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COASTAL AND MARINE ECOLOGY

Seasonal impoundment alters patterns of tidal wetland plant diversity across spatial scales

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Citation: Jones, S. F., C. N. Janousek, M. L. Casazza, J. Y. Takekawa, and K. M. Thorne. 2021. Seasonal impoundment alters patterns of tidal wetland plant diversity across spatial scales. Ecosphere 12(2):e03366. 10.1002/ecs2.3366

Abstract. Understanding patterns of biodiversity is a key goal of ecology and is especially pressing in the current human-caused biodiversity crisis. In wetland ecosystems, human impacts are centered around hydrologic manipulation including the common practice of wetland diking and impoundment. Constraining how wetland management influences plant biodiversity patterns across spatial scales will provide information on how best to modify actions to preserve biodiversity and ecosystem function in managed wetlands. Here, we compare patterns of plant diversity and species presence, abundance, and community composition at several spatial scales among tidal wetlands along an estuarine salinity gradient and managed wetlands that were formerly tidal. Managed impounded wetlands had decreased alpha and gamma diversity of rare species, with less than 60% of the species richness found in tidal brackish wetlands at several spatial scales. There was little change in the overall pattern of alpha, beta, and gamma diversity for common species in impounded wetlands; however, dominant tidal brackish species, primarily perennial rhizomatous graminoids, were replaced with management target plants and non-native annual grasses in impounded wetlands. This species replacement led to over 60% of impounded sites being classified as containing novel plant assemblages. An additional 25% of impounded sites were classified as containing tidal saline plant assemblages, suggesting potential soil salinization. Along the estuarine gradient, patchiness and codominance of common plant species drove high diversity and turnover in tidal brackish wetlands, while it remains unclear whether tidal fresh or brackish wetlands maximize rare plant diversity. With reduced species richness, altered functional dominants, and novel or saline assemblages, impounded brackish wetlands may require careful water management to balance native plant biodiversity, associated ecosystem processes, and waterfowl requirements.

Key words: alpha diversity; beta diversity; coastal wetland; community composition; San Francisco Bay Delta; waterfowl management; wetland impoundment.

Received 19 March 2020; accepted 30 August 2020; final version received 20 November 2020. Corresponding Editor: Debra P. C. Peters.

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Introduction

Understanding spatial and temporal patterns of biodiversity is a key goal of ecology. Naturalists and ecologists have been fascinated by the striking patterns of species occurrence and abundance for millennia (Egerton 2001) and have expanded the idea of biodiversity and how it relates to

ecosystem function from species diversity to functional trait and phylogenetic diversity (Díaz and Cabido 2001, Donoghue 2008). Methods to rigorously quantify biodiversity patterns have been recently refined (Jost 2007, Chao et al. 2014*a*) and discussion continues on which metrics or combinations of metrics are most appropriate to document biodiversity change, including the possibility and utility of moving beyond single diversity metrics (Hillebrand et al. 2018).

Describing the patterns and drivers underpinning biodiversity is especially pressing as human pressure on natural ecosystems increases globally (Worm et al. 2006, Cardinale et al. 2012). The alteration of species presence, abundance, and community composition can lead to novel or no-analog ecosystems, with largely unknown effects on overall ecosystem function (Hobbs et al. 2006, Williams and Jackson 2007, Cloern et al. 2016). Additionally, the effects on biodiversity and ecosystem function may depend on the spatial scale altered by human activity (Wanner et al. 2013; Gonzalez et al. 2020). If anthropogenic impacts to biodiversity differ across spatial scales, cross-scale studies will be necessary as the scale of input data may determine whether impacts to biodiversity are detectable. An understanding of the spatial scales at which biodiversity loss is due to human activity is also crucial to develop effective solutions to modify human activity to reduce biodiversity conflict (Young et al. 2010).

In wetlands, human disturbance often involves hydrologic modifications. Wetlands have been diked, drained, and otherwise hydrologically manipulated for centuries across the globe (Zedler and Kercher 2005, Gedan et al. 2009). Investigating the response of wetland diversity to hydrologic modification is tractable partially because wetland plants have strong responses to hydrologic stress (Mitsch and Gosselink 2007), and wetlands typically have a limited pool of foundational species, especially in estuaries (Sharpe and Baldwin 2009). Wetlands also often occur as discrete patches across landscapes, allowing comparison among distinct sites that have similar environmental drivers (Grewell et al. 2007). Wetland impoundment, which typically changes inundation frequency and duration and decreases salinity in coastal wetlands by muting or reducing tidal influence, is one of the more common practices of hydrologic manipulation, often in combination with waterfowl management (Montague et al. 1987, Ackerman et al. 2014).

While impoundment effects have been studied on the Atlantic (Portnoy and Giblin 1997, Elsey-Quirk and Adamowicz 2016, Loder et al. 2019) and Gulf (Nyman et al. 1993, Boumans and Day 1994) coasts of North America, the effects of wetland impoundment on Pacific coast plant communities are still largely unknown (but see Busnardo et al. 1992 and Sinicrope et al. 1992 for effects on biogeochemistry). Further, although novel community states may be expected after impoundment, it is still unclear whether wetland impoundment fundamentally alters how diversity changes from plot to landscape scales and whether rare or common species are the primary drivers of changes in diversity. This gap is especially problematic considering coastal wetlands on a large portion of the Pacific Coast have a Mediterranean climate; coastal wetlands in Mediterranean settings may experience inherently different environmental fluctuations (e.g., high variability in salinity due to wet–dry season dynamics; Takekawa et al. 2013) compared with coastal wetlands in more humid/temperate climates. Wetland impoundment in a Mediterranean estuarine setting may therefore exert diversity effects that differ in magnitude or type compared with impoundment in more temperate settings.

We studied 48 nontidal managed wetlands (hereafter "impounded wetlands") to investigate how waterfowl-focused management affects patterns of plant diversity, species presence and abundance, and community composition in Suisun Marsh, California, USA. Here, we define impounded wetlands as diked areas with water control structures that can be opened or closed to tidal waters based on management decisions. We compared patterns of plant diversity at several spatial scales among impounded wetlands and tidal wetlands along an estuarine salinity gradient in the San Francisco Bay-Delta Estuary. We asked the following: (1) How has wetland management for waterfowl habitat influenced the overall patterns of plant diversity and the relationships between diversity and spatial scale? (2) Are changes in diversity being driven by rare, common, and/or dominant species? (3) How has

management altered plant presence and abundance, and is there evidence of novel assemblages? and (4) How can spatial patterns of diversity, species presence and abundance, and community composition inform impounded wetland water management to preserve plant diversity across the broader estuarine landscape?

Methods

Site descriptions

The San Francisco Bay-Delta is a large inland deltaic estuary located in central California, USA (Fig. 1). This area has a Mediterranean climate with warm, dry summers and cool, wet winters. The estuary contains a strong salinity gradient from east to west with tidal freshwater wetlands where the Sacramento and San Joaquin rivers converge, seasonally dynamic tidal brackish wetlands in Suisun Marsh, and fully saline tidal wetlands in San Francisco Bay, each with their own characteristic vegetation (Fig. 2). Suisun Marsh is the largest brackish wetland complex in California (Moyle et al. 2014), with ~60,000 acres of total wetland area. Of this, approximately 75% is managed with water control structures as seasonal impounded wetlands to enhance wintering waterfowl production. Salinity in Suisun Marsh varies seasonally and interannually due to changes in freshwater river inflows and management for human uses (Kimmerer et al. 2013).

We sampled impounded brackish wetlands across Suisun Marsh; these wetlands are managed by individual landowners, flooded in fall to create shallow ponds for wintering waterfowl, and drained in the spring. The former tidal wetland soils dry out by the end of the summer (Moyle et al. 2014). We also sampled tidal wetlands across the estuarine salinity gradient as a comparison to impounded wetlands: saline marsh at San Pablo (38.12° N, 122.47° W, average summer salinity 20.2 ppt, marsh platform average 8% flooded), brackish marsh at Rush Ranch (38.19° N, 122.02° W, average summer salinity 7.9 ppt, marsh platform average 5% flooded), and fresh marsh at Miner Slough (38.23° N, 121.67° W, average summer salinity 0.0 ppt, marsh platform average 41% flooded; Fig. 1). Tidal brackish wetlands represent the pre-management condition of impounded wetlands in Suisun Marsh, while tidal fresh and tidal saline wetlands represent conditions that may occur as salinity changes in response to hydrological management activity.

