

Alternative stable states of tidal marsh vegetation patterns and channel complexity

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ABSTRACT

Intertidal marshes develop between uplands and mudflats, and develop vegetation zonation, via biogeomorphic feedbacks. Is the spatial configuration of vegetation and channels also biogeomorphically organized at the intermediate, marsh-scale? We used high-resolution aerial photographs and a decision-tree procedure to categorize marsh vegetation patterns and channel geometries for 113 tidal marshes in San Francisco Bay estuary and assessed these patterns' relations to site characteristics. Interpretation was further informed by generalized linear mixed models using pattern-quantifying metrics from object-based image analysis to predict vegetation and channel pattern complexity. Vegetation pattern complexity was significantly related to marsh salinity but independent of marsh age and elevation. Channel complexity was significantly related to marsh age but independent of salinity and elevation. Vegetation pattern complexity and channel complexity were significantly related, forming two prevalent biogeomorphic states: complex versus simple vegetation-and-channel configurations. That this correspondence held across marsh ages (decades to millennia) and at both high and low marsh elevations suggests the following: (1) marshes of shared physiography can exhibit highly variable ecosystem structures; (2) young marshes are not necessarily simple nor necessarily develop vegetation complexity with age and elevation; (3) Bay marshes should continue to exhibit both simple/complex configurations in the future despite a likely shift toward low marshes; (4) salt marshes may tend to occupy two alternative stable states characterized by linked complexity in vegetation and channel organization. This final point may help fill the gap at the marsh scale between biogeomorphic models explaining marsh occurrence at larger coastal and smaller vegetation patch scales. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS tidal; marsh; estuary; biogeomorphic; vegetation zonation; stable state; San Francisco Bay; object-based image analysis

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INTRODUCTION

Coastal and estuarine salt marshes exist in the balance of biological and geomorphological dynamics. These wetland ecosystems are densely vegetated by emergent macrophytes between mean sea level and the mean elevation of the high tide. The persistence of intertidal elevations over time, and therefore of the wetland itself, is controlled by mineral sediment deposition and erosion, organic matter production and accumulation, and relative sea level rise (Morris *et al.*, 2002). These biotic and abiotic controls form coupled biogeomorphic processes, e.g. elevation and the depth of tidal flooding partly control vegetation biomass while vegetation biomass promotes sediment accretion to raise intertidal elevations (Morris, 2007). Simulations of these biogeomorphic feedbacks consistently produce multiple, alternative stable states at the scale of the

coastline, i.e. distinct subtidal basins, unvegetated low-elevation tidal flats, and vegetated high-elevation marshes (Figure 1a). As highlighted in recent reviews of such analyses (Fagherazzi *et al.*, 2012; Moffett *et al.*, 2015), emphasis has so far been on understanding coastline-scale equilibria and the persistence of vegetated versus unvegetated intertidal coastline states in the face of future sea level rise and human-altered sediment supplies.

But within a single estuary system, are all vegetated coastline equilibrium states similar? How much biogeomorphic variation is there within and among marsh sites? A comprehensive and spatially integrative conceptual framework has so far been elusive. In particular, we seek an understanding of dynamic biogeomorphic feedbacks and tidal wetland equilibrium states that accommodates both geographic variation and spatial scaling. Understanding sources of geographic variation in intertidal marsh organization is key, as it is this that allows us to place uncertainty bounds on presumed or modeled outcomes of (natural or restored) marsh development trajectories.

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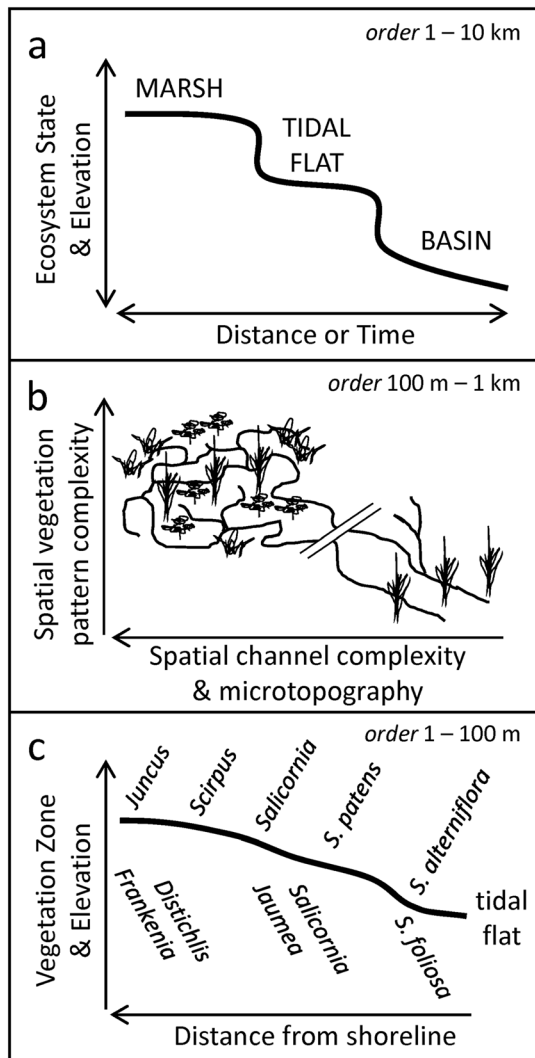


Figure 1. Conceptual models of alternative stable marsh states at different scales. (a) Alternative marsh, tidal flat, and subtidal basin ecosystem states at the coastline scale. (b) Alternative states at the marsh scale of linked vegetation and channel organization, both in either complex or simple spatial configurations. (c) Vegetation zones as multiple stable states at the sub-marsh scale, with representative zones by plant genus as if for United States east coast, above marsh surface profile line, and for United States west coast, below profile line.

As noted and well-described by Da Lio *et al.* (2013), biogeomorphic conceptual and numerical models of intertidal ecosystem states need to connect scales spanning from a local vegetation patch, to vegetation zones at the sub-site scale, to the overall coastline ecosystem character. The current state-of-the-science has alternative equilibrium states expressed and modeled at the coastline scale as subtidal, tidal flat, or marsh ecosystems, with the ecosystem collapsed to a unitary point in zero dimensions with the potential to become stable in any of these three states (Da Lio *et al.*, 2013). In reality, of course, the finer scales and patterns composing an intertidal ecosystem should be nested within this ‘point’. For example, the

equilibrium marsh state should be further organized at the sub-site scale into distinct vegetation zones.

Multiple equilibrium theory has also been applied to explain this vegetation zonation at the sub-marsh scale. Vegetation zonation within marsh sites is characterized by dominant plant species occupying different, discrete intertidal elevation ranges and sets of environmental conditions (Johnson and York, 1915) (Figure 1c). The locations and extent of vegetation zones are generally limited by a combination of stress tolerance and interspecific competition (Emery *et al.*, 2001; Bertness and Ewanchuk, 2002; Pennings *et al.*, 2005; Morris, 2006), although there can be additional factors, e.g., nutrient status (Deegan *et al.*, 2007, 2012). Intertidal vegetation zones are typically conceptualized as shore-parallel bands at different elevations. The state-of-the-science is able to simulate strikingly realistic salt marsh vegetation zonation along 1D, shore-perpendicular transects, accounting for multiple vegetation categories and stochasticity in interspecific competition (Da Lio *et al.*, 2013; Marani *et al.*, 2013). This and other field and modeling results have led to the proposal by multiple authors that a multi-modal histogram of intertidal elevations, with corresponding and distinct vegetation zones aligned with each histogram mode, is an indicator of multiple concurrent biogeomorphic states at the sub-site scale of the vegetation zones (Marani *et al.*, 2007, 2010; Carniello *et al.*, 2009; D’Alpaos *et al.*, 2012; Wang and Temmerman, 2013).

But what of marsh biogeomorphic organization at the intermediate scale of a whole marsh site? If coastal-scale biogeomorphic balances support a stable vegetated coastline including many marshes, and zone-scale biogeomorphic processes induce terracing and vegetation banding within a marsh, what biogeomorphic organization at the marsh scale reconciles these larger and smaller scale dynamics?

One plausible hypothesis, deterministically based on this background, is that each salt marsh site within a common coastal system should occupy a similar overall intertidal position and should be configured into similar numbers, types and distributions of banded vegetation zones. However, a competing hypothesis of heterogeneous vegetation and channel organization, which may vary from site-to-site, is suggested by other research (Figure 1b). Zedler *et al.* (1999) reflected on the prevalence of the elevation-based zonation conceptual model in the literature and showed that although correlations of plant species with elevation might serve as general guidelines for some species’ distribution, salt marsh vegetation patterning exhibits lateral variations in response to a combination of effects that include microtopography and tidal channels. This may result in non-distinct vegetation ‘zone’ elevation ranges and complex two-dimensional marsh organization. In other words, the lateral heterogeneity that configures marshes at the sub-site scale, which is not yet captured by

zero-dimensional and one-dimensional multiple equilibrium theory models, may be key to thoroughly understanding these systems.

Furthermore, it is commonly assumed that accreting salt marshes will develop more detailed, varied vegetation zonation as they mature to higher elevations (Atwater *et al.*, 1979; Cornu and Sadro, 2002) and that more mature salt marsh channel networks will exhibit more branching, looping and overall variation because of the accumulated effects of past tidal actions, relative sea level/subsidence changes and disturbances (Kirwan *et al.*, 2008). It is uncertain, however, whether these assumptions hold empirically, whether these developments in vegetation configuration and channel geometry do in fact occur concurrently over time, and whether such a temporal trend can be reconciled with the coastline scale and sub-site scale theories of marsh organization into multiple equilibria by biogeomorphic feedbacks.

It is important to understand how much variation exists in the heterogeneity, or complexity, of marsh vegetation configurations because features such as patch area-to-perimeter ratio, total edge length, patch compactness, and patch size have real implications for interspecific plant interactions, as well as faunal habitat (e.g., Moffett *et al.*, 2014 and references therein). Variability in channel network geometries likewise can both provide information on individual marsh morphodynamic processes as well as diagnostic information to test general geomorphic hypotheses (e.g., Marani *et al.*, 2003).

In this study, we tested the two alternative hypotheses for marsh organization at the site scale: (1) There is relative uniformity in the patterns of vegetation configuration and channel geometry among a large number of salt marsh sites in the same physiographic coastal system, as suggested from the background on multiple stable states at zone and coastline scales, or (2) there is substantial variation in the biogeomorphic organization of marshes within a common physiographic coastal system, perhaps related to effects of microtopography and tidal channels. We also tested whether the degree of complexity in marsh vegetation patterns and channel geometries is related to each other and to relative marsh age or other site characteristics.

