain a desired mix of habitats, including tidal creeks, mudflat, and marsh plain habitats (Vivian-Smith, 2001; Wallace et al., 2005; Weinstein et al., 2005; Williams, 2001). Given the tight coupling between elevation and habitat type, restoration projects require careful consideration of design elevation to support habitat creation in desired locations (Haltiner et al., 1996; Williams, 2001; Zedler et al., 1999). Here, we document the unplanned, long-term habitat conversion of tidal creek and mudflat habitat to *Spartina*-dominated salt marsh at San Dieguito Wetlands (SDW) in Southern California. We confirmed that the *Spartina* spp. in the tested wetlands was the native *S. foliosa*, and to our knowledge, no non-native or hybrid *Spartina* spp. have been documented at other Southern California wetlands (personal communication, Brian Ort, Christine Whitcraft, Doug Gibson). Habitat conversion was likely due to flaws in restoration

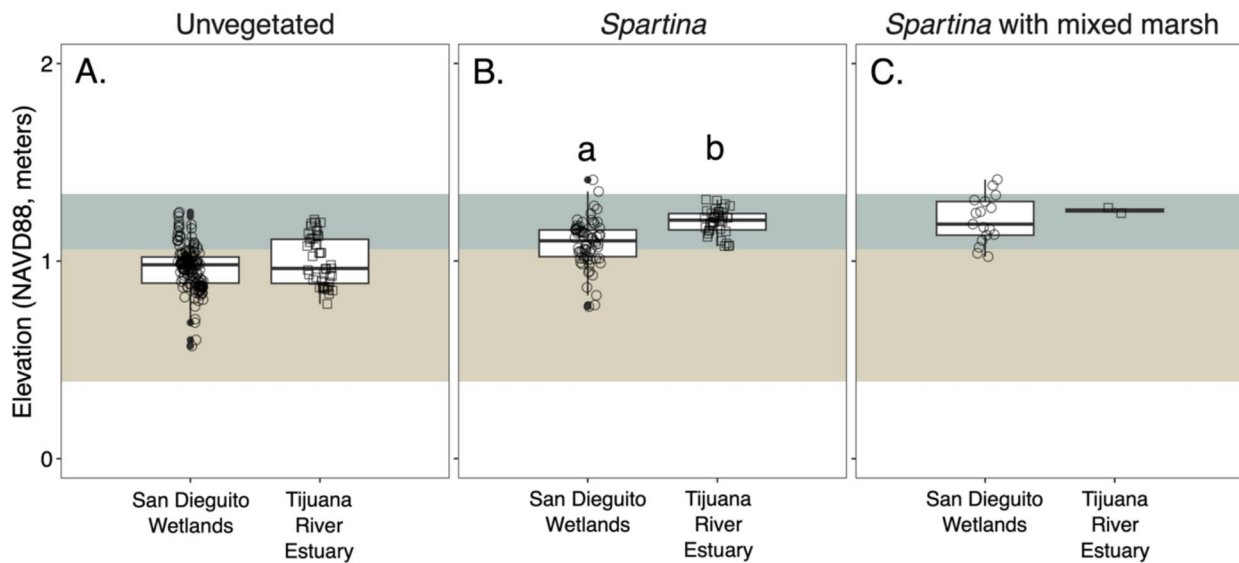


Fig. 4 **A** Unvegetated areas in mudflats at the restored San Dieguito Wetlands (SDW) occurred at comparable elevations to natural mudflats at Tijuana River Estuary (TJE). **B** At SDW, *Spartina foliosa* extended below the design elevations for low marsh habitat at SDW (green band, 1.1–1.3 m NAVD88) to lower elevations than natural mudflats at TJE, overlapping with the design elevations for mudflat

at SDW (tan band, 0.4–1.1 m NAVD88). **C** *Spartina foliosa* with mixed marsh occurred at comparable elevations in mudflats at SDW and TJE, though few examples of this vegetation type were present at TJE. Lowercase letters represent significant differences between wetlands within a panel