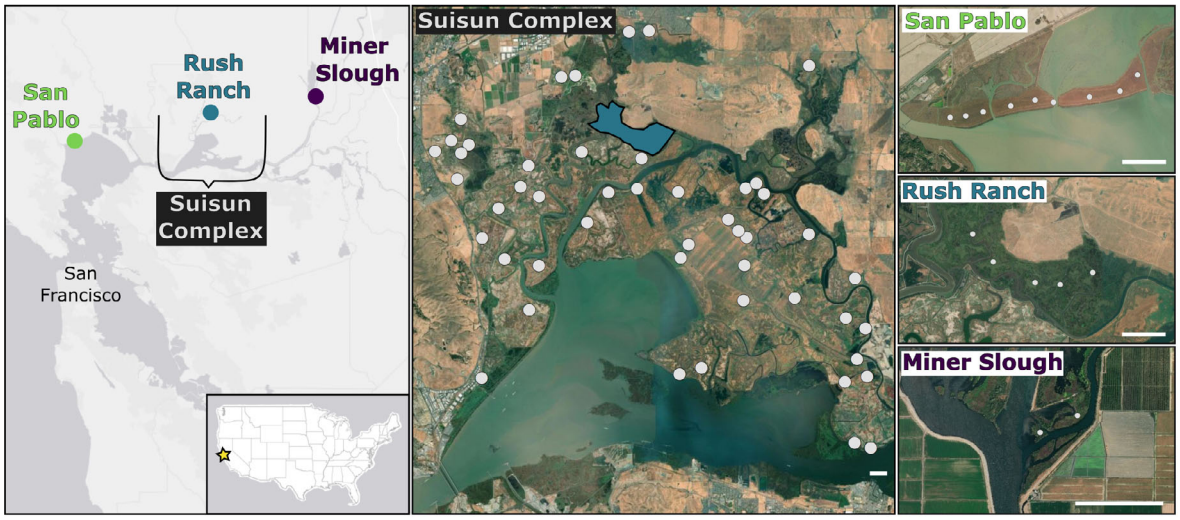

Fig. 1. Locations of San Pablo (tidal saline), Rush Ranch (tidal brackish), the Suisun Marsh Complex (impounded brackish), and Miner Slough (tidal fresh) wetlands within the broader San Francisco Bay-Delta Estuary, California, USA, and maps of site locations used in this study. Note that Rush Ranch is located within the Suisun Marsh Complex (center panel). Small white bar in site panels represents 1 km distance.

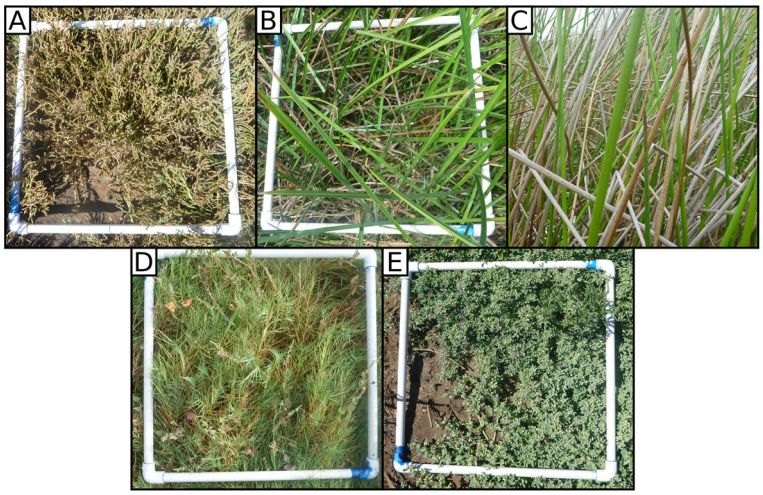

Fig. 2. Representative plot photographs of dominant plant species found throughout San Francisco Bay-Delta tidal wetlands and Suisun Marsh impounded wetlands. (A) *Salicornia pacifica*; (B) *Schoenoplectus americanus*; (C) Tules (*Schoenoplectus californicus* and/or *Schoenoplectus acutus*); (D) *Distichlis spicata*; and (E) *Sesuvium verrucosum*.

Data collection and sampling design

Between 2016 and 2018, we collected plant community data using standard 0.5×0.5 m quadrats along transects at sites within four distinct wetland types across the San Francisco Bay-Delta: brackish impounded, tidal fresh, tidal brackish, and tidal saline wetlands (Fig. 1). Surveys consisted of 1–2 observers identifying every plant to the lowest possible taxonomic level (usually species) and visually estimating percent cover of every species present. When species identification was uncertain, voucher specimens were taken (physical and/or photograph vouchers) for later identification using the Jepson Flora manual (Baldwin et al. 2012*a*), and taxonomic names were confirmed with Jepson eFlora (Baldwin et al. 2012*b*). Species difficult to identify in the field were grouped for standardization across surveys, including non-flowering annual grasses (grass spp.) and *Schoenoplectus acutus* and *Schoenoplectus californicus* (tules).

We sampled several sites within each wetland type: 48 brackish impounded, 2 fresh tidal, 5 brackish tidal, and 9 saline tidal sites (Fig. 1). Within each site, we established transects to span in situ hydrologic gradients; tidal sites were sampled from low marsh fringing the main tidal channel to the upland transition edge, and impounded sites were sampled from low interior pond bottoms to just below the levee berm. Transects therefore varied in length and number depending on site-specific shape. This approach allowed us the flexibility to capture the full variability of hydrologic conditions within a site, an important consideration as hydrology is a strong driver of wetland plant presence and abundance (Mitsch and Gosselink 2007). Additionally, sampling across the entire elevation gradient in impounded sites ensured we captured variability in hydrology despite lacking explicit hydrologic data from individual landowners. Quadrats were sampled every 10–25 m along each transect.

To investigate how patterns of diversity varied across spatial scales, we aggregated data at four scales using ArcGIS (Esri, Redlands, California, USA). These scales differed in order of magnitude, with plots representing patterns at submeter scales, patches representing hundreds of square meters, sites representing hectares, and regions representing square kilometers. Plots consisted of individual quadrats. To ensure valid comparisons across sites that varied in shape, we first standardized sampling intensity so that all sites contained ~25 plots (impounded brackish $\bar{x} = 24$; tidal fresh $\bar{x} = 23$; tidal brackish $\bar{x} = 26$; tidal saline $\bar{x} = 27$), sampled at the hectare scale. Plots were randomly removed from sites that contained higher sampling intensity than

targeted. After standardization of site sampling intensity, sites were divided into patches manually in ArcGIS, so that each patch contained ~6 plots (impounded brackish $\overline{x} = 6.1$; tidal fresh $\overline{x} = 6.6$; tidal brackish $\overline{x} = 6.1$; tidal saline $\overline{x} = 6.5$), sampled at the hundreds of square meters scale. Plots were manually grouped into patches by one analyst, as differences in site shape presented site-specific clustering challenges.

At the region scale, we grouped sites into nearby clusters of 5, sampled at the square kilometers scale. For the contiguous tidal wetlands, this grouping was straightforward; there were enough sites for one tidal brackish region ($n = 129$ plots) and one tidal saline region ($n = 137$ plots). The tidal fresh wetland type did not contain enough data ($n = 46$ plots) to form a region and was therefore excluded from figures and analyses at that scale. For impounded brackish wetlands distributed throughout Suisun, clustering sites into regions was more difficult. Impounded sites that were far removed from other sites and could not form a close cluster were excluded from regional analysis ($n = 18$ sites), to avoid sampling larger spatial areas for impounded wetlands than tidal wetlands. This process produced 6 impounded brackish regions ($\overline{x} = 125$ plots). After grouping, sampling intensity and relative spatial area was consistent within all four spatial scales across wetland types.

Patterns of diversity

Alpha, beta, and gamma.—To determine the patterns of plant diversity across wetland types and spatial scales, we calculated the effective number of species (Hill 1973) for alpha, beta, and gamma diversity using diversity partitioning (Jost 2007) via package vegetarian in R version 3.6 (Charney and Record 2012, R Core Team 2020). This approach allows the calculation of independent alpha- and beta-diversity metrics and is becoming standard practice in ecology (Ellison 2010, Chao et al. 2014*b*). Alpha diversity and gamma diversity represent the effective number of species; we termed the effective number of species at the plot-, patch-, and site-scale alpha diversity, and the effective number of species at the region-scale gamma diversity. Beta diversity represents the effective number of compositional units (here termed assemblages) and was calculated within patches, sites, and regions. Diversity metrics were calculated on each individual plot, patch, site, or region, and then, average diversity across all plots, patches, sites, or regions within each wetland type was calculated for comparisons. All diversity metrics were calculated for order $q = 0$ (species richness; all species weighted equally and sensitive to rare species), $q = 1$ (exponential of Shannon's index; all occurrences weighted equally), and $q = 2$ (inverse of Simpson's index; sensitive to the most abundant species; Jost 2007, Chao et al. 2014*a*). By calculating diversity along the q gradient, we tested the influence of rare ($q = 0$), common ($q = 1$), and dominant ($q = 2$) species on diversity patterns (Morris et al. 2014, Thorn et al. 2020). This multimetric approach allowed a broader understanding of diversity patterns than using a single metric, as each diversity metric reveals different information about community responses (Morris et al. 2014).

Statistics.—For plot-, patch-, and site-scale analyses, we compared alpha-diversity and beta-diversity metrics across wetland types at each q value using a mixed-effects model framework (package nlme in R: Pinheiro et al. 2019). Wetland type was treated as a fixed effect, and site ID was treated as a random effect. After specifying the random effects, structures for variance modeling were compared using restricted maximum likelihood (REML) and AIC_c scores; for final models, variance was allowed to differ by wetland type. When final random effects including error structure were specified, wetland type was tested using maximum likelihood (ML). Significant differences between wetland types were detected by contrasting the Tukey-adjusted estimated marginal means ($\alpha = 0.05$) on the final mixed models (package emmeans in R; Lenth 2020). For regional scales, we compared gamma-diversity and beta-diversity metrics between impounded brackish and tidal brackish wetland types using one-sample t tests in R. This approach was necessary as only impounded brackish wetlands contained replication at the regional scale. We compared the distribution of gamma and beta diversity of impounded brackish regions ($n = 6$) to the

value of gamma and beta diversity of the tidal brackish region.