DATA AND METHODS

Study area

The unifying physiographic system targeted by this study was the San Francisco Bay estuary. Originally several fluvial valleys, the estuary was established as a coastal embayment during the rapid sea level rise of the early Holocene, about 10,000 years ago (Atwater *et al.*, 1979; Helley *et al.*, 1979; Goals Project, 1999). Today, the Sacramento and San Joaquin rivers are the major fluvial

systems joining with the bays to comprise the estuary. These rivers drain about 40% of the state of California and join in a single delta just prior to flowing into the embayment. Beginning perhaps 6000 years ago, the growth of marshes began to keep pace with slowing sea level rise in the delta. Sustained shore-fringing marshes were established 2000–3000 years ago in the four sections of the San Francisco Bay estuary, Suisun Bay, North (San Pablo) Bay, Central Bay, and South Bay. The rate of sea level rise during these recent millennia has been approximately 2 mm year^{-1} (Atwater *et al.*, 1979; Goals Project, 1999).

In contrast to marshes overlying a gradually sloping, clastic coastal plain such as on the United States east coast, the marshes of San Francisco Bay estuary are nearly topographically flat (Atwater *et al.*, 1979). This is explained by the development of the estuary's marshes from the settling of fine sediments in the gradually subsiding and relatively quiescent Bay (Gilbert, 1917). The Bay is impounded behind the Coast Range mountains, which host San Francisco and Marin Counties, and which arise from the compression between the North American and Pacific plates at the San Andreas fault. The ranges surrounding the Bay cause some of the resulting shorelines to be fairly steep and absent of salt marshes. The modern estuary overlies about 10 m of estuarine sediments, beneath which are alluvial deposits and more estuarine sediments, in alternation (McGann *et al.*, 2002). The deposition of these layers was jointly controlled by past tectonic, sea level, and climate variations (Koltermann and Gorelick, 1992).

The climate of the region is semi-arid and Mediterranean, with moderate temperatures, dry summers and wet winters. Climate proxy records suggest substantial variability in temperature, water balance, salinity, and sediment loads throughout the Holocene, but relatively stable conditions since 1850 (Malamud-Roam *et al.*, 2007). North, Central, and South Bays are saline, except around the mouths of some smaller streams. The low salinity of Suisun Bay is controlled by seasonal high freshwater discharge from the Sacramento–San Joaquin Delta during the winter and spring (Goals Project, 1999), although the seasonal hydrograph is highly modified by reservoir storage and diversions (Nichols *et al.*, 1986; Knowles, 2002). In contrast, far South Bay can become hypersaline because of evapoconcentration and little freshwater inflow.

Beginning in the mid-19th century, the estuary has undergone enormous anthropogenic change. Between about 1850 and 1980, approximately 95% of 2200 km² of original tidal marshes in the estuary were converted to other land uses by draining, filling, or impoundment. At the same time, hydraulic mining during the California Gold Rush (1853–1884) and subsequent erosion during additional urban and agricultural development throughout the

extensive watershed, contributed an anomalous, nine-fold increase in sediment supply between about 1850 and 1900 over prior 'natural' supply levels (Wright and Schoellhamer, 2004). This resulted in about 0.25–1.0 m of new sediment accumulated by 1900, with the larger values closer to the delta (Nichols *et al.*, 1986). This large supply of sediment facilitated the development of new marshes over perhaps 5% of the original area (Atwater *et al.*, 1979; Goals Project, 1999), with development and restoration continuing today. Recent sediment supply has decreased to less than a third of the peak and is decreasing further over time (Wright and Schoellhamer, 2004). This history of marsh destruction, fragmentation, impoundment, site-specific anthropogenic restoration, and natural redevelopment has resulted in the marshes of the estuary being generally isolated sites of relatively small extent (1s–100s hectares per site). Although these anthropogenic influences are particular to San Francisco Bay estuary, they are by no means unique. Globally, estuaries and coastal marshes are extensively impacted by anthropogenic activities ranging from direct draining and filling of marshes, to relative sea level rise caused by pumping-induced subsidence, to the indirect effects of upstream control of water and sediment fluxes to the coastline (Millennium Ecosystem Assessment, 2005).

With extensive shallow shoals and mudflats, especially in the South Bay, the estuary hosts abundant areas susceptible to sediment accretion raising them to near mean water level. Pioneer California cordgrass vegetation (*Spartina foliosa*) colonizes mudflats once they have accreted to about mean tide level (Atwater *et al.*, 1979). From there, positive feedbacks between cordgrass growth, patch expansion, and sedimentation can promote rapid vertical and lateral marsh expansion. Recent sedimentation rates in marshes of the estuary range from about 1–5 mm year⁻¹ in natural marshes keeping pace with sea level rise (Patrick and DeLaune, 1990; Watson, 2004), to 22–39 mm year⁻¹ in sites recovering from subsidence caused by groundwater pumping (Patrick and DeLaune, 1990; Watson, 2004), to a temporary extreme of perhaps 450 mm year⁻¹ in a very rapidly accreting restoration site (Goals Project, 1999). Mineral sedimentation is likely supplemented by *in situ* organic sediment production (Culbertson *et al.*, 2004). Key marsh flora and fauna, habitats, and biogeography of species of special status are summarized in existing documents (Goals Project, 2000; H.T. Harvey and Associates, 2005).

Study sites and data sources

We identified 62.65 km² of fully saline and tidal marshlands around San Francisco Bay estuary, which we delineated as polygon outlines in ArcGIS 10 (ESRI, Redlands, CA, USA) as 113 vegetated marsh sites

(Figure 2). The total spatial scope of the study was provided by a set of high-resolution (0.3 m) natural color (RGB) aerial photography images, which were used as the basis for categorizing marsh vegetation configuration and channel complexity. These categories were then used to test whether marshes across this physiographic region were generally of a common form, or of diverse vegetation and channel configurations, consistent with the hypotheses from our introduction.

The aerial images were NGA 2004 USGS High-Resolution Orthoimages, produced for the National Geospatial-Intelligence Agency and US Geological Survey by EarthData International of Maryland, LLC, and provided to the project by the San Francisco Estuary Institute, Oakland, CA (EarthData International, 2004). Example sites are presented in Figure 3. Some large, highly distinct sections of larger marshes, or sections of larger marshes with different marsh age or elevation, were delineated separately. The Supporting Information includes detailed maps of all delineated sites (Figure S1).

The 113 selected marsh sites were known to be fully tidal based on the mapping of 'Modern Baylands' by the San Francisco Estuary Institute (Grossinger, 1998a, 1998b; Goals Project, 1999). The shorelines of North (San Pablo), Central and South San Francisco Bays are saline (Goals Project, 1999) and included 97 of the sites (46.58 km²). Brackish marshes within Suisun Bay near the San Joaquin/Sacramento River delta and within the mouth of Coyote Creek in far southern San Francisco Bay were represented by 16 sites (16.08 km²). Brackish marshes could be further identified as they exhibit dense, extensive stands of Alkali Bulrush (*Scirpus maritimus*). Alkali Bulrush is a dominant species in brackish habitats in this region (H.T. Harvey and Associates, 2005), and its stands appeared a highly distinctive dark-purple in the aerial imagery.

To enable testing whether the complexities of marsh vegetation configuration and channel geometry were related to relative marsh age, we classified the age of each marsh. The marshes of San Francisco Bay broadly fall into two age groups: 'old', existing for more than 165 years, since before the anthropogenic changes beginning with the California Gold Rush, and 'young', also known as 'centennial', developed within the last 165 years. Relative marsh age (young or old) and relative marsh elevation within the tidal range (high or low-mid) were identified for each study site from existing maps (Grossinger, 1998a, 1998b; Goals Project, 1999).

Given that sites ranged from relatively pristine islands to fully enclosed, impounded tidal wetlands, we sought to quantify this impoundment effect to determine if it is also related to marsh vegetation configuration or channel complexity. An impoundment index was determined by imagery inspection to quantify the degree of site enclosure

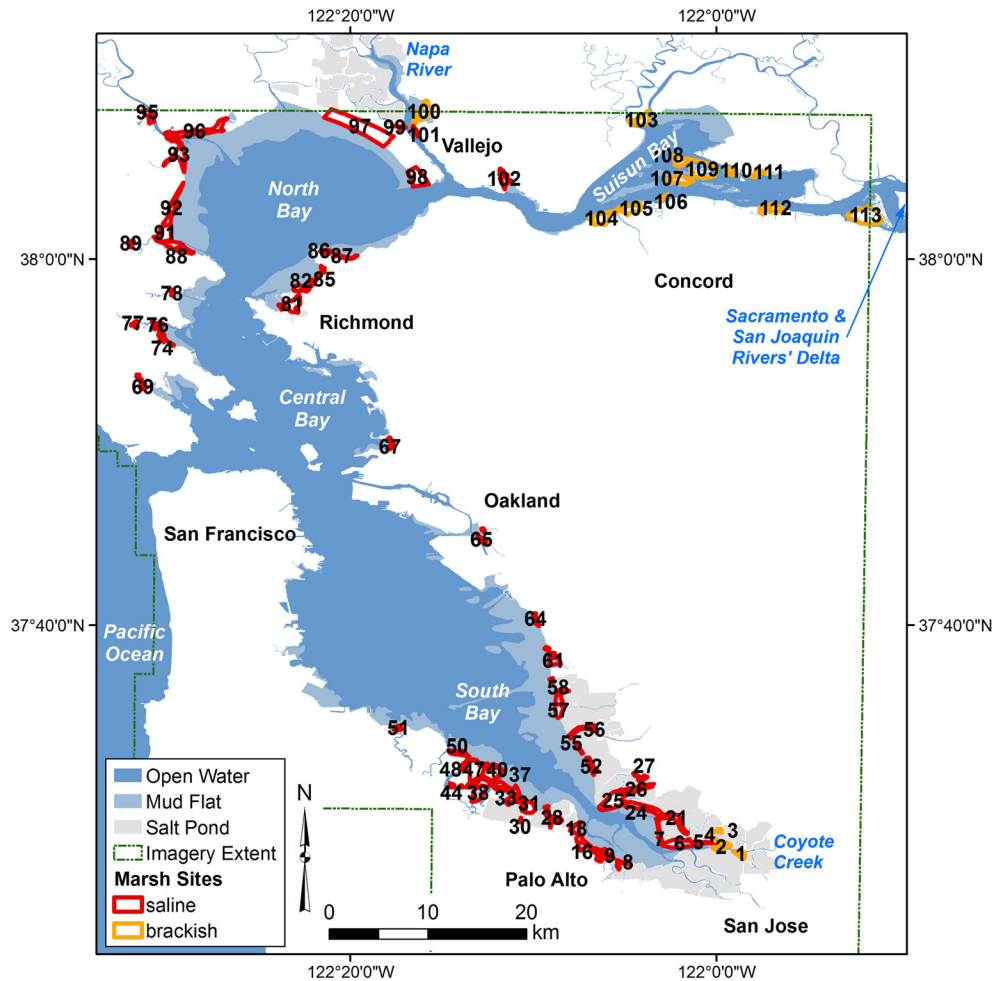


Figure 2. Map of San Francisco estuary study region and 113 analysed tidal marsh sites. Bay map is from National Wetlands Inventory (USFWS, 2006). Aerial photography imagery extent is from EarthData International (2004). Marsh sites digitized by authors. Detailed sub-region maps and images of each site are provided in the Supporting Information.