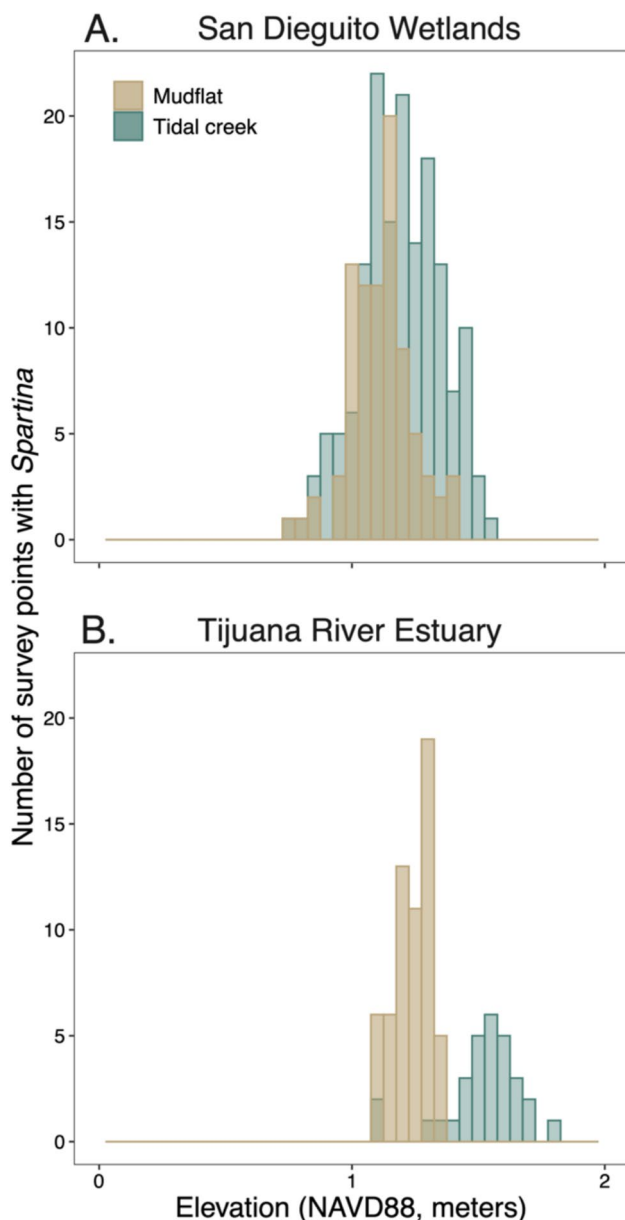


Fig. 5 At the **A** restored San Dieguito Wetlands (SDW), the distribution of survey points with *Spartina foliosa* present overlapped in elevation for tidal creek and mudflat habitats. In comparison, at the **B** natural Tijuana River Estuary (TJE), survey points with *S. foliosa* present were located at higher elevations in tidal creek habitat relative to mudflat habitat. *Spartina foliosa* in restored tidal creeks at SDW extended to lower elevations compared to natural tidal creeks at TJE

design and insufficient information about the elevation range of *S. foliosa* at the site prior to wetland restoration. Restored tidal creek and mudflat habitat were built at elevations that fell within the site's elevation range of *S. foliosa*. Furthermore, the elevation range of *S. foliosa* extended lower at SDW than other wetlands in California, expanding the range of elevations susceptible to *Spartina* encroachment. These results illustrate the need to consider

the site-specific elevation ranges of desired target species when designing restoration projects to guard against habitat conversion.

Spartina foliosa was planted soon after wetland construction to jumpstart low marsh development. Despite slow growth from 2012 to 2017, *S. foliosa* increased rapidly in 2018 following a high rainfall year (NWS, 2024). Freshwater inputs can accelerate *S. foliosa* growth; large rainfall events drive habitat conversion in Southern California wetlands by relieving salinity stress and increasing substrate elevations via sedimentation (Cahoon et al., 1996; Ward et al., 2003; Zedler, 1983). Other wetland restoration projects have similarly found delayed *Spartina* spp. growth (> 7 years) followed by rapid expansion (Haltiner et al., 1996; Race, 1985; Wolters et al., 2008). *Spartina foliosa* may be slow to colonize new marsh areas due to dispersal limitation, which can produce erratic seedling establishment (Callaway & Joselyn, 1992; Morzaria-Luna & Zedler, 2007). As the population of *S. foliosa* increases at a given site, the overall rate of establishment will increase due to a combination of clonal growth and greater local seed supply. Indeed, we observed *S. foliosa* establishment from seed in SDW following initial planting (H.M. Page & S.C. Schroeter, personal observation). Siting restoration projects next to natural *S. foliosa* sources can support tidal dispersal to newly restored locations (Morzaria-Luna & Zedler, 2007).