Species presence, abundance, and community composition

Species presence and abundance.—To determine how wetland types differed in plant species presence and abundance, we compared average plant cover of dominant species. We calculated average percent cover for every species at the patch scale ($n = 259$ total patches); we chose the patch spatial scale as a middle ground between capturing the inherent variability within wetland types while avoiding inflated variability from using small spatial scale (i.e., <1 m^2) data. We determined dominant species by compiling species with more than 15% average cover in at least one wetland type. For the impounded brackish type, plants targeted by managers as waterfowl food plants were combined into one group, termed management associates. We combined management associates as one class as this group of species is managed in a portfolio approach where each individual species typically makes up a small fraction of percent cover within individual sites. As individual land managers may target one suite of management associates over another, sites differ in their composition of plants meant to enhance waterfowl production; however, the class of management associates should make up a substantial proportion of plant cover in impounded brackish wetlands if management is effective. The management associates class included *Atriplex prostrata*, *Bolboschoenus maritimus* subsp. *paludosus*, *Cotula coronopifolia*, *Crypsis schoenoides*, *Polypogon monspeliensis*, and *Sesuvium verrucosum*. Due to its invasion of tidal brackish wetlands and uncertain native status, percent cover of management associates was calculated with and without *A. prostrata*.

Community composition.—We visualized multivariate plant community data at the site scale using stable, two-dimensional solutions of nonmetric multidimensional scaling (NMDS) with function metaMDS from the vegan package in R (Oksanen et al. 2019) based on a Bray–Curtis dissimilarity matrix of chord-transformed plant cover. We used site data for community composition as the larger spatial scale better represented wetland assemblages than the patch data used to explore individual species cover patterns. We calculated centroids and 95% confidence ellipses for each region; using regions allowed comparisons that accounted for sampling intensity and overall spatial coverage of sampling within and among wetland types. The tidal fresh wetland type did not have sufficient data at the regional scale, so ellipses were not calculated. Centroids and ellipses were overlaid on sites using vegan in R.

To identify how impounded wetlands differed from tidal wetlands in community composition, we classified all sites into a wetland assemblage using cluster analysis (package vegclust in R; De Cáceres and Wiser 2013; $m = 1.2$, dnoise = 0.8, nstart = 50). We started by classifying tidal wetland sites according to their wetland type in a fixed a priori classification, using percent plant cover data that were chord-transformed (Oksanen et al. 2019). We then used noise clustering to classify impounded sites, using the previous a priori tidal classification clusters as fixed centroids (De Cáceres and Wiser 2013). Impounded sites were classified as any of the tidal assemblages, or as novel, nontidal assemblages. We forced assemblage membership to be crisp, not fuzzy. To describe any novel assemblages, we tabulated species constancy and average percent plant cover within each assemblage.

Statistics.—To test whether wetland types differed in percent cover of dominant species at the patch scale, we used a mixed-effects model framework (package nlme in R). Percent cover values were logit-transformed before analysis for all species; a small offset value (0.001) was added to avoid logit transformation of 0. Model outputs were back-transformed before presentation. Wetland type was treated as a fixed effect, and patch ID nested within site ID was treated as a random effect. After specifying the random effects, error structures were compared using REML and AIC_c scores; for final models, variance was allowed to differ for each wetland type. When final random effects including error structure were specified, wetland type was tested using ML. To assist with model convergence when a wetland type contained only zeros for a species, a small

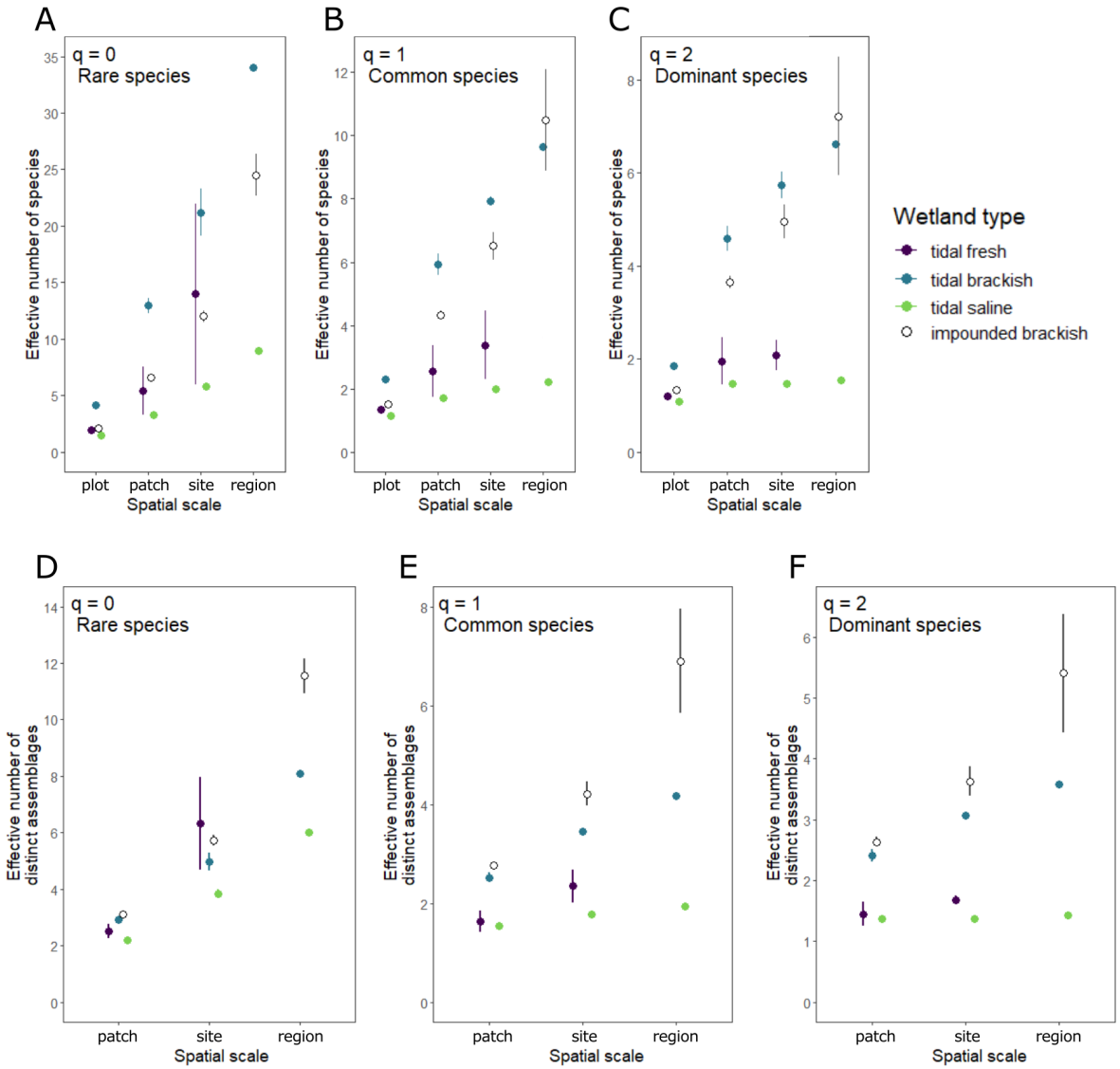

Fig. 3. Plant community alpha, beta, and gamma diversity for three tidal wetland types along a San Francisco Bay-Delta estuarine gradient and an impounded brackish wetland complex, at four spatial scales. Effective numbers of species (alpha and gamma diversity) are shown along a q gradient in panels (A) $q = 0$: species richness where all species are weighted equally (sensitive to rare species); (B) $q = 1$: exponential of Shannon's index where all occurrences are weighted equally; and (C) $q = 2$: inverse of Simpson's index (sensitive to most abundant species). Effective numbers of distinct assemblages (beta diversity) are shown along a q gradient in panels (D) $q = 0$; (E) $q = 1$; and (F) $q = 2$. Note change in y-axis between panels. Error bars are standard errors. Note lack of error bars for tidal brackish and tidal saline wetland types at the regional scale ($n = 1$), and absence of tidal fresh wetland type at the regional scale from lack of data.

amount of random noise was added to each observation. Random noise was added with a mean = 0 and standard deviation = 0.0001 (1/100th of 1 percent cover) following a Gaussian distribution. Noise was added only for modeling purposes; untransformed data are