by levees. Islands had zero surrounding levees and an impoundment index of zero. Marsh sites that were developed outward from one backshore levee had an impoundment index of one. Irregularly shaped sites (e.g. roughly triangular) were scored according to the apparent proportion of the marsh boundary confined by levees. A site fully surrounded by levees, with substantial breaches only for passage of tidal channels, was scored with an impoundment index of four, regardless of site shape. The Supporting Information provides a comprehensive table of sites and site location, salinity, age, elevation, and impoundment characteristics (Table S1).

A combination of categorization and quantitative metrics was used to assess the spatial characteristics of the vegetation configurations and channel geometries of the 113 marsh sites, as exhibited in the aerial imagery. The vegetation configuration and channel geometry categorization methodology using a consistent decision-tree procedure was adapted and updated from preliminary efforts

briefly reviewed in (Moffett *et al.*, 2015). The present study was expanded to include more marsh sites throughout the region, including brackish sites. This study also included robust statistical hypothesis testing, quantitative analysis of metrics describing marsh heterogeneity, and linear modeling of the degree of complexity of vegetation configurations and channel geometries in relation to those metrics, which were not part of the earlier preliminary trial.

Categorization of marsh vegetation patterns and channel geometry

Vegetation patterns and channel geometry were categorized in a standardized manner using a consistent decision-tree procedure (Figure 4). The procedure was developed as an hierarchical, *a priori* categorization method meeting the needs for practicality, commonality, flexibility, comprehensiveness, simplicity, and systematization (as per terminology and criteria in the definitions of land cover

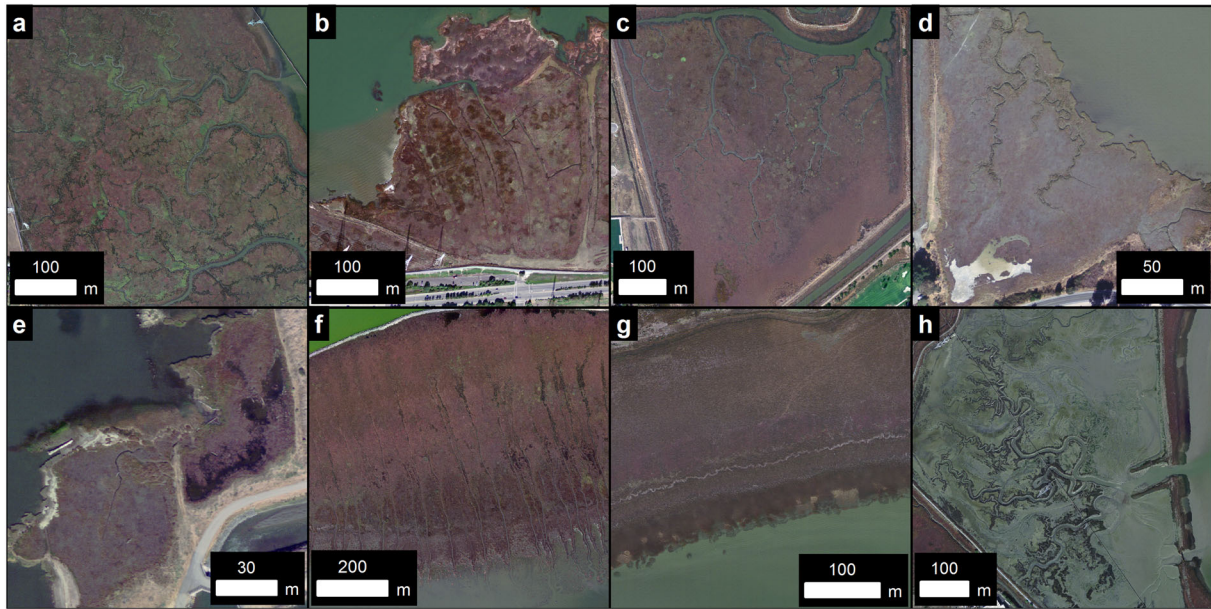


Figure 3. Examples of vegetation and channel pattern categories as observed in aerial photography. (a) Laumeister tract: vegetation 'mosaic', channels 'dendritic-looped'. (b) Seal Slough marsh: vegetation 'mosaic', channels 'linear'. (c) Faber tract: vegetation 'mosaic-solid', channels 'dendritic'. (d) Marin triangle marsh: vegetation 'solid', channels 'sinuous'. (e) Hayward's Landing: vegetation 'solid-banded', channels 'sinuous'. (f) Calaveras Point: vegetation 'banded', channels 'perpendicular'. (g) Petaluma River mouth north side: vegetation 'banded', channels 'none'. (h) Cooley Landing pond: vegetation 'developing', channels 'dendritic-looped'. All images are oriented with North at top.

classification systems by Di Gregorio and Jansen (2000)). The categorization procedure was focused on identifying different ways that discrete vegetation units within a marsh site might be spatially configured; our analysis did not study the plant diversity or species composition of the marsh. The categorization of marsh vegetation patterns was based on the presumption that different vegetation zones appear spectrally different in the RGB imagery, so color variation could be interpreted in terms of vegetation configuration.

To categorize the vegetation pattern of a site, first, the major color element of the marsh was identified, i.e., the color covering most of the interior marsh area, away from narrow buffers along the edges of channels, levees, and the shoreline. If the site were mostly covered by one, fairly uniform color, with little color or shade variation, it was categorized as the 'solid' vegetation pattern (Figure 3d). If minor color or shade variations appeared striated in a shore-parallel manner beyond a narrow buffer at the shoreline, the site was categorized as the 'solid-banded' vegetation pattern. If the site exhibited strong color variations oriented as shore-parallel bands, then the site was categorized as the 'banded' vegetation pattern, even if there was additional patchiness, e.g. around dissecting channels. If the site exhibited substantial color variations, but there was no notable preferential orientation of the color patches relative to the shoreline (i.e. the site appeared starkly mottled), then it was categorized as the 'mosaic' vegetation pattern. If a majority of the site appeared as one

visually smooth, fairly uniform color, but the site included notable sections of strongly patchy colors, or included faint patchiness in color or shade over a majority of the area, then the site was categorized as the 'mosaic-solid' vegetation pattern. If the site exhibited a large fraction of mudflat sparsely colonized by marsh vegetation, it was categorized as the 'developing' vegetation pattern. These six vegetation pattern classes were then combined into 'complex' (mosaic or mosaic-solid) and 'simple' (solid, solid-banded, banded or developing) vegetation pattern groups (Figure 4). Although qualitative, in practice it was straightforward to separate the marshes into discriminatory vegetation pattern categories using this decision-tree procedure (Figure 4).

Tidal channels were clearly visible in the high-resolution imagery, either as narrow curvilinear features among the vegetation or as lines of bare mud. Channel geometry categorization began by identifying whether the dominant channel shape was highly sinuous, straight, or whether channels appeared absent (channel category 'none'). Most sinuous channels also exhibited substantial network branching. If this branching was of a distributary style, the site was categorized as having a 'dendritic' channel geometry. If some of the branches of adjacent tidal drainages connected together in the inland portions of the marsh to form interconnected, looping networks [a feature geomorphologically enabled in marshes by vegetation, bi-directional tidal flow and disturbance (Kirwan *et al.*, 2008)], then the site was categorized as having a 'dendritic-

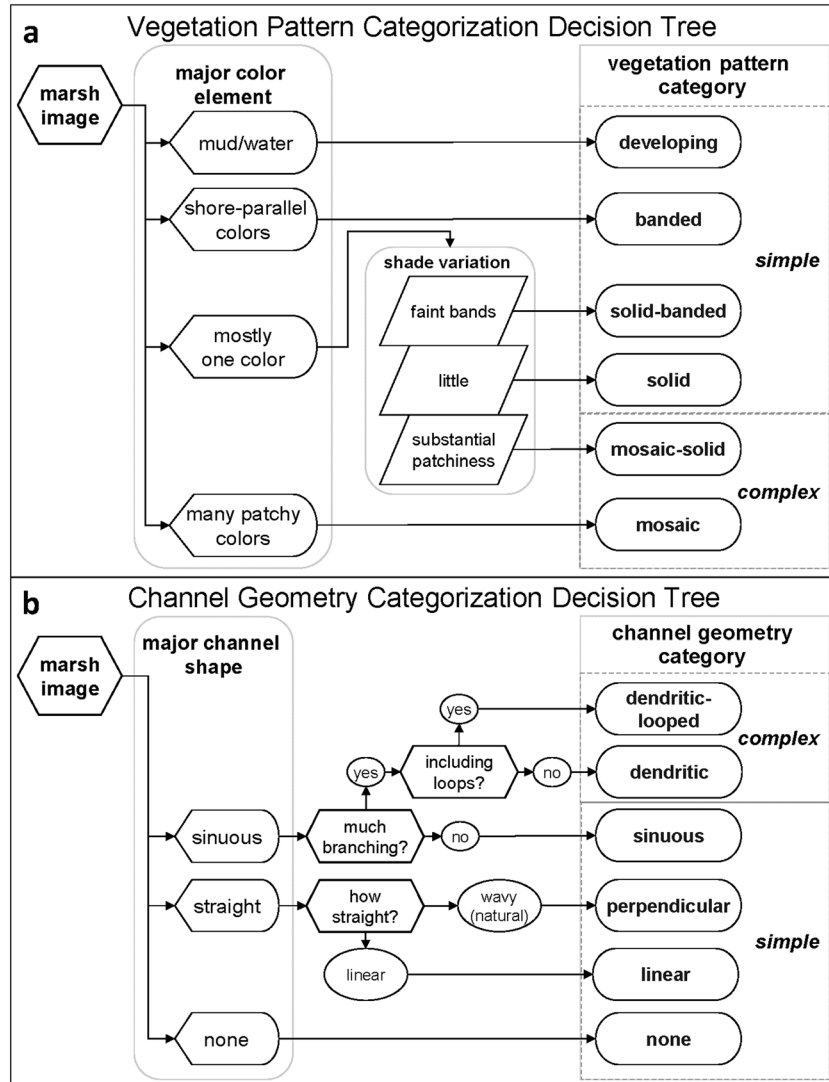


Figure 4. Framework for distinguishing marsh (a) vegetation pattern categories and (b) channel network type categories based on imagery inspection.