Although *S. foliosa* plantings can help increase vegetation cover in restored salt marsh areas (Zedler, 1993), the rapid growth of this species can hinder progress towards restoration goals if *S. foliosa* encroaches into other habitat types. At SDW, *S. foliosa* expanded into areas built as tidal creek and mudflat habitat via multiple mechanisms. Unvegetated areas in tidal creeks were located at higher elevations relative to other wetlands, indicating that tidal creeks were likely built too high and too shallow at SDW relative to natural creeks (Beheshti et al., 2022). Higher, shallower creeks often have tidal asymmetries favoring flood dominance that promote sediment accretion and continued shallowing over time (Friedrichs & Perry, 2001). Thus, tidal creek geomorphology may have contributed to *S. foliosa* encroachment into tidal creeks at SDW by maintaining shallow, high conditions within the range of elevations that can support *S. foliosa*. In contrast, elevations of unvegetated mudflat areas were comparable between SDW and TJE, suggesting that these habitats were built similarly to natural mudflats.

Tidal creek and mudflat elevations at SDW overlapped with the vertical range of *S. foliosa* observed at the site, supporting its expansion into both of these habitats. Thus, there was likely a mismatch between the design elevation for *S. foliosa* relative to the actual vertical range of the species at the site post-construction. We expect additional conversion of tidal creek and mudflat habitat to low marsh at SDW in the future, as much of these remaining

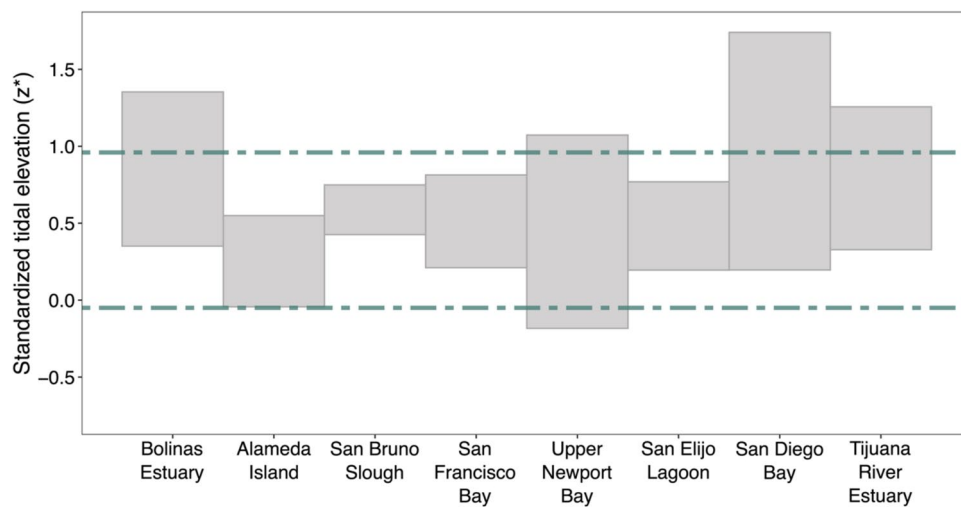


Fig. 6 Comparison of *Spartina foliosa* elevation distribution at the restored San Dieguito Wetlands (SDW; this study, dashed lines) relative to other California wetlands, from Bolinas Estuary to Tijuana River Estuary (gray rectangles). Wetlands are organized from Northern to Southern California from left to right. The elevation bound-