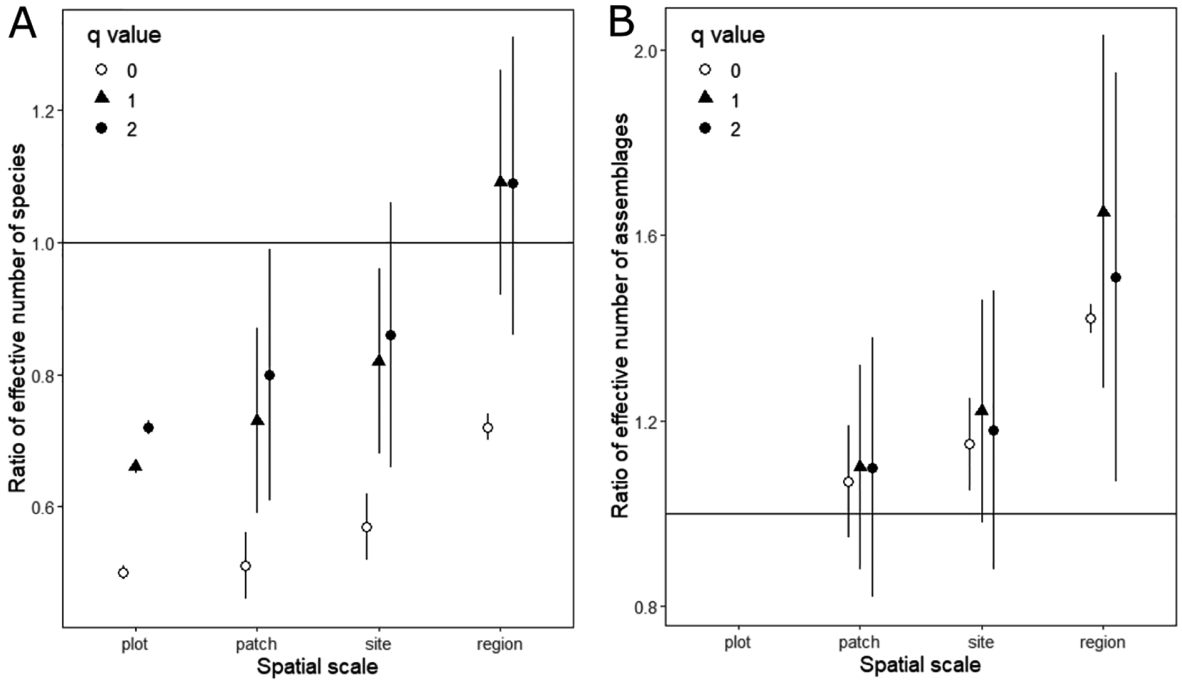

Fig. 4. Ratios of diversity values comparing impounded brackish to tidal brackish wetland types from the San Francisco Bay-Delta. (A) Alpha and gamma diversity and (B) beta diversity. Error bars are ratio variance.

presented in figures. Significant differences between wetland types were detected by contrasting pairwise Tukey-adjusted estimated marginal means ($\alpha = 0.05$) on the final models (package emmeans in R).

Results

Patterns of diversity

Impounded vs. tidal brackish wetlands.—The differences in alpha and gamma diversity between impounded and tidal brackish wetlands depended on spatial scale and whether rare, common, or dominant species were emphasized when calculating effective number of species (Figs. 3, 4; overall model parameters and estimated marginal means in Appendix S1: Tables S1–S3). Differences between wetland types were primarily driven by rare species, and the effects were more pronounced at small spatial scales (Fig. 4). Impounded brackish wetlands contained fewer plant species ($q = 0$) at all spatial scales ($P < 0.01$ in all cases), including only 57% of the effective number of species as tidal brackish wetlands at the site scale (Fig. 4). Impounded brackish wetlands contained a lower effective number of common species ($q = 1$) at site and smaller spatial scales ($P < 0.02$ in all cases), and a lower effective number of dominant species ($q = 2$) at plot scales ($P < 0.001$), but not at larger spatial scales.

Impounded brackish wetlands had higher beta diversity than tidal brackish wetlands, especially at the regional scale (Figs. 3, 4; Appendix S1: Tables S1–S3). Differences were primarily driven by spatial scale, with no difference in the effective number of assemblages between impounded and tidal brackish wetlands at patch ($P > 0.2$ in all cases) and site ($P > 0.1$ for $q = 0$ and $q = 2$) scales, except for common species at the site scale ($P = 0.02$). At the regional scale, whether impounded brackish wetlands had more distinct assemblages was dependent on which species were emphasized (Fig. 4; total assemblages $q = 0$: $P = 0.003$; common assemblages $q = 1$: $P = 0.05$; dominant assemblages $q = 2$: $P = 0.12$).

Tidal wetlands along the estuarine gradient.—Tidal fresh and brackish wetlands had high levels of diversity depending on which species were emphasized. Tidal brackish wetlands

contained higher alpha diversity than tidal fresh or tidal saline wetlands when common ($q = 1$) and dominant ($q = 2$) species were emphasized, regardless of spatial scale ($P < 0.001$ in all cases; Fig. 3a–c; Appendix S1: Tables S1, S2). Tidal fresh and saline wetlands contained ~1/3 of the alpha diversity compared with tidal brackish wetlands at the site scale when emphasizing dominant species (tidal fresh $\overline{x} = 2.1$, tidal saline $\overline{x} = 1.5$, tidal brackish $\overline{x} = 5.7$). When rare ($q = 0$) species were emphasized, however, tidal fresh wetlands did not differ from tidal brackish wetlands in alpha diversity at larger spatial scales (plot $P = 0.002$; patch $P = 0.002$; site $P = 0.65$), while tidal saline wetlands remained low in diversity (site-scale alpha diversity at $q = 0$: tidal fresh $\overline{x} = 14.0$, tidal saline $\overline{x} = 5.7$, tidal brackish $\overline{x} = 21.2$).

A similar pattern emerged with beta diversity. Tidal brackish sites had higher beta diversity than tidal fresh or tidal saline sites when considering common ($q = 1$) and dominant ($q = 2$) distinct assemblages ($P < 0.001$ in all cases; Fig. 3d–f; Appendix S1: Tables S1, S2), regardless of spatial scale. Tidal fresh and saline wetlands contained ~1/2 of the beta diversity compared with tidal brackish wetlands at the site scale when emphasizing dominant species (tidal fresh $\overline{x} = 1.7$, tidal saline $\overline{x} = 1.4$, tidal brackish $\overline{x} = 3.1$). When rare ($q = 0$) species were emphasized, however, tidal fresh wetlands did not differ from tidal brackish wetlands in beta diversity at the patch or site scales (patch $P = 0.34$; site $P = 0.70$), while tidal saline wetlands remained low in beta diversity (site-scale beta diversity at $q = 0$: tidal fresh $\overline{x} = 6.3$, tidal saline $\overline{x} = 3.9$, tidal brackish $\overline{x} = 5.0$).

Species presence, abundance, and community composition

Impounded vs. tidal brackish wetlands.—Despite a lack of difference in the effective number of dominant species between impounded brackish and tidal brackish wetlands (Figs. 3, 4), the identity of species present and their relative abundance was markedly different between wetland types (Fig. 5). Both brackish wetland types were codominated by several species, with no one species having greater than 35% average cover. Tidal brackish assemblages were codominated by *Schoenoplectus americanus*, *Distichlis spicata*, *Salicornia pacifica*, and *Juncus balticus* subsp. *ater* (Fig. 5; Appendix S1: Tables S4, S5). In contrast to tidal brackish assemblages, impounded brackish assemblages had effectively no *S. americanus* ($P < 0.0001$) or *J. balticus* subsp. *ater* plant cover ($P < 0.0001$), had decreased *D. spicata* cover ($P = 0.05$), and had higher cover of management associates ($P = 0.3$ with *A. prostrata*, $P < 0.0001$ without *A. prostrata*; Fig. 5; Appendix S1: Tables S4, S5). *Salicornia pacifica*, a salt and drought-tolerant perennial succulent, was a codominant in both impounded and tidal brackish wetlands (Fig. 5).

Plant community composition in impounded wetlands partially overlapped both tidal brackish and tidal saline wetland types (Fig. 6). Impounded sites were classified into distinct wetland assemblages: novel impounded assemblages with no tidal analog ($n = 29$, 60% of impounded sites), tidal saline assemblages ($n = 12$, 25% of impounded sites), and a single tidal brackish assemblage ($n = 1$, 2% of impounded sites; Table 1). No impounded sites were classified as containing tidal fresh assemblages, and six sites remained unclassified as outliers or rare assemblages (13% of impounded sites). Two distinct novel impounded assemblages were identified: one which contained a mix of tidal brackish plants, non-native annual grasses, and management associates (Table 1 impounded novel assemblage; $n = 19$, 40% of impounded sites); and one which was dominated by management associates with *S. pacifica* as a minor component (Table 1 impounded targets assemblage; $n = 10$, 21% of impounded sites; Table 1).