looped' channel geometry. If the sinuous channels were dominantly of a meandering shape and exhibited little branching, the channel geometry was categorized as 'sinuous'. If the channels were very straight and perpendicular to the shoreline, with only slight (apparently natural) waviness, the site was categorized as having a 'perpendicular' channel geometry. If the channels appeared unnaturally linear (from anthropogenic drainage engineering or mosquito ditching), the site was categorized as having a 'linear' channel geometry. These six channel geometry categories were then combined into 'complex' (dendritic or dendritic-looped) and 'simple' (sinuous, perpendicular, linear or none) channel pattern groups (Figure 4). Again, although qualitative, in practice it was straightforward to separate the marshes into discriminatory channel geometry categories using this decision-tree procedure (Figure 4).

The categorization of marsh sites by vegetation configuration, as viewed in aerial imagery, was compared with a categorization using the same procedure, but based on published vegetation maps, to assess whether the imagery-based categorization was capturing previously identified site characteristics. Of the 113 marsh sites, 22 had one or more published vegetation maps or detailed vegetation transects from the time of, or soon after, the imagery used in the analysis, for a total of 25 published comparative datasets (Table S1). The published maps were assessed using the same vegetation pattern categorization procedure as noted previously for the imagery. Assessment of the published maps was conducted independently, blind to the outcomes from the image assessment. The resulting correspondence of imagery-based and publication-based vegetation pattern categorizations was quantified using a confusion matrix and metrics of overall, producer, user,

and kappa (coefficient of agreement) accuracy (Landis and Koch, 1977).

Null hypotheses were posed that all categories of marsh salinity (saline/brackish), age (young/old), elevation (low/high), vegetation pattern complexity (complex/simple) and channel complexity (complex/simple) were independent. Fisher's exact tests ('fishertest' MATLAB v.R2014b, MathWorks, Natick, MA, USA) were used to evaluate whether the null hypotheses could be rejected. The maximum statistical significance level required to reject the null hypothesis in each case was $\alpha=0.01$. This maintained a family level significance at 0.1, including the Bonferroni correction for the 10 comparisons, which is known to be conservative (Rice, 1989).

Pattern relations to quantitative metrics of site heterogeneity

In addition to testing for relationships among categorical site characteristics, we tested whether the complexities of vegetation patterns and channel geometries were related to objective metrics quantifying site area, channel density, and the configuration (e.g., relative homogeneity, patch shape) of vegetation and channels within each marsh. Marsh configuration was quantified using object-based image analysis (OBIA; eCognition Developer and Server v.9 software, Trimble Navigation Limited, Sunnyvale, CA, USA) (Baatz and Schäpe, 2000; Benz *et al.*, 2004). The spatial features in the imagery suggestive of vegetation

patches and zones were extracted using the automated eCognition multi-resolution segmentation algorithm. The algorithm divided each marsh site into numerous objects (i.e., coherent polygon features) by iteratively merging similar adjacent pixels, or proto-objects, until the objects had grown to such a size as to encompass a designated degree of image (color) heterogeneity and shape complexity (Benz *et al.*, 2004) (Figure 5). Multi-resolution segmentation algorithm parameters were chosen based on prior determination of optimal salt marsh vegetation zone extraction from this RGB imagery data source: scale parameter 100, shape/color weighting 0.1/0.9 and smoothness/compactness weighting 0.3/0.7 (Moffett and Gorelick, 2013).

A variety of quantitative metrics were evaluated for each of the 75,191 objects resulting from the OBIA, which together composed the 113 marsh sites. The metrics, calculated for each image object, were aggregated to the site level by calculating the mean and standard deviation of the object-based metric values within each site. The object-growing approach of MRSA means that smaller final objects were more spectrally heterogeneous per unit area than larger objects. (See MRSA summary description in Moffett and Gorelick (2013) and original work by Baatz and Schäpe (2000) and Benz *et al.* (2004).) Also, channels tended to constrain object boundaries, because incorporating a spectrally contrasting channel segment within an object incurred a substantial increase in the object heterogeneity score and limited further object

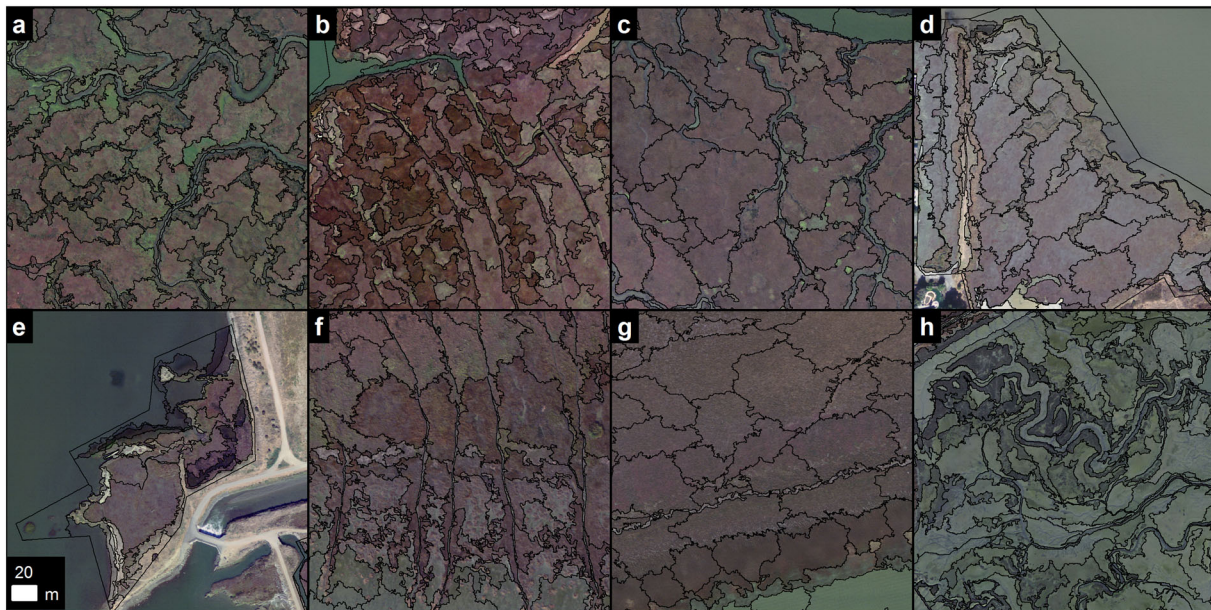


Figure 5. Examples of objects produced by the eCognition multi-resolution segmentation algorithm, for subregions of the sites depicted in Figure 3. The algorithm produces objects such that the area within an object is more similar to itself than the object is to its neighbours, and maximum object size is limited by a specified heterogeneity threshold. Each example is displayed at the same scale, as indicated in (e). The different sizes and shapes of objects reflect differences in marsh vegetation patterning among sites. As in Figure 3, the site vegetation patterns were classified as (a) 'mosaic', (b) 'mosaic', (c) 'mosaic-solid', (d) 'solid', (e) 'solid-banded', (f) 'banded', (g) 'banded' (h) and 'developing'. All images are oriented with North at top.

growth. Extending from these ideas, nine site-level, OBIA-derived metrics were hypothesized to be related to vegetation pattern complexity: mean and standard deviation of object size, mean and standard deviation of object compactness, mean and standard deviation of object shape index, standard deviation of object brightness, standard deviation of object hue and standard deviation of object main direction (metrics defined in Table I). Seven site-level metrics were hypothesized to be related to channel complexity: mean and standard deviation of object size, mean and standard deviation of object compactness, mean and standard deviation of object shape index and standard deviation of object main direction.

In addition to the OBIA-derived metrics to quantify aspects of marsh configuration, site area and site channel density index were quantified. Site area was calculated based on the polygon outlines of the 113 sites using the 'area' option in the 'Calculate Geometry' function of ArcGIS 10 (ESRI, Redlands, CA, USA). Site channel density index was calculated based on a digital map (i.e., GIS line segments data file) of the stream and tidal channel networks throughout the study region, which was obtained from the San Francisco Estuary Institute online resources (SFEI, 2015). This channel dataset was developed as part of the Bay Area Aquatic Resources Inventory by digitization based on a combination of

National Agriculture Imagery Program 1-m resolution aerial imagery from 2005 or 2009, digital images of 1:24,000 scale USGS Topographic Quadrangles, and ground truth data (SFEI, 2011). For reference, these Bay Area Aquatic Resources Inventory GIS data are shown overlain on the imagery for each site in Figure S2. Although this GIS data did not represent all the channels visible in the aerial imagery used in this study, the pre-existing GIS data were useful as a standardized source for developing an index of channel occurrence per site.

To calculate the channel density index, the GIS streams map was intersected with the marsh site outlines map in ArcGIS 10 (ESRI, Redlands, CA, USA) to omit portions of channel segments outside each designated marsh site. The remaining segment lengths were then summed within each marsh site, and this total divided by site area, to calculate a channel density index [channel density index = total stream length/site area (m ha^{-1})]. This channel density index was therefore calculated the same way as a Horton drainage density (Horton, 1945; Marani *et al.*, 2003), but termed an index because of the potential lack of representation of the finest-scale channels in the calculations. Because of missing small channels at the scale below that used for digitization, and because of the data format as very small and topologically disconnected line segments, strict calculations of channel density, sinuosity, fractal dimension, or other such metrics were not feasible.