ary of *S. foliosa* documented in this study at SDW is lower than all other sites, aside from Upper Newport Bay (Thorne et al., 2016). See Table S2 for the references associated with each wetland. Panels for San Diego Bay and Tijuana River Estuary include data from multiple studies. Data for San Elijo Lagoon is added from the current study

habitats fall within the elevation range of *S. foliosa* at the site. Once established, *S. foliosa* can further accelerate habitat conversion by locally increasing sedimentation as plant stem densities increase, creating a positive feedback loop that builds higher elevations and supports additional *Spartina* colonization (Cahoon et al., 1996; Friedrichs & Perry, 2001; Gleason et al., 1979; Stumpf, 1983). *Spartina foliosa* encroachment into mudflat habitat can also occur in response to extreme sedimentation events associated with winter storms that can increase substrate elevations to overlap with the elevation range of *S. foliosa* (Cahoon et al., 1996; Ward et al., 2003).

It is unclear how much tidal creek and mudflat habitat at SDW has accreted in response to *S. foliosa* encroachment. We are currently working to quantify sediment accretion in tidal creek and mudflat areas with and without *S. foliosa* at SDW by developing digital elevation models, measuring feldspar markers over time, and creating an elevation time series in consistent locations with RTK-GPS. These efforts are necessary to understand trajectories of tidal creek and mudflat habitat relative to continued *S. foliosa* expansion and how these habitat shifts will respond to predicted sea-level rise. It is currently unknown whether sedimentation rates at SDW will outpace sea-level rise, which will influence how the current habitat configuration will change as sea levels increase. As in many other coastal wetlands, mudflat and subtidal habitat area is expected to increase at SDW with sea level rise, and there is limited area available for marsh migration at the lagoon (ESA, 2018). Thus, over time, it is possible that currently encroached areas may convert back to tidal creek or mudflat habitat.

Finally, the lower elevation boundary for *S. foliosa* at SDW extends below that documented at seven out of eight California wetlands, exacerbating salt marsh encroachment at the site. The plasticity of *S. foliosa*'s elevation range across wetlands is supported by prior work that found the vertical niche breadth of most salt marsh plants—including *S. foliosa*—varies along the US West Coast (Janousek et al., 2019). Variation in species-specific elevation limits could be due to differences in abiotic tolerance, species interactions, latitude, substrate texture, distance to mouth, or site-specific differences in the relationship between elevation and inundation frequency (Janousek et al., 2019; Zedler et al., 1999). At SDW, tidal regime likely contributes to the lower-than-expected vertical range for *S. foliosa* at the site. Relative to TJE, SDW marshes spend less time submerged at lower elevations (Fig. S5; 0.4–1.5 m NAVD88), which could support greater growth at lower elevations (i.e., reduced hypoxic exposure, etc.). *Spartina* spp. may also have a particularly large vertical niche relative to other salt marsh plants due to lack of competition with other species in the low marsh (Chapman, 1940; Janousek et al., 2019; Sánchez et al., 1996). Additionally, plants may grow at different elevation ranges at restored wetlands relative to natural wetlands, so it is important to account for a wide range of elevations in wetland restoration plans and understand site-specific plant distributions (Zedler et al., 1999). Although site-specific information on planting elevations can be challenging to obtain prior to restoration, we recommend measuring these elevations from the closest natural populations to the restoration site prior to construction and conducting small scale experiments (e.g., marsh organs) at the restoration site to

determine the realized niche of salt marsh plants prior to construction and grading.

Management Trade-Offs

Managing habitat conversion in wetland restoration projects is challenging. Salt marsh and mudflat are both desired habitat types in restoration plans, and both habitats are inherently valuable (Foster et al., 2013). Conversion of tidal creeks and mudflat to salt marsh alters the important wetland functions provided by these lost habitats. For example, salt marsh encroachment and associated sediment accretion can impede fish and invertebrate access to tidal creeks by changing channel dimensions, reducing available habitat, and altering tidal inundation and water flow (Desmond et al., 2000; Friedrichs & Perry, 2001; Minello & Webb, 1997; Wallace et al., 2005). Fish composition is linked to topographic complexity of tidal creeks, and narrow, shallow creeks with encroached vegetation may have different fish communities than wider, deeper creeks (Haltiner et al., 1996; Williams & Zedler, 1999). Salt marsh encroachment can also reduce mudflat, a regionally rare, vulnerable and often overlooked habitat type that has been substantially degraded worldwide (Murray et al., 2019). Mudflat provides important feeding grounds for resident and migrating shorebirds (Burger et al., 1997; Galbraith et al., 2002). That said, salt marsh also provides valuable ecosystem services in coastal wetlands, including habitat provisioning for other sensitive species of conservation concern, including the Ridgway's Rail and Belding's savannah sparrow (Massey et al., 1984; Powell, 1993; Zedler, 1993).