Tidal wetlands along the estuarine gradient.—Tidal fresh and tidal saline patches were dominated by a single species or species group that made up the majority of total plant cover: tules in tidal fresh patches (average 72% cover) and *S. pacifica* in tidal saline patches (average 75% cover; Fig. 5; Appendix S1: Tables S4, S5). This was in contrast to the codominance of several species observed in tidal brackish patches (Fig. 5). Tules and *S. pacifica* were minor components of other wetlands but were found in the highest abundance within tidal fresh (tules, $P < 0.0001$

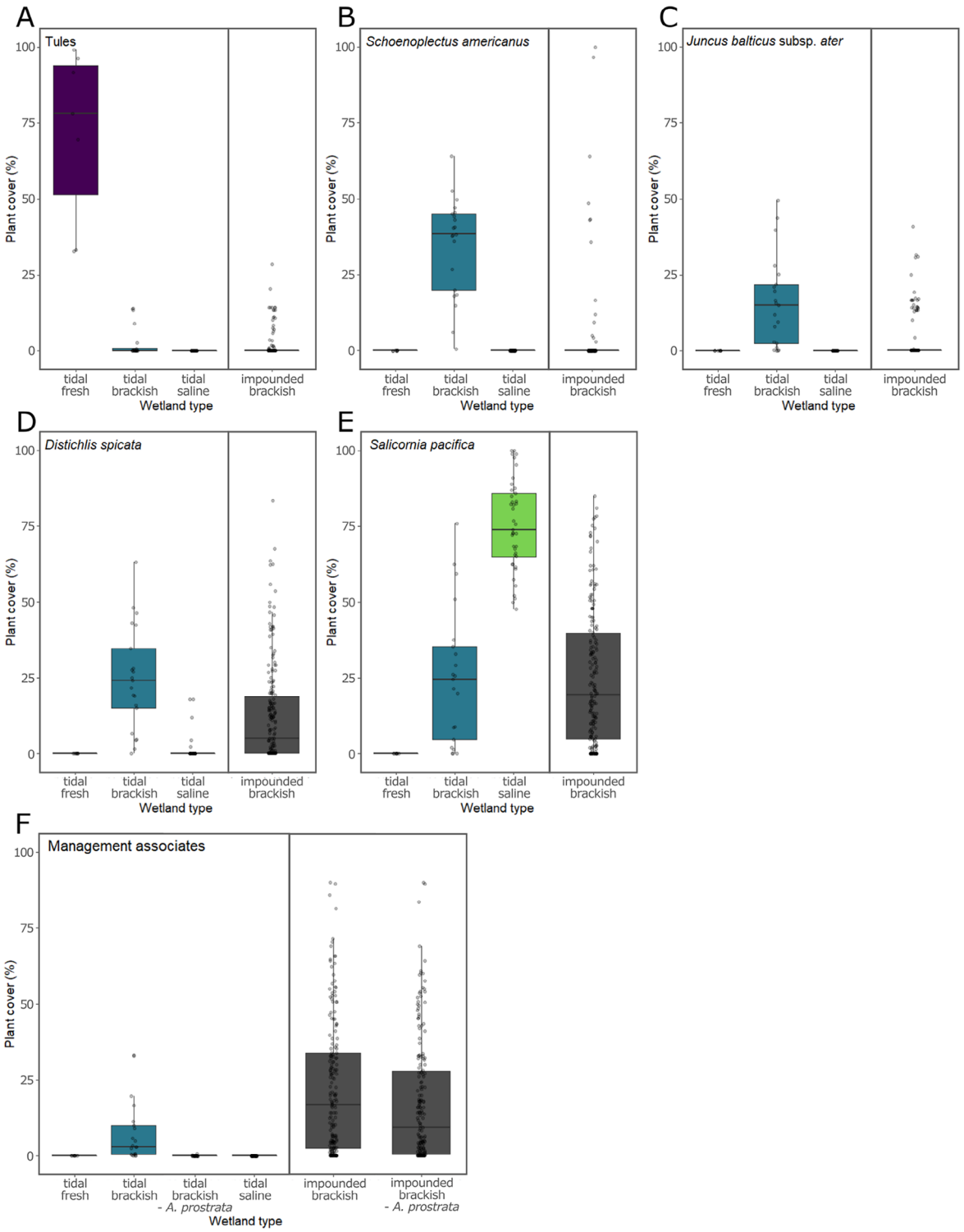

Fig. 5. Plant species cover for three tidal wetland types along a San Francisco Bay-Delta estuarine gradient, and an impounded brackish wetland complex. Percent cover at the patch scale for (A) Tules (*Schoenoplectus acutus* and *Schoenoplectus californicus*), (B) *Schoenoplectus americanus*, (C) *Juncus balticus* subsp. *ater*, (D) *Distichlis spicata*, (E)

Fig. 5 *(Continued)*

Salicornia pacifica, and (F) Management associates (*Bolboschoenus robustus*, *Cotula coronopifolia*, *Crypsis schoenoides*, *Polypogon monspeliensis*, and *Sesuvium verrucosum*). Management associates for tidal and impounded brackish wetlands shown with and without *Atriplex prostrata*. Boxes are the first and third quartiles around the median, and whiskers are 1.5 × the interquartile range. Dots are individual patches (tidal fresh $n = 7$, tidal brackish $n = 21$, tidal saline $n = 48$, impounded brackish $n = 190$).

compared with all other wetland types) or tidal saline (*S. pacifica*, $P < 0.0001$ compared with all other wetland types) wetland types. The tidal fresh wetland type was more compositionally dissimilar from the other tidal wetland types, while the tidal saline wetland

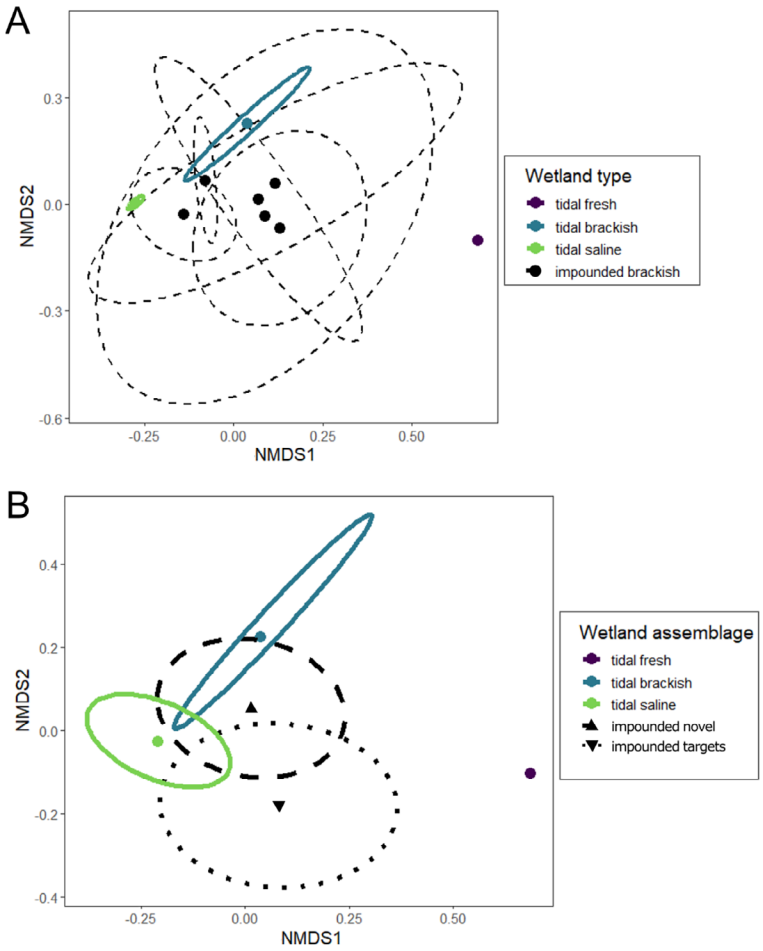

Fig. 6. Nonmetric multidimensional scaling of plant community composition for three tidal wetland types along the San Francisco Bay-Delta Estuary gradient and Suisun Marsh impounded brackish wetlands. (A) Site-scale regions and (B) site scale with impounded sites classified into wetland assemblages. Centroids represent (A) means of each region or (B) means of each classified wetland assemblage. Ellipses represent 95% confidence intervals for (A) each region, color-coded by overall wetland type, and (B) each classified wetland assemblage, color-coded by overall wetland type. Note lack of ellipse around tidal fresh sites due to lack of sufficient data.

Table 1. Mean percent cover (± standard error; $n = 12$ tidal saline, $n = 19$ impounded novel, $n = 10$ impounded targets) of key species or species groups within classified impounded wetland assemblages with more than one representative.

Classified wetland assemblage	*Distichlis spicata*	Grass	*Juncus balticus* ssp. *ater*	Management associates	*Salicornia pacifica*	*Schoenoplectus americanus*	Tules
Tidal saline	6.5 ± 1.9	1.2 ± 0.6	0.4 ± 0.4	18.3 ± 3.8	46.7 ± 2.7	0.0 ± 0.0	0.0 ± 0.0
Impounded novel	23.2 ± 2.9	13.5 ± 3.0	3.9 ± 1.3	13.1 ± 0.8	24.4 ± 2.6	0.4 ± 0.3	0.7 ± 0.3
Impounded targets	3.3 ± 1.0	3.7 ± 1.8	3.1 ± 2.0	45.7 ± 4.4	15.1 ± 2.7	0.4 ± 0.3	3.6 ± 1.3

Notes: Classified using noise clustering (vegclust in R). A single impounded site containing an assemblage classified as tidal brackish is not shown due to lack of replication.

type was compositionally similar to the tidal brackish wetland type (Fig. 6).