Table I. Quantitative metrics of marsh configuration included to predict site vegetation and channel pattern complexity using generalized linear mixed-effects models (GLMM).

Metric	Definition	GLMM relationship to pattern complexity: complex/simple	
		Vegetation	Channels
area	Site area in hectares (ha)	(none)	(none)
chden	Channel density index = total stream length / site area (m ha^{-1})	(none)	+/-
msize	$mean_{obj}$ (size in number of pixels)	(none)	+/-
sdsiz	$stdev_{obj}$ (size in number of pixels)	-/+	(none)
mcompact	$mean_{obj}$ (compactness), where [compactness = length * width/area] and length and width are the major and minor axis lengths of the object (first and second eigenvalues)	(none)	+/-
sdcompact	$stdev_{obj}$ (compactness)	(none)	-/+
mSI	$mean_{obj}$ (shape index), where [shape index = object border length / ($4 \sqrt{\text{object area}}$)] and shape index is a measure of object border smoothness, with a minimum value of 1 for a square	(none)	(none)
sdSI	$stdev_{obj}$ (shape index)	+/-	(none)
sdbright	$stdev_{obj}$ (brightness), where brightness = weighted sum of mean red, green and blue intensity values within an object	-/+	(none)
sdhue	$stdev_{obj}$ (hue), where hue = mean object red, green and blue values transformed onto a rainbow color scale from 0 to 1	(none)	(none)
sddir	$stdev_{obj}$ (main direction), where main direction = direction (0 to 180°) of the major axis of the object (first eigenvector)	-/+	(none)

Object-based metric definitions are as in the eCognition reference book (Trimble, 2014). Abbreviations $mean_{obj}(var)$ and $stdev_{obj}(var)$ indicate the mean and standard deviation, respectively, of the object-level values of *var*, taken over all the objects composing a site. A GLMM relationship coded as '+/-' indicates that a larger value of the metric was significantly related to complexity and a smaller value to simplicity; a relationship coded as '-/+' is the opposite.

Table II. Relationships among marsh salinity, age, elevation, and impoundment characteristics and vegetation and channel pattern complexity categorization: Numbers shown are the number of 113 total sites in each combination of categories.

	Relative salinity		Relative age		Relative elevation		Impoundment index				Vegetation complexity			Total
	Saline	Brackish	Old	Young	High	Low-mid	0	1	2	3	4	Complex	Simple	
Relative salinity	Saline		37	60	83	14	9	38	12	29	9	57	40	97
Relative age	Brackish		11	5	14	2	7	4	1	3	1	15	1	16
	Old	11			48	0	12	14	8	13	1	35	13	48
Relative elevation	Young	5			49	16	4	28	5	19	9	37	28	65
	High	83	14	49			13	40	12	26	6	60	37	97
Impoundment index	Low-mid	14	2	16			3	2	1	6	4	12	4	16
	0	9	7	4	13	3						14	2	16
	1	38	4	28	40	2						29	13	42
	2	12	1	8	12	1						6	7	13
	3	29	3	13	26	6						17	15	32
Vegetation complexity	4	9	1	9	6	4						6	4	10
	Complex	57	15	35	60	12	14	29	6	17	6			72
	Simple	40	1	13	37	4	2	13	7	15	4			41
	Complex	56	9	35	53	12	11	22	7	19	6	50	15	65
Channel complexity	Simple	41	7	13	44	4	5	20	6	13	4	22	26	48
	97	16	48	65	16	16	42	13	32	10	72	41	113	

The relations of these OBIA-derived object, area and channel density metrics to site vegetation and channel complexity were tested using generalized linear mixed-effects models [GLMM; (Zuur *et al.*, 2009)]. In each of the two models (for vegetation pattern complexity or channel complexity), the response variable was categorical, taking values of 'complex' (1) or 'simple' (0). The GLMM analysis was conducted using the MATLAB v.R2014b function 'fitglm' (MathWorks, Natick, MA, USA), with binomial distribution, logit link, and Laplace fit method. The fixed effects included in the initial model iteration were site area, channel density index, and the OBIA-derived metrics hypothesized to be related to marsh configuration (Table I). The GLMM analysis was conducted in a sequential hierarchical manner, to identify the metrics that were significant contributors to a predictive model. In each GLMM iteration, the fixed effect with the largest *P*-value was removed from the model. Subsequent iterations continued until the *P*-values for all contributing fixed effects were <0.1 . Site ID number was included as a random effect in each model. The final GLMM results were further confirmed by comparison with an automated stepwise generalized linear model procedure, which lacked the random effect of site ID. The generalized linear model analysis was conducted using the MATLAB v.R2014b function 'stepwiseglm' (MathWorks), with binomial distribution, logit link, linear terms only, and terms with *P*-value >0.1 iteratively removed.

RESULTS

Marsh site characteristics

The site characteristics of the 113-site sample population of marshes are tallied in Table II. A preponderance of sites (97/113) was in the saline category, as saline tidal marshes were the more common estuarine habitat and the intended focus. Similar proportions of sites were in the old (>165 year; 48/113 sites) and young (<165 year; 65/113 sites) marsh age categories overall, but there was a larger fraction of young sites among saline sites (60/97) and a larger fraction of old sites among brackish sites (11/16). Many more sites were in the high-elevation category (97/113) than in the low-to-mid elevation category (16/113), overall and within both salinity categories. All sites in the low-mid elevation category corresponded with young marsh age (16/16). Nearly equal proportions of high marsh sites occurred in the old and young marsh age categories, both overall (48/97 old, 49/97 young) and among only saline sites (37/83 old, 46/83 young). The marshes in each salinity, age and elevation category spanned all five degrees of impoundment. Marsh age and elevation were significantly related, both among all sites (Table IV) and among saline sites only (Table S2).

Vegetation organization

The total number of sites identified with each vegetation pattern category, and the categories' relationships to other site characteristics, are tallied in Table III. The most abundant vegetation pattern identified in the region was the 'mosaic' category, accounting for almost half of sites overall (52/113, 46%; Table IV). The proportion of sites with a 'mosaic' vegetation pattern was somewhat less among only saline sites (38/97, 39%; Table S3). The distributions of sites among the six vegetation pattern categories were similar between old and young marsh age groups and between high and low-mid elevation sites.

At the coarser level of analysis, just comparing 'complex' versus 'simple' vegetation pattern categories, more sites exhibited a complex vegetation pattern than a simple vegetation pattern for every category of relative marsh salinity, age, elevation and every impoundment index except 2 (Table II). The occurrence of a high proportion (more than two-thirds) of sites exhibiting a complex vegetation pattern was particularly notable within old marshes, low-mid elevation marshes, islands (impoundment index 0), and laterally unrestricted fringing sites (impoundment index 1). Islands had the most reliably complex vegetation configuration (14/16, 88% of island sites). Overall, more sites exhibited a complex vegetation configuration (72/113, 64%; Table II) than a simple vegetation configuration. The proportion of sites of complex vegetation configuration was somewhat less among only saline sites (57/97, 59%; Table S2). The complexity (complex/simple) of the marsh vegetation patterns was significantly related to salinity but statistically independent of relative marsh age and relative marsh elevation, both among all sites (Table IV) and among saline sites only (Table S4).

Comparison of the imagery-based vegetation pattern complexity categorizations to categorizations based on 25 published site maps was favourable, with an overall correspondence of 76%, an average user accuracy of 76%, an average producer accuracy of 77%, and a kappa (K) coefficient of agreement of 69% (Table V). The 'producer accuracy' estimates the probability that the complexity (complex/simple) assigned based on the published site map was also assigned based on the imagery, so a high value suggests few false negatives in the categorization. The 'user accuracy' estimates the probability that a complexity assignment based on the imagery was the same as the complexity assignment based on the published site map, so a high value suggests few false positives in the categorization. A kappa coefficient of agreement of 0.61–0.80 (including our 0.69) is generally considered 'substantial' agreement (Landis and Koch, 1977). To the degree that the imagery-based and published map-based categorizations differed, this was likely due in part to variations among the

Table III. Numbers shown are the number of marsh sites in each specific vegetation and channel pattern category and relationships to site characteristics.

	Relative salinity				Relative age				Relative elevation				Impoundment index				Channel pattern class			
	Saline	Brackish	Old	Young	High	Low-mid	0	1	2	3	4	Dendritic-looped	Dendritic	Sinuuous	Perpendicular	Linear	None	Complex	Simple	Total
Vegetation pattern class																				
Complex	38	14	24	28	43	9	10	21	4	13	4	23	11	5	5	3	5			52
Mosaic-solid	19	1	11	9	17	3	4	8	2	4	2	11	5	0	3	1	0			20
Simple	12	0	4	8	10	2	1	1	1	8	1	3	3	3	2	1	0			12
Solid	9	0	4	5	9	0	0	4	2	3	0	1	3	2	1	2	0			9
Solid-banded	17	1	5	13	17	1	1	8	4	4	1	2	1	2	7	1	5			18
Banded	2	0	0	2	1	1	0	0	0	0	2	2	0	0	0	0	0			2
Developing	36	6	25	17	36	6	10	17	4	8	3									42
Dendritic-looped	20	3	10	13	17	6	1	5	3	11	3									23
Dendritic	11	1	5	7	12	0	2	4	1	3	2									12
Sinuuous	15	3	0	18	16	2	1	11	4	1	1									18
Perpendicular	7	1	6	2	7	1	0	1	1	5	1									8
Linear	8	2	2	8	9	1	2	4	0	4	0									10
None	97	16	48	65	97	16	16	42	13	32	10	42	23	12	18	8	10			113
Total																				

Table IV. Results of Fisher's exact tests for relationships between marsh site characteristics, vegetation pattern complexity and channel complexity.

	Salinity	Age	Elevation	Vegetation complexity	Channel complexity
Salinity					
Age	0.0291				
Elevation	1.0000	0.0001*			
Vegetation complexity	0.0095*	0.1130	0.4056		
Channel complexity	1.0000	0.0068*	0.1742	0.0008*	

*Reported values are significance (P values), with a value $P < 0.01$ required for rejection of the null hypothesis (for $\alpha = 0.1/10$, with Bonferroni correction for 10 comparisons). Asterisks indicate significant results.

Table V. Comparison of site vegetation pattern complexity assignment based on imagery to assignment based on published site maps.