Given the trade-offs between habitat types, managing salt marsh encroachment in wetland restoration requires consideration of restoration objectives and desired outcomes at the system-level (Williams & Faber, 2001). For example, in assessing the performance of SDW, we evaluate the holistic wetland community (birds, fishes, invertebrates) and their associated functions (Page et al., 2022). These wetland functions may interact or respond differently to salt marsh encroachment. In making complex management decisions, it is important to determine which restoration objectives are most important (Williams & Faber, 2001). It may be necessary to re-evaluate objectives given project progression, especially when unpredictable processes, such as salt marsh encroachment, can alter restoration trajectories (Mitsch & Wilson, 1996; Moreno-Mateos et al., 2015). Indeed, this work highlights the challenges of trying to meet fixed habitat area targets in an inherently dynamic system. Additionally, understanding the mechanisms leading to habitat conversion (e.g., graded elevations) can support adaptive management of the desired habitat. For example, tidal creeks at SDW could be deepened to match the elevational profiles of tidal creeks in modeled equilibrium conditions that will not support salt marsh growth.

Conclusions

Given the linkages among tidal elevation, habitat type, and salt marsh plant zonation (Bertness & Ellison, 1987; Pennings & Callaway, 1992; Silvestri et al., 2005; Vivian-Smith, 2001; Williams, 2001), consideration of project design elevations relative to expected elevation ranges of wetland plants is essential for meeting project objectives and ensuring that vegetation can establish and grow in desired locations. Restoration projects should be designed to mimic the hydrology, position, and dimensions of natural tidal creeks and mudflats (Williams & Zedler, 1999). Restored wetlands that are not built in dynamic equilibrium with local physical processes may quickly develop to be different from their initial design and away from expected equilibrium conditions (Friedrichs & Perry, 2001; Wallace et al., 2005). At SDW, tidal creeks were likely designed too shallow and were unable to maintain their geomorphology as tidal creeks. Combined with the wide elevation range of *S. foliosa* at SDW, these accretive conditions facilitated *S. foliosa* establishment and expansion into areas designed as tidal creeks and mudflat. Our work reinforces the importance of considering the physical aspects of wetland hydrology and elevation relative to the requirements of desired habitat types for successful wetland restoration.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-025-01576-3>.

Acknowledgements We thank Brian Ort and Tobias Rohmer with the Invasive Spartina Project for their help with processing and interpreting the *Spartina* genetics results. We thank Lee Harrison and Garrett Reynolds for helping collect field data.

Author Contribution Conceptualization: KMB, HMP, RSS; methodology: AD, HMP, KMB, RSS; data acquisition and management: AD, DH, DW, EB, JCH, MT, KMB, RJ, RSS, SCS; supervision: AD, DH, KMB, RSS; formal analysis and investigation: DW, KMB, RSS; writing—original draft preparation: RSS; writing—review and editing: all authors; funding acquisition: HMP, KMB, RSS, SCS; All authors read and approved the final manuscript.

Funding Funding was provided by Southern California Edison (SCE) as required by the California Coastal Commission under SCE's coastal development permit (No. 6–81-330-A, formerly 183–73) for Units 2 and 3 of the San Onofre Nuclear Generating Station.

Data Availability Data are publicly available on the Environmental Data Initiative Data Portal (<https://doi.org/10.6073/pasta/efd746b655f98e5f127589366b569b10>).

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Competing Interests The authors declare no competing interests.

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