Discussion

Seasonal impoundment alters patterns of diversity

Differences between impounded and tidal brackish wetlands in alpha and gamma diversity depended on spatial scale and whether diversity metrics emphasized rare, common, or dominant plant species. Overall, impounded brackish wetlands contained less than 60% of alpha diversity of tidal brackish wetlands at site and smaller spatial scales, when weighting all species equally ($q = 0$). Impoundment can reduce total plant diversity in tidal wetlands, especially compared with nearby high marsh (Sturdevant et al. 2002, Whitcraft et al. 2011). The typical hydrologic regime of high tidal marsh habitat, infrequent but regular inundation, appeared to be lost in impounded wetlands. High marsh in tidal wetlands can be a hotspot for rare species (Grewell et al. 2007). The marsh platform of Pacific coast tidal saline and brackish marshes can be quite high in the tidal frame, with only fringing low marsh (Atwater and Hedel 1976, Janousek et al. 2019), so a reduction in diversity after seasonally prolonged flooding reduces high marsh habitat is expected. That the reduction in species diversity in impounded wetlands disproportionately affects rare species at all spatial scales poses conservation challenges, as several rare and endangered species are found in Suisun Marsh, including Soft Bird's Beak (*Chloropyron molle* subsp. *molle*) and the Suisun Thistle (*Cirsium hydrophilum* var. *hydrophlilum*). Further, as rare species are more vulnerable to extinction and make up a substantial portion of global biodiversity (Enquist et al. 2019), large-scale management practices that preferentially reduce rare species from the landscape may be at odds with the preservation of plant diversity.

The difference between impounded and tidal brackish wetlands in beta diversity primarily depended on spatial scale. Impounded wetlands had approximately 50% more distinct plant assemblages at the regional scale compared with tidal brackish wetlands (i.e., higher between-site turnover). Impounded brackish wetland sites differed markedly from one another in plant diversity and composition, likely due to lack of hydrologic connectivity and individual management. This contrasted with greater connectivity among remaining tidal wetlands in the estuary (Moyle et al. 2014). Tidal brackish wetland sites were all similar, containing assemblages of codominant species driven by local abiotic and biotic gradients. That local gradients largely control community diversity has been shown in other wetlands on the U.S. Gulf and Southern Atlantic Coasts (Guo et al. 2015). The greater isolation of seasonally impounded sites likely increased species turnover and the importance of stochastic events for determining species composition.

Altered patterns of alpha, beta, and gamma diversity in impounded wetlands are likely a result of management actions that changed abiotic drivers and disturbance regimes. Impounded wetland management is informed by regional planning documents and best available science (USBR 2013), but it is up to individual landowners or managers to decide when and what management actions get implemented on the landscape. Unfortunately, soil salinity and hydrologic regime data are lacking for the impounded wetlands in this study, so tying specific changes in diversity to, for example, increased salinity is difficult and

requires inference. Landscape-scale soil type and associated variables (i.e., drainage, flooding frequency) are available (e.g., SSURGO database) but are not always useful for investigating plot- and patch-scale drivers of plant distribution and abundance. We suggest that heightened disturbance and the disappearance of specific abiotic niches may be responsible for the large decrease in species richness in impounded wetlands. Salinity and flooding regime data in impounded managed wetlands, however, are needed to verify this inference with field data.

Seasonal impoundment alters species presence, abundance, and community composition

Alpha and gamma diversity of dominant species ($q = 2$) did not differ between impounded and tidal brackish wetland types. However, species presence, relative abundance, and community composition differed between wetland types at all scales. Impounded patches had effectively no *S. americanus* or *J. balticus* subsp. *ater*, both native perennial rhizomatous graminoids which together made up more than 40% of average tidal brackish plant cover. Instead, impounded patches had substantial cover of a suite of plants that were primarily non-native annual graminoids or forbs which were mostly absent from tidal brackish patches. Although the overall diversity of dominant plants did not differ between impounded and tidal brackish wetlands, the species identity and functional attributes of dominant plants did differ. As species presence, relative abundance, and functional traits can alter ecosystem function (Lefcheck et al. 2015, Stotz et al. 2019), management-induced changes in dominant plant composition likely affect important ecosystem processes, including carbon cycling (Kroeger et al. 2017), climate change resilience (Stagg et al. 2016), and long-term restoration potential (Wolff et al. 2019). As the functional traits of rhizomatous perennial graminoids found in tidal brackish wetlands and non-rhizomatous annual graminoids or perennial forbs found in impounded brackish wetlands are not equivalent, changes in dominant species could lead to important, but understudied, shifts in ecosystem function (Hooper et al. 2005).

Plant community composition was altered in impounded wetlands, such that the majority of impounded sites were classified as containing novel plant assemblages without a tidal analog. The only site classified as containing a tidal brackish plant assemblage was in the Hill Slough complex, which has muted tidal hydrology and is undergoing restoration. The novel plant assemblages came in two forms. One novel assemblage that we infer to be representative of drier, more saline conditions contained a mix of *D. spicata*, *S. pacifica*, non-native annual grasses, and management associates. The other novel assemblage that we infer to be representative of wetter, more fresh conditions was dominated by management associates. In wetlands managed to produce waterfowl, only 21% of plant assemblages at the site scale were dominated (46% average plant cover) by management associates, showing the difficulty of converting brackish tidal wetlands to meet management targets across the landscape. It is unclear whether the novel plant assemblages identified here are transitory and maintained by constant management activity, or whether the legacy of management has created novel plant assemblages that will persist over time.

A sizable fraction of impounded wetland sites (25%) were classified as containing tidal saline plant assemblages, dominated by *S. pacifica*. The occurrence of tidal saline plant assemblages where there would previously have been tidal brackish plant assemblages may indicate unintentional salinization of regions of Suisun Marsh. The Mediterranean climate of the region may exacerbate the typical moist soil management practice of drawdown in the spring, as late drawdown in Suisun Marsh coincides with the hot, dry Californian season where no freshwater precipitation and reduced river flow are entering the region (Kimmerer et al. 2013). Pilot data from adjacent impounded and brackish wetlands indicate that impounded wetlands can have higher overlying water salinity in the fall and spring (S. F. Jones, *unpublished data*), but spatially and temporally distributed sampling campaigns are necessary to validate these findings across Suisun Marsh. These tidal saline impounded wetlands may also give a glimpse into what managers are facing in the near future with predicted decreases in freshwater availability and increases in

summer temperatures over the next century (Ackerly et al. 2018). Tracking impounded wetlands over time, coupled with on-the-ground soil sampling, will be key to detecting the influence of increasing salinity on plant communities in Suisun Marsh, similar to work on the development of abandoned agricultural fields with salinization in the Chesapeake Bay, Maryland, USA (Gedan and Fernández-Pascual 2019).

Diversity along the estuarine gradient

Along the estuarine salinity gradient in tidal wetlands, diversity depended on spatial scale and whether metrics emphasized rare ($q = 0$), common ($q = 1$), or dominant ($q = 2$) species. We found higher alpha, beta, and gamma diversity in a brackish tidal wetland compared with other tidal wetland types when considering the effective number of common and dominant species, especially at larger spatial scales. Tidal brackish dominants were distributed patchily in the current study, with *S. americanus*, *S. pacifica*, *D. spicata*, and *J. balticus* subsp. *ater* (and *Jaumea carnosa*) dominating specific plots but not having more than 35% average cover at the patch or larger spatial scales. This was in stark contrast to tidal fresh wetlands (dominated by tules) and tidal saline wetlands (dominated by *S. pacifica*) that basically contained one or two dominant species. Tidal brackish wetlands with intermediate salinity may be expected to have high diversity according to the stress gradient hypothesis (Huston 1979, Menge and Sutherland 1987, Crain et al. 2004) because they have lower salinity stress than tidal saline wetlands (increasing the available pool of potential dominant species) and potentially lower interspecific competition than tidal freshwater wetlands (decreasing the number of individual dominant species). The patchy distribution of codominant plant species may also be due to high spatial heterogeneity at the freshwater/marine ecotone in, for example, soil salinity, which is known to structure wetland plant communities (Watson and Byrne 2009, Weilhoefer et al. 2013, Janousek and Folger 2014). In Suisun Marsh for example, vegetation assemblages occur as patchy mosaics that are thought to arise from spatial heterogeneity in soil salinity and asymmetric competition (Whitcraft et al. 2011, Moyle et al. 2014). Surface water salinity in Suisun Marsh varies temporally and spatially at several scales (Kimmerer et al. 2013), although patch-scale soil salinity data are scarce.

Unlike patterns of diversity using metrics that emphasize common or dominant species, total species richness was equivalent between tidal fresh and brackish wetlands. Tidal fresh wetlands did contain more species that were found in no other wetland types, including a unique suite of woody wetland plants that can tolerate flooding but not salinity. The dual effects of flooding and salinity stress gradients on estuarine plant community structure make spatial comparisons of plant community structure challenging. This interaction of factors may be especially important in the San Francisco Bay-Delta, as many tidal freshwater marshes are either degraded or do not have a high elevation platform, and have been so for decades (Atwater and Hedel 1976). In the current study, the tidal fresh wetland was on average lower in the tidal frame than other tidal wetland types. This may have influenced observed diversity patterns as higher, less frequently flooded marshes are typically more diverse than lower, more flooded marshes (Janousek and Folger 2014). The tidal fresh wetland sampled here was also typical of Bay-Delta tidal freshwater wetlands in that it was small in total area, limiting the possibility for extensive replication of patches and sites. This limited the precision of diversity estimates. With scarce tidal freshwater wetland data available, a broader effort is needed to clarify overall patterns of tidal estuarine plant diversity, perhaps by combining several large datasets (e.g., Vasey et al. 2012, the current study). We hypothesize that diversity when emphasizing rare species is maximized in tidal fresh wetlands, or is at least equivalent between tidal fresh and brackish wetlands (Sharpe and Baldwin 2009).