		Map-based pattern			User accuracy:	User average:
		Complex	Simple	Total		
Image-based pattern	Complex	8	4	12	67%	76%
	Simple	2	11	13	85%	
Total		10	15	25		
Producer accuracy:		80%	73%			
Producer average:		77%			K:	69%

Numbers of sites independently assigned to complex or simple pattern type from each data source are tabulated, and kappa coefficient of agreement (K) is reported.

methods used to develop the published maps and in the final resolution and detail of the published maps compared with the imagery.

The GLMM for predicting vegetation pattern complexity from objective quantitative metrics of marsh configuration found that only four of the metrics were significant fixed-effect contributors, each with an individual P value < 0.1 (Table S5). The Supporting Information provides a comprehensive table of the metric values for each site (Table S1). The successful GLMM for vegetation pattern complexity [veg. complexity was either complex (=1) or simple (=0)] was the linear combination of the standard deviation of object size (sdsiz), the standard deviation of object shape index (sdSI), the standard deviation of object direction (sddir) and the standard deviation of mean object brightness (sdbright):

$$\text{veg. complexity} = 4.4 - 0.00025 \text{ sdsiz} + 3.7 \text{ sdSI} - 0.083 \text{ sddir} - 0.078 \text{ sdbright} \quad (1)$$

such that the probability (π_i) that a marsh exhibited a complex vegetation pattern was

$$\pi_i = \frac{e^{\text{veg.complexity}}}{1 + e^{\text{veg.complexity}}} \quad (2)$$

The signs of the interactions are summarized in Table I. The total covariance attributed to the random effect of the

marsh site ID was negligible (Table S5). The automated stepwise GLM, which omitted the site effect, reduced to the same model as the GLMM. These four quantitative variables, therefore, were the only ones significantly useful for discriminating complex versus simple marsh vegetation configurations within the sample population of 113 marshes.

Channel network types

The total number of sites in each channel geometry category, and the categories' relationships to other site characteristics, are tallied in Table III. The most abundant channel network type identified in the region was the 'dendritic-looped' category, accounting for more than a third of sites both overall (42/113, 37%; Table III) and among only saline sites (36/97, 37%; Table S3). The distributions of marshes across all six specific channel geometry categories were relatively consistent (Table III); an important exception was that all sites in the 'perpendicular' channel category were young sites.

Overall, more sites exhibited a complex channel geometry (65/113, 58%; Table II) than a simple channel geometry, and this proportion was equivalent among only saline sites (56/97, 58%; Table S2). A high proportion (more than two-thirds) of sites exhibiting a complex channel geometry was particularly notable within old marshes, low-mid elevation marshes and islands (impound-

ment index 0). Because in this sample population all old marshes were high-elevation and all low-mid-elevation marshes were young (Table II), this means that complex channel networks were prevalent among old-and-high marshes and also among low-and-young marshes. More sites exhibited complex channel patterns than simple channel patterns for every category of relative marsh salinity, elevation, and impoundment index, and for old but not young marsh age. The degree of complexity in these channel geometry categories was significantly related to marsh age but statistically independent of relative marsh salinity and relative marsh elevation, both among all sites (Table IV) and among saline sites only (Table S4).

The GLMM for predicting channel pattern complexity from objective quantitative metrics of marsh configuration found that only four of the metrics were significant fixed-effect contributors, each with an individual P value < 0.1 (Table S5). The successful GLMM for channel geometry complexity [chan. complexity was either complex (=1) or simple (=0)] was the linear combination of the channel density index (chden), the mean object size (msize), the mean object compactness (mcompact) and the standard deviation of compactness (sdcompact):

$$\text{chan. complexity} = -18 + 0.010 \text{ chden} + 0.00021 \text{ msize} + 6.9 \text{ mcompact} - 2.5 \text{ sdcompact} \quad (3)$$

such that the probability (π_i) that a marsh exhibited a complex channel pattern was

$$\pi_i = \frac{e^{\text{chan.complexity}}}{1 + e^{\text{chan.complexity}}} \quad (4)$$

The signs of the interactions are summarized in Table I. The total covariance attributed to the random effect of the marsh site ID was negligible (Table S5). The automated stepwise GLM, which omitted the site effect, reduced to the same model as the GLMM. These four quantitative variables, therefore, were the only ones significantly useful for discriminating complex versus simple marsh channel geometries within the sample population of 113 marshes.

Relations between complexity of vegetation patterns and channel geometries

The largest single subset of sites (23/113, 20%) exhibited both the complex 'mosaic' vegetation configuration and complex 'dendritic-looped' channel geometry (Table III). In contrast, the sites with a simple 'banded' vegetation configuration were mostly occupied by 'perpendicular' channels or no channels, all of which were young marsh sites. Overall, almost every combination of vegetation pattern and channel geometry was exhibited by at least one site, excepting sites with no channels, the rare 'developing' vegetation pattern class and the anomalously absent

mosaic-solid vegetation pattern/sinuuous channel geometry combination (Table III); this was also true among only saline sites (Table S3).

Overall, vegetation pattern complexity and channel geometry complexity were significantly related, both among all sites (Table IV) and among saline sites only (Table S4). This significant relationship was based on there being more sites with a complex vegetation configuration and complex channel geometry (complex/complex), or with a simple vegetation configuration and simple channel geometry (simple/simple), than either mixed (simple/complex) combination (Table II).

DISCUSSION

Marsh site characteristics of the San Francisco Bay estuary

The preponderance of high marsh sites in both the old and young age groups of our sample population of marshes was consistent with the physiography and recent history of the San Francisco Bay estuary. In their comprehensive summary of the estuary's natural history, Atwater *et al.* (1979) suggested that the surprisingly flat marshes of San Francisco Bay estuary are mostly at the elevation of mean higher high water, the mean of the higher of the two daily semi-diurnal tides, although with notable site-to-site variations. Some of this elevation variation depends on marsh age, as indicated by the significant relationship we quantified between elevation and age. In the San Francisco Bay estuary, a bimodal distribution of marsh elevation could easily have been caused by the destruction of all but about 100 km² of the old high marsh areas of the estuary since about 1850 and the simultaneous development of a similar area of young low marshlands with sediment from recent industry and development in the watershed. The somewhat similar proportions of old (42%) and young (58%) marsh sites in our sample population therefore likely reflect relatively representative sampling of this bimodal distribution of marsh age.

The significant relationship between marsh age and elevation in our sample population was consistent with the marshes of San Francisco Bay estuary having been in an accretionary mode during the 150 years of recently elevated sediment supply, and indeed over recent millennia since the last eustatic high. Although the accretion of low marshes to become high marshes is not surprising, it is not a foregone conclusion. Simulations by Mariotti and Carr (2014) demonstrated how marshes and mudflats can achieve multiple different equilibrium states under different scenarios of sea level rise, sediment supply and wind-wave erosion. The processes contributing to state stability or transition include vertical marsh accretion, but also relative vertical

marsh subsidence, marsh drowning and lateral marsh retreat or expansion either to a bistable marsh/mudflat equilibrium or to complete conversion to one or the other state (Mariotti and Carr, 2014). In fact, multiple predictions suggest that San Francisco Bay estuary marshes may be substantially lost in the future because of combined effects of declining sediment supply and rising sea level (Knowles, 2010; Schoellhamer *et al.*, 2012; Stralberg *et al.*, 2011). The possible future of the estuary, in light of this background and the results of the study, is discussed further in the succeeding text (Section on Implications for Estuarine Wetland Futures).

Vegetation configurations and relations to site characteristics

The substantial variations in vegetation configurations among marsh sites in San Francisco Bay estuary led us to reject the first hypothesis posed in the introduction, that there should be relative uniformity in vegetation patterns among a large number of sites within the same system because of shared biogeomorphic feedback processes and critical points. Instead, the results supported the second hypothesis posed in the introduction, that there is substantial variation in the organization of marsh vegetation within a common physiographic coastal system, related to factors such as microtopography.

The relationships of vegetation pattern complexity to quantitative metrics of marsh cover heterogeneity derived from OBIA and identified as significant by GLMM were informative and could be interpreted in relation to patterns observable in aerial imagery. The complexity of marshes' vegetation configurations was negatively related to the standard deviation of object size, meaning that the more complex 'mosaic' and 'solid-mosaic' type vegetation patterns had an overall less variable (more uniform) vegetation patch and zone size than simpler (e.g., 'solid' or 'banded') pattern types. Marshes exhibiting the more simple vegetation configurations characteristically had many large, fairly homogenous marsh areas interspersed by small anomalous vegetation patches (e.g. *Grindelia stricta* bushes), which likely caused their higher standard deviations in object size. Vegetation pattern complexity was also positively related to the standard deviation of the object shape index, a measure of object border smoothness, meaning that objects with less smooth borders comprised sites with complex vegetation patterning. This was caused by the highly crenulated zone shapes and puzzle-like intermingling of vegetation types in sites with complex vegetation patterning (Figure 3). Both of these interpretations about vegetation patch shape are again consistent with the hypothesis that there is substantial variation in the organization of marsh vegetation that might be related to small local factors such as

microtopography (Zedler *et al.*, 1999) or distance to channel (Sanderson *et al.*, 2000).

Vegetation pattern complexity was also negatively related to the standard deviation of object main direction, suggesting less variation in the cardinal orientation of objects within complex sites than simple sites. The explanation for this is unknown; we had hypothesized that greater vegetation pattern complexity would have a more random distribution of object orientations and simpler vegetation patterns, especially banded patterns, would have more consistent object orientations, but the demonstrated relationship was in the opposite sense. Vegetation pattern complexity was negatively related to the standard deviation of object brightness, meaning that greater brightness variation related to simpler vegetation patterning. This was likely a consequence not so much of the vegetation patterning itself, but instead of a greater tendency for sites with simple vegetation patterning to also contain highly contrasting, bright salt pannes and dark high marsh ponds. Whether this apparent correspondence between pannes and simpler vegetation configurations is a general phenomenon, and whether there is a biogeomorphic reason for it, are unknown.