Comparing diversity between tidal wetland types requires an approach that incorporates several diversity metrics, which can differentiate rare and dominant species patterns. Other studies have shown oligohaline and brackish tidal wetlands can have alpha and gamma diversity on par with freshwater tidal wetlands (e.g., Sharpe and Baldwin 2009 in Chesapeake Bay, USA; Suchrow et al. 2015 in the Wadden Sea, Germany; and Watson and Byrne 2009 in San Francisco Bay, USA), but it is unclear whether those patterns were driven by rare or dominant

species. This distinction is important, because it gives a more complete understanding of tidal wetland patterns of diversity than simply identifying where species richness is maximized. While total richness may truly be higher in tidal fresh wetlands with many species that cannot tolerate salinity stress, the diversity of the dominant plants driving ecosystem function is higher in tidal brackish wetlands in this estuary.

Conclusions

We show that the magnitude of differences in diversity depended on spatial scale and the metric of diversity used. Species richness or individual species presence using plot data alone can be poor predictors of biodiversity change, regardless of temporal scale (Hillebrand et al. 2018, Alvarez et al. 2019). Further, small or nonexistent changes in overall diversity metrics may mask large changes in species presence, abundance, and community composition that likely influence ecosystem function. Assessing diversity at multiple spatial scales enabled more detailed examination of differences in how diversity is structured across coastal wetland types. Tierney et al. (2018) similarly found that swamps that had been classified as one wetland type at large spatial scales actually contained several distinct wetland assemblages at smaller scales; it was the unique combination of assemblages that differentiated wetlands. In that work, as here, a combination of diversity metrics at several spatial scales was required to disentangle patterns in plant diversity, important for management and conservation applications that are concerned with regional biodiversity or the spatial scaling of diversity patterns. In the present study, sampling within sites is probably sufficient to capture patterns of diversity within tidal wetlands (unless specific rare species are sought), but sampling across many sites is necessary in impounded wetlands due to the increased turnover at large scales. To successfully detect shifts in ecosystem structure and function that can result from changing climate, other anthropogenic disturbance, or restoration, sampling across a range of spatial scales and incorporating multiple metrics of diversity that emphasize both rare and common species should be considered.

Impounded wetlands shifted from rhizomatous perennial graminoids to largely annual graminoids or perennial forbs. In addition to altered abiotic conditions of flooding and potentially salinity, this biotic shift likely altered ecosystem function as rhizomatous perennial graminoids are functionally distinct from annual graminoids and perennial forbs. Soil biogeochemistry and nutrient cycling are influenced by changing environmental conditions, and the management of impounded brackish wetlands in a Mediterranean climate is shifting nutrient cycling in unknown ways (see Hinckley et al. 2019 for responses in a humid climate setting). Changes in plant functional groups may also cascade to influence animal community structure and function (Johnson and Montalbano 1984, Eberling et al. 2020). Ecosystem processes support plant biomass and seed production and therefore can influence the end goal of managers: thriving waterfowl populations. Biogeochemical and other process-based studies are necessary to investigate how the alteration of environmental conditions and plant functional traits with current management practices are influencing nutrient cycling and other ecosystem functions.

The differences we report in plant diversity and assemblages between impounded and tidal wetlands in a Mediterranean climate contrast with the lack of plant responses after waterfowl management reported in more temperate/humid climates (e.g., U.S. Gulf Coast; Nyman et al. 1993) or in fresher settings (Evans-Peters et al. 2012). The combination of hot, dry summers and a surrounding brackish salinity leads to high evaporation stress in the summer in Suisun Marsh, which has the potential to increase soil salinity on drained wetlands. Investigations of soil salinity in tidal and impounded wetlands over time may detect if seasonal impoundment is leaving a persistent soil salinity legacy in these wetlands. The combination of brackish salinity and Mediterranean climate has restricted the influence of waterfowl management given current infrastructure, as 25% of impounded sites contained nontarget tidal saline plant assemblages, approximately equal to the 21% of sites that contained a target plant assemblage. As tidal restoration is implemented in Suisun Marsh over the remaining 25-yr horizon of the Suisun Marsh habitat management, preservation, and restoration plan (USBR 2013), habitat

managers may consider creating a mosaic of habitat that supports rare plant diversity, wetland ecosystem function, and the ecological requirements of waterfowl in a Mediterranean climate.

Acknowledgments

Scott F. Jones, John Takekawa, and Karen Thorne conceived the ideas and designed methodology; Chris Janousek, Michael Casazza, Karen Thorne, and John Takekawa supervised data collection or collected data; Scott F. Jones analyzed the data; and Scott F. Jones led the writing of the manuscript. All authors contributed critically to the text and gave final approval for publication. We would like to thank land managers from California Department of Fish & Wildlife, NOAA National Estuarine Research Reserve, U.S. Fish & Wildlife Service, Solano Land Trust, private landowners, and Suisun Resource Conservation District (Steve Chappell) for facilitating site access. We express thanks to Anna Kennedy, Kylie Mosher, Nina Tortosa, Brandon Drucker, Karen Backe, Chase Freeman, and Kevin Buffington, who assisted with the study. We thank the editor, anonymous reviewers, Meagan Gonneea (USGS) and Robert Klinger (USGS), for constructive comments that improved the manuscript. Funding was provided by the USGS Priority Ecosystem Science, California Department of Water Resources, and NOAA EESLR cooperative agreement NA15NOS4 780171. Support was also provided by the U.S. Geological Survey Western Ecological Research Center, UC Davis Center for Aquatic Biology and Aquaculture, and the John Muir Institute of the Environment. Any use of trade, product, or firm names are for descriptive purposes only and do not imply endorsement by the U.S. Government.

Literature Cited

Ackerly, D., A. Jones, M. Stacey, and B. Riordan. 2018. San Francisco Bay Area Summary Report. California's Fourth Climate Change Assessment. University of California, Berkeley, California, USA.

Ackerman, J., M. Herzog, G. Yarris, M. Casazza, E. Burns, and J. Eadie. 2014. Waterfowl ecology and management. Pages 103–132 *in* Suisun Marsh: ecological history and possible futures. University of California Press, Berkeley, California, USA.

Alvarez, S. A., S. J. Gibbs, P. R. Bown, H. Kim, R. M. Sheward, and A. Ridgwell. 2019. Diversity decoupled from ecosystem function and resilience during mass extinction recovery. Nature 574:242–245.

Atwater, B. F., and C. W. Hedel. 1976. Distribution of seed plants with respect to tide levels and water salinity in the natural tidal marshes of the northern San Francisco Bay estuary, California. U.S. Geological Survey, Menlo Park, California, USA.

Baldwin, B. G., D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken. 2012*a*. The Jepson manual: vascular plants of California, thoroughly revised and expanded. University of California Press, Berkeley, California, USA.

Baldwin, B. G., D. Goldman, D. J. Keil, R. Patterson, and T. J. Rosatti. 2012*b*. The Digital Jepson manual: vascular plants of California. University of California Press, Berkeley, California, USA.

Boumans, R., and J. Day Jr. 1994. Effects of two Louisiana marsh management plans on water and materials flux and short-term sedimentation. Wetlands 14:247–261.

Busnardo, M. J., R. M. Gersberg, R. Langis, T. L. Sinicrope, and J. B. Zedler. 1992. Nitrogen and phosphorus removal by wetland mesocosms subjected to different hydroperiods. Ecological Engineering 1:287–307.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Chao, A., C.-H. Chiu, and L. Jost. 2014*a*. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annual Review of Ecology, Evolution, and Systematics 45:297–324.

Chao, A., N. Gotelli, T. Hsieh, E. Sander, K. Ma, R. Colwell, and A. Ellison. 2014*b*. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45–67.

Charney, N., and S. Record. 2012. vegetarian: jost diversity measures for community data. R package version 1.2. https://CRAN.R-project.org/package=vegetarian

Cloern, J. E., et al. 2016. Human activities and climate variability drive fast-paced change across the world's estuarine-coastal ecosystems. Global Change Biology 22:513–529.

Crain, C. M., B. R. Silliman, S. L. Bertness, and M. D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85:2539–2549.

De Cáceres, M., and S. K. Wiser. 2013. How to use the vegclust package (ver. 1.6.5). https://CRAN.R-project.org/package=vegclust

Díaz, S., and M. Cabido. 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646–655.

Donoghue, M. 2008. A phylogenetic perspective on the distribution of plant diversity. Proceedings of the National Academy of Sciences USA 105: 11549–11555.

Eberling, A., E. W. Lind, S. T. Meyer, A. D. Barnes, E. T. Borer, N. Eisenhauer, and W. W. Weisser. 2020. Contrasting effects of plant diversity on β- and γ-diversity of grassland invertebrates. Ecology 101: e03057.

Egerton, F. 2001. A history of the ecological sciences, part 2: Aristotle and Theophrastus. Bulletin of the Ecological Society of America 82:149–152.