Relationship of vegetation configuration to salinity. Within the sample population of marsh sites, vegetation pattern complexity and site salinity were positively related. Given the exogenous control of salinity by freshwater discharge from the Sacramento–San Joaquin Delta or Coyote Creek (Goals Project, 1999), it is clear that this significant relationship is due to the influence of salinity on vegetation, not vice versa. Brackish marsh plant species richness is generally greater than that of salt marshes (Atwater *et al.*, 1979). In salt marshes, salinity is well known to influence plant community composition at both site and sub-site scales, especially as related to intertidal elevation (Chapman, 1940). Overall, the significant relationship between vegetation pattern complexity and relative marsh site salinity was strongly driven by the complex vegetation pattern of almost every brackish site and the greater representation of simple vegetation patterns among saline sites. It must be emphasized, however, that these results should only be interpreted categorically. The salinity categorization was only available at the site scale as binary brackish/saline categories, and vegetation complexity (complex/simple) was not graded by degree. Therefore, although binary vegetation pattern complexity and binary site salinity were categorically related, a conclusion that fresher marshes are generally more complex or that saltier marshes are generally simpler is not supported, nor testable, with these data. Also, it should be appreciated that salinity typically varies across a marsh site and has strong relationships to vegetation composition and configuration (e.g. Callaway *et al.*, 1990).

Relationship of vegetation configuration to elevation. Our finding that the complexity of marsh vegetation configuration was unrelated to marsh elevation may appear counter-intuitive at first; it is typically assumed that higher (and older) marshes are more complex in both composition and configuration. However, abundant literature only exists to substantiate the former, elevation–composition relationship. For example, in an experimental manipulation of adjacent marsh restoration sites to different initial elevations, Cornu and Sadro found that vegetation density, diversity and richness became greater at high-elevation sites compared with low sites (Cornu and Sadro, 2002). However, density, diversity and richness are measures of marsh cover composition, which is fundamentally different from marsh cover configuration. The two-dimensional configuration of salt marsh topographic and vegetation heterogeneity across whole marsh sites in western North America has been assessed by only a few studies (Morzaria-Luna *et al.*, 2004; Varty and Zedler, 2008; Moffett *et al.*, 2012). Such two-dimensional complexity in salt marsh vegetation organization has been hypothesized to relate to spatial variations in microtopography (Zedler *et al.*, 1999), cumulative distance to channel (Sanderson *et al.*, 2000) and salt exchange with tidal waters (Moffett *et al.*, 2010). It is quite possible, and even likely, that the salt marsh sites in San Francisco Bay estuary that exhibit simple vegetation patterns, especially the ‘solid’ vegetation pattern category, also exhibit less microtopographic heterogeneity, but the very high resolution, accurate topographic data that would be required to test this are currently unavailable. The important point here, however, is that increasing diversity of marsh vegetation *composition* with elevation (e.g., Cornu and Sadro, 2002) does not necessarily mean that the complexity of marsh vegetation *configuration* need also increase with elevation.

To illustrate the important difference between composition and configuration, consider a chess board: with two alternating colors (composition), each square on the board can be distinguished from its neighbours via a checkered pattern (configuration) that has a complex visual texture of 64 ‘patches’. On the other hand, a board with the same total number of red and black squares (same composition) could be colored half red and half black with a dividing line in the center and have a very simple overall configuration of just two ‘zones’. When considering configuration versus composition of multiple plant species, the possibilities are more diverse (i.e., more than two colors could appear on the board), but the overall concept is the same: vegetation diversity need not be indicative of configurational marsh complexity, or vice versa. For example, it is theoretically possible that a marsh could be characterized by a very diverse, rich, and dense but well-mixed vegetation assemblage, and that assemblage could be quite uniformly spread across the whole marsh, in which case the marsh

would have a very simple vegetation configuration. Alternatively, each species could be present in small monospecific patches that together form a detailed mosaic of heterogeneous marsh cover, in which case the marsh would have a complex vegetation configuration.

It is also possible that the origins and geomorphic history of marsh sites play a role in whether they exhibit a strong relationship between marsh elevation and vegetation pattern complexity. Sites already ‘on’ a terrestrial shoreline that morphologically take on, or are given, a higher or lower elevation [as in the study by Cornu and Sadro (2002)] might be more likely to exhibit a positive relationship between marsh elevation and vegetation pattern complexity because of the pre-existing elevation gradient, the preexisting species or seed bank or differences in how water, sediment and interspecific interactions occur on an existing emergent shoreline or upland margin compared with other potential tidal marsh settings. It could be that sites that grow by vertically accreting on mudflats or by prograding outward from shorelines might instead have the opportunity to develop both complex channel networks and a variety of patchy, complex vegetation configurations, perhaps via more pronounced vegetation–geomorphology feedbacks. Such biogeomorphic feedbacks have been well-described at the scale of vegetation patches and zones by marsh models that do incorporate elevation-dependent processes to simulate the spatial arrangement of vegetation zones along a transect (e.g. Marani *et al.*, 2013; Da Lio *et al.*, 2013). Because such transect models do not yet assess the overall degree of two-dimensional vegetation configurational complexity within a simulated marsh, however, their results cannot yet be compared with or used to evaluate this study’s finding of no significant empirical relationship between marsh elevation and vegetation configurational complexity.

Relationship of vegetation configuration to marsh age.

Our finding that the complexity of marsh vegetation configuration was unrelated to marsh age (like elevation) may also appear counter-intuitive at first; it is commonly assumed that marsh vegetation will develop toward a more nuanced, complex system over time, as a patchwork of interspecific interactions, micro-habitat variations and small disturbances will progressively generate complexity as the site ages. For example, Tuxen *et al.* (2010) showed that among a subset of marsh sites in the northern San Francisco estuary, older sites exhibited more vegetation classes and greater vegetation diversity. Again, site composition (number of classes, diversity) need not necessarily be related to or to, nor indicative of, site configuration. As in the chess-board example, great pattern complexity can in fact be generated by only two colors (species), whereas even many plant species can be configured into simple patterns (e.g., mixed into a

homogeneous assemblage, or configured in large monospecific zones). Therefore, even if plant species and class (i.e., assemblage) diversity increases with age, it does not necessarily follow that the overall marsh configuration needs to grow more complex with age.

Also, sites of different ages need not exhibit a similarly complex configuration for the same reasons. For example, the statistical (GLMM) model results indicated that a complex vegetation configuration was associated with more uniform vegetation patch sizes and detailed (crenulated), rough vegetation patch and zone borders. In young or low marshes with such complex vegetation patterning, the relatively uniform patch sizes might be caused by a tendency toward clonal modes of expansion in stressed pioneer and low-elevation plants. In old or high marshes with such complex vegetation patterning, however, a history of interspecific interactions, disturbance and channel dissection might cause complicated patch and zone boundaries but tend to limit zones to more uniform sizes over time.

Regardless of mechanism, the evidence from our sample population of 113 marshes rejects the prevailing tendency to assume that older and higher marshes have necessarily more complex vegetation configurations than younger marshes. It would be useful to test whether this evidence holds in other regional marsh systems around the world, and whether specific mechanisms controlling vegetation configuration, as well as composition, in marshes of different ages can be more clearly distinguished in future research.

Channel geometries and relations to site characteristics

The complexity of marsh channel geometry was significantly related to site age (by Fisher's exact test) and channel density index (by GLMM) but not salinity or elevation, in contrast to the significant relationships of vegetation pattern complexity to site salinity but not site age or elevation.

Some researchers have suggested that aging channel networks may become more meandering, develop loops, abandon smaller-order channels and so develop lower density [e.g., (Allen, 2000)]. On the other hand, more disturbance can generate both more complex and dissecting, space-filling channelization (Kirwan *et al.*, 2008). The positive relationship between channel density index and channel geometry complexity in our data suggests that the network pruning mechanism has not been a prominent factor in the San Francisco Bay estuary to date, but the effects of disturbance may have been important.

In the quantitative statistical (GLMM) model, channel geometry complexity (complex/simple) was also positively related to mean object size, in addition to channel density index, and negatively related to the standard deviation of

object compactness. Together, these results indicated that sites with a simple channel network were composed of smaller and more internally heterogeneous marsh surface features on average, with greater variation in feature compactness. The reasons for these relationships are unknown; we hypothesized the opposite relationships. Channel pattern complexity was also positively related to mean object compactness, which can be explained because simple channel patterns among marshes in our sample population were more likely to consist of roughly parallel channels, which would constrain objects to be more elongated and less compact, and allow more complex channel patterns to be related to more compact objects. Together, these results suggest that marsh channel evolution over time, and of channel-inter-channel area relationships, may be useful areas for further research (e.g., D'Alpaos *et al.*, 2005, 2007a, 2007b).

Relationship of channel geometry to marsh age. Complex channel geometry occurred in a majority of old sites and simple channel geometry in a majority of young sites. It is logical that channel complexity may take time to develop; Allen (2000) cited proposals by Yapp from the early 20th century that channel pattern complexity should increase with marsh age and marsh elevation. Marsh channels may also accumulate complexity via disturbance over time (Kirwan *et al.*, 2008). More regionally relevant, the analysis of two North Bay marshes presented in a student manuscript by Hall found channel sinuosity and channel order to generally increase with marsh age and drainage density to increase until about 150 years and then decrease (Hall, 2004). Allen (2000) reported a similar pattern of first increasing and then decreasing channel density for English salt marshes, also with peak density at about 150 years for marshes with clay/silt substrate. However, channel density may be more constant in some settings: Marani *et al.* (2003) quantified a power law relationship between total network length and marsh basin area (the ratio of which would equal our channel density index), which was consistent between repeated analysis separated by decades in time, for two salt marshes of the Venice Lagoon. In general, though, the significant positive relationship we identified between channel network complexity and site age is in agreement with previous literature.

In contrast, the causes of sustained channel simplicity are less clear, for those marshes not following this trend (13/48 old marshes in the sample with simple channel geometries). Atwater *et al.* (1979) anecdotally noted that some older marshes exhibited straighter, less meandering channels than the typical old marsh site in the estuary and proposed a relationship between rapid early marsh formation and straight channels, irrespective of present marsh age. Rather than control by the rate of development, we propose that the means of development and the slope of

the developing marsh surface may control channel complexity. We observe that young marshes in the estuary can develop by two means, either aggrading from a mudflat or prograding from an established shoreline. Our anecdotal observations in the estuary agree with published concepts that suggest that relatively flat, aggrading young marshes can inherit the mudflat's intertidal channels, which may be complex because of tidally asymmetric flows and shallow topographic relief (Cornu and Sadro, 2002). New marsh areas that fill in formerly disturbed, subsided or impounded areas can also develop complex (or simple) channel networks depending on topographic and sediment features (D'Alpaos *et al.*, 2007b). In contrast, prograding young marshes (i.e., expanding shorelines) or aggrading locations with steeper slopes (e.g., elongated mud-bars) develop straighter rill-runoff channels. Low, flat, intertidal topography with developing vegetation and a strong tidal oscillation across it can also form straight channels aligned with the direction of tidal flows (Temmerman *et al.*, 2007). Further discussion of types of tidal channel formation is available by Perillo and Iribarne (2003). That both aggradational and progradational mechanisms of young marsh development are prevalent in the San Francisco Bay estuary explains how the proportion of complex versus simple channel patterns in the young marshes of our sample population could be nearly equal (30/65, 46% complex; 35/65, 54% simple).