Ellison, A. 2010. Partitioning diversity. Ecology 91:1962–1963.

Elsey-Quirk, R., and S. Adamowicz. 2016. Influence of physical manipulations on short-term salt marsh morphodynamics: examples from the North and Mid-Atlantic Coast, USA. Estuaries and Coasts 39:423–439.

Enquist, B. J., et al. 2019. The commonness of rarity: global and future distribution of rarity across land plants. Science Advances 5:eaaz0414.

Evans-Peters, G. R., B. D. Dugger, and M. J. Petrie. 2012. Plant community composition and waterfowl food production on Wetland Reserve Program easements compared to those on managed public lands in western Oregon and Washington. Wetlands 32:391–399.

Gedan, K., and E. Fernández-Pascual. 2019. Salt marsh migration into salinized agricultural fields: a novel assembly of plant communities. Journal of Vegetation Science 30:1007–1016.

Gedan, K. B., B. Silliman, and M. Bertness. 2009. Centuries of human-driven change in salt marsh ecosystems. Marine Science 1:117–141.

Gonzalez, A., et al. 2020. Scaling-up biodiversity-ecosystem functioning research. Ecology Letters 23:757–776.

Grewell, B. J., J. C. Callaway, and J. W. R. Ferren. 2007. Estuarine wetlands. *In* M. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial vegetation of California. University of California Press, Oakland, California, USA.

Guo, H., et al. 2015. Geographic variation in plant community structure of salt marshes: species, functional and phylogenetic perspectives. PLOS ONE 10:e0127781.

Hill, M. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432.

Hillebrand, H., et al. 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. Journal of Applied Ecology 55:169–184.

Hinckley, B., J. Etheridge, and A. Peralta. 2019. Wetland conditions differentially influence nitrogen processing within waterfowl impoundments. Wetlands 40:1117–1131.

Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Janousek, C. N., and C. L. Folger. 2014. Variation in tidal wetland plant diversity and composition within and among coastal estuaries: assessing the relative importance of environmental gradients. Journal of Vegetation Science 25:534–545.

Janousek, C. N., K. M. Thorne, and J. Y. Takekawa. 2019. Vertical zonation and niche breadth of tidal marsh plants along the northeast Pacific coast. Estuaries and Coasts 42:85–98.

Johnson, F. A., and F. Montalbano. 1984. Selection of plant communities by wintering waterfowl on Lake Okeechobee, Florida. Journal of Wildlife Management 48:174–178.

Jones, S. F., C. N. Janousek, M. L. Casazza, J. Y. Takekawa, and K. M. Thorne. 2020. Impounded and tidal wetland plant diversity and composition across spatial scales, San Francisco Bay-Delta, California, USA (2016–2018): U.S. Geological Survey data release.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Kimmerer, W. J., M. L. MacWilliams, and E. S. Gross. 2013. Variation of fish habitat and extent of the low-salinity zone with freshwater flow in the San Francisco Estuary. San Francisco Estuary and Watershed Science 11:1–16.

Kroeger, K., S. Crooks, S. Moseman-Valtierra, and J. Tang. 2017. Restoring tides to reduce methane emissions in impounded wetlands: a new and potent blue carbon climate change intervention. Scientific Reports 7:11914.

Lefcheck, J. S., J. Byrnes, F. Isbell, L. Gamfeldt, J. Griffin, N. Eisenhauer, M. Hensel, A. Hector, B. Cardinale, and J. Duffy. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6:6936.

Lenth, R. 2020. emmeans: estimated marginal means, aka least-squares means. R package version 1.4.4. https://CRAN.R-project.org/package=emmeans

Loder, A., I. Spooner, N. McLellan, J. Kurek, and M. Mallory. 2019. Water chemistry of managed freshwater wetlands on marine-derived soils in coastal Bay of Fundy, Canada. Wetlands 39:521–532.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Mitsch, W., and J. Gosselink. 2007. Wetlands. Fourth edition. Wiley, Hoboken, New Jersey, USA.

Montague, C., A. Zale, and F. Percival. 1987. Ecological effects of coastal marsh impoundments: a review. Environmental Management 11:743–756.

Morris, E. K., et al. 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecology and Evolution 4:3514–3524.

Moyle, P. B., A. D. Manfree, and P. L. Fielder. 2014. Suisun Marsh: ecological history and possible futures. University of California Press, Berkeley, California, USA.

Nyman, J., R. Chabreck, and N. Kinler. 1993. Some effects of herbivory and 30 years of weir management on emergent vegetation in brackish marsh. Wetlands 13:165–175.

Oksanen, J., et al. 2019. vegan: community ecology package. https://CRAN.R-project.org/package=vegan

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2019. nlme: linear and nonlinear mixed effects models. R package version 3.1. https://CRAN.R-project.org/package=nlme

Portnoy, J. W., and A. E. Giblin. 1997. Effects of historic tidal restrictions on salt marsh sediment chemistry. Biogeochemistry 36:275–303.

R Core Team. 2020. R: a language and environment for statistical computing, 3.6. R Foundation for Statistical Computing, Vienna, Austria.

Sharpe, P. J., and A. H. Baldwin. 2009. Patterns of wetland plant species richness across estuarine gradients of Chesapeake Bay. Wetlands 29:225–235.

Sinicrope, T. L., R. Langis, R. M. Gersberg, M. J. Busnardo, and J. B. Zedler. 1992. Metal removal by wetland mesocosms subjected to different hydroperiods. Ecological Engineering 1:309–322.

Stagg, C. L., D. R. Schoolmaster, S. C. Piazza, G. Snedden, G. D. Steyer, C. J. Fischenich, and R. W. McComas. 2016. A landscape-scale assessment of above-and belowground primary production in coastal wetlands: implications for climate change-induced community shifts. Estuaries and Coasts 40:856–879.

Stotz, G. C., E. Gianoli, and J. F. Cahill Jr. 2019. Biotic homogenization within and across eight widely distributed grasslands following invasion by *Bromus inermis*. Ecology 100:e02717.

Sturdevant, A., C. B. Craft, and J. N. Sacco. 2002. Ecological functions of an impounded marsh and three natural estuarine marshes along Woodbridge River, NY/NJ Harbor. Urban Ecosystems 6:163–181.

Suchrow, S., M. Stock, and K. Jensen. 2015. Patterns of plant species richness along environmental gradients in German North Sea salt marshes. Estuaries and Coasts 38:296–309.

Takekawa, J., K. Thorne, K. Buffington, K. Spragens, K. Swanson, J. Drexler, D. Schoellhamer, C. Overton, and M. Casazza. 2013. Final report for sea-level rise response modeling for San Francisco Bay estuary tidal marshes. Pages 161. Open File Report 2012–1081. U.S. Geological Survey, Sacramento, California, USA.

Thorn, S., A. Chao, M. Bernhardt-Romermann, Y.-H. Chen, K. Georgiev, C. Heibl, J. Muller, H. Schafer, and C. Bassler. 2020. Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. Ecology 101:e02949.

Tierney, D., G. Wardle, and P. Erskine. 2018. The intersection of diversity metrics and spatial mapping: a case study of regional vegetation patterns for a complex community. Plant Ecology 219:1169–1183.

USBR (U.S. Bureau of Reclamation). 2013. Suisun Marsh habitat management, preservation and restoration plan. USBR, Washington, D.C., USA.

Vasey, M. C., Parker, V. T., Callaway, J. C., Herbert, E. R. & Schile, L. M. 2012. Tidal wetland vegetation in the San Francisco Bay-Delta Estuary. San Francisco Estuary and Watershed Science 10. https://doi.org/10.15447/sfews.2012v10iss2art2

Wanner, A., S. Suchrow, K. Kiehl, W. Meyer, N. Pohlmann, M. Stock, and K. Jensen. 2013. Scale matters: impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes. Agriculture, Ecosystems & Environment 182:69–79.

Watson, E. B., and R. Byrne. 2009. Abundance and diversity of tidal marsh plants along the salinity gradient of the San Francisco Estuary: implications for global change ecology. Plant Ecology 205:113.

Weilhoefer, C. L., W. G. Nelson, P. Clinton, and D. M. Beugli. 2013. Environmental determinants of emergent macrophyte vegetation in Pacific Northwest estuarine tidal wetlands. Estuaries and Coasts 36:377–389.

Whitcraft, C. R., B. J. Grewell, and P. R. Baye. 2011. Estuarine vegetation at rush ranch open space preserve, San Francisco Bay National Estuarine Research Reserve, California. San Francisco Estuary and Watershed Science 9:6j89531r.

Williams, J., and S. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.

Wolff, B. A., S. B. Duggan, and W. H. Clements. 2019. Resilience and regime shifts: Do novel communities impede ecological recovery in a historically metal-contaminated stream? Journal of Applied Ecology 56:2698–2709.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Young, J., M. Marzano, R. White, D. McCracken, S. Redpath, D. Carss, C. Quine, and A. Watt. 2010. The emergence of biodiversity conflicts from biodiversity impacts: characteristics and management strategies. Biodiversity and Conservation 19:3973–3990.

Zedler, J., and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30:39–74.

Data Availability

Data are available from Jones et al. 2020: .https://doi.org/10.5066/P9ZG1Y72

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3366/full