That a majority of old marsh sites in the sample population exhibited complex channel patterns is to be expected [e.g., according to the "Pethick-Steel-Pye Model" by Pethick (1969) and Steel and Pye (1997), as summarized by Allen (2000)]. The correspondence is explained by their accumulation over time of more numerous perturbations from past tidal actions, relative sea level/subsidence changes, and disturbances, which can cause complex channel branching, looping, and overall variation (Kirwan *et al.*, 2008). However, a large fraction of old sites also exhibited simple channel patterns (13/48, 27%). It is not likely that these old sites escaped the influences that perturbed the majority of the old marshes' channels. Instead, we attribute this result to marshes under some conditions being 'locked in' to their early tidal network structure. Mechanistically, this could occur in part because of reach-scale morphodynamics, whereby bank undercutting, slumping and redevelopment can maintain channels in stable locations over time amid other drivers of change (Gabet, 1998). Vegetation is also known to generally stabilize channels. This conclusion agrees with another anecdotal implication by Atwater *et al.* (1979), that old marshes that initially formed with straight channels may still today exhibit similar straight channels.

Relationship of channel geometry to marsh elevation. That channel pattern complexity was unrelated to marsh elevation contrasted with findings from the multi-elevation experimental manipulation of marsh restoration sites by

Cornu and Sadro (2002), who found that channels were more sinuous and less linear at higher elevation sites compared with low-elevation sites. Although sinuous and straighter ('perpendicular') channels were combined in our 'simple' channel geometry category, both high and low marsh sites within our sample population had very similar proportions of each of the channel pattern classes (Table III).

That sites with no tidal channels occurred almost exclusively at higher site elevations in the estuary (9/10 sites) was consistent with existing literature. Because comparative marsh restorations have shown that channels develop on restored marsh plains placed below, but not at, mean higher high water (Cornu and Sadro, 2002), this suggests that there is not enough hydrodynamic energy very high in the tidal prism to cause notable channelization if not pre-existing. However, none of the nine sites at high-elevation but exhibiting no channels in our sample population was restored; in fact, only the one site with no channels but at a lower site elevation had a site restoration history. This argues for a natural corollary to the experimental manipulation, perhaps that these sites lacking channels may have originally developed to a high elevation so extraordinarily rapidly that channels were unable to become established.

Alternative stable biogeomorphic marsh states

The very strong relationship between vegetation patterns and channel complexity observed in our sample population of marsh sites suggests two key conclusions. It suggests that salt marshes in the San Francisco Bay estuary exhibit at least two alternative, stable biogeomorphic states, represented by *either* complex vegetation-and-channel configurations *or* simple vegetation-and-channel configurations.

That the two states are mutually exclusive alternatives was supported by the statistical analysis. Two of the four marsh states possible in our classification occurred disproportionately often; these were the states of 'complex vegetation pattern with complex channel network configuration' and 'simple vegetation pattern with simple channel network configuration'. The two states 'complex vegetation pattern with simple channel network configuration' and 'simple vegetation pattern with complex channel network configuration' occurred with less frequency than statistically expected. We note that our binary complex/simple method of classifying marsh states was not the cause of the apparently dichotomous result. *A priori* it was also possible that there would be no significant relationship between vegetation patterning and channel complexity (e.g., if there were similar proportions of simple and complex channel networks among both simple and complex vegetation patterns) or that a relationship could have been negative instead of positive. Instead, a strong

positive association between vegetation pattern complexity and channel network complexity was statistically supported. As all the sites shared a common physiography and regional history, the statistical evidence indeed pointed to two mutually exclusive (alternative) states.

That both states are apparently stable is evidenced by the presence of both states among young marshes (aged <165 years) and the persistence of both states among a number of old, even ancient, marsh sites. It is further supported by the statistical independence of marsh vegetation pattern complexity from marsh age, although this does not rule out the possibility that a site might theoretically switch between simple and complex configurational states multiple times in a century or millennium. Pollen records in the San Francisco Bay estuary suggest that some sites may have had stable vegetation composition (although that cannot necessarily represent stable configuration, as noted previously) over multiple millennia, whereas others may be stable over only centuries or decades because of higher frequency salinity changes (Byrne *et al.*, 2001; Malamud-Roam and Ingram, 2004; Watson, 2004). Also, over decades to a century, it seems tidal channel locations at least also remain relatively stable in these estuarine wetlands, despite substantial human influences such as truncation by levees (e.g. Watson, 2004; Hermstad *et al.*, 2009; Moffett *et al.*, 2012). Given the strong statistical link between vegetation and channel configurations, the relative stability of overall channel configurations over time, and the lack of significant association between marsh age and marsh vegetation configuration, we suggest that the preponderance of evidence indeed points to the two alternative marsh states tending to remain stable over time. This is further suggested by past restoration experience in the estuary, which has shown that sites that developed either thorough (>50%) or sparse (<50%) vegetation cover have remained in that state for decades after restoration (Williams and Orr, 2002).

We also suggest more generally that both simple and complex states of vegetation configuration are independently viable and one need not necessarily develop gradually from the other. Although channel complexity tends to develop over time, and occurred in a higher proportion of older marshes, vegetation pattern complexity frequently occurred even in young marshes and was not significantly related to marsh age. It follows from this evidence that channel complexity need not be a prerequisite to vegetation complexity, or vice versa, although both likely co-evolve via biogeomorphic coupling.

As already established, vegetation patterns and channel complexity are apparently influenced by different aspects of a site's characteristics: Channel complexity is related to site age but not salinity, while vegetation pattern complexity is related to salinity but not to site age. That

vegetation and channel complexity are then so strongly related without being jointly controlled by a common site characteristic suggests a causal link between vegetation and channel patterns. We adopt the proposal of Zedler *et al.* (1999) that salt marsh vegetation patterning exhibiting two-dimensional heterogeneity in its organization does so in response to a combination of the effects of microtopography and tidal channels. Sanderson *et al.* (2000) also noted that vegetation buffers (of ~1–15 m width) around tidal channels may have distinct species composition and form a striking element of the overall marsh configuration, lending another mechanism for linking the channel network and vegetation pattern complexity. Vegetation cover heterogeneity, in turn, can promote further channel development (Temmerman *et al.*, 2005, 2007). However, this study did not quantify the disturbance history of the marsh sites; it is likely that a history of disturbance would promote both channel complexity (Kirwan *et al.*, 2008) and a complex patchwork of vegetation recolonizing the disturbed locations.

Whereas the coastal scale state differentiation of marshes, tidal flats and subtidal basins will impose some constraints on the marsh elevation, whether high or low, and interspecific interactions and species-specific stress responses will impose some controls on vegetation zone distribution within the marsh (Figure 6), we propose that the channel network responds at the intermediate scale to both these 'top-down' and 'bottom-up' influences, thereby providing the functional link across scales.

Implications for estuarine wetland futures

This conceptual model, of alternative stable states in tidal marsh biogeomorphic configurations at the marsh scale, has key implications for past and future estuarine wetland dynamics. The historical context and large proportion of high marshes in both old and young age groups in the San Francisco estuary suggests that the observed relationship between marsh age and elevation was not developed because of a large number of formerly low marshes accreting to higher elevations over the last 150 years, but rather because of the maintenance of many old marshes at higher elevations while young marshes accreted to a variety of site-specific elevations, both high and low. The observed correspondence of young low-elevation sites and old high-elevation sites in our data set is therefore likely a transient relationship, albeit representative over perhaps 150 years (~1850–2004). Although a result derived from a particular regional case study, this idea that marshes may not exhibit increasing vegetation pattern complexity with time is a result with general and global theoretical applicability to better understanding our coastal zones.

If this is so more generally, high and low marshes are likely to respond differently to forecasted future changes in

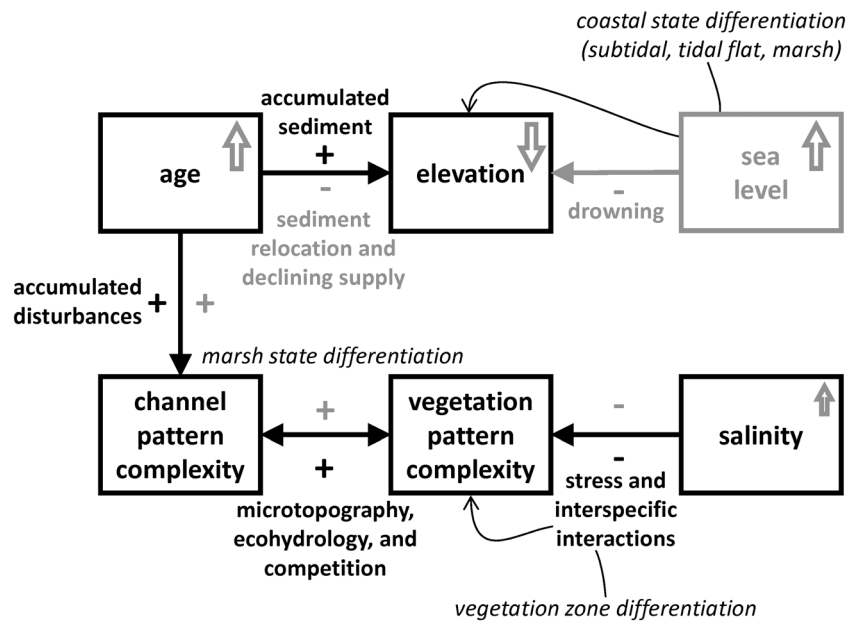


Figure 6. Conceptual model of interactions among marsh site characteristics, in boxes, and vegetation and channel pattern complexity in the San Francisco Bay estuary. Directions of interactions follow solid arrows, with adjacent text indicating type of interaction process and sign of interaction. For example, site age has a positive relationship with greater channel pattern complexity because of accumulation of disturbances over time. Additional influences expected to develop in the future, in gray, include higher sea level, which will drown high marshes, declining sediment supply, relocation of sediments from eroding higher to accreting lower elevations, and possible increases to system salinity from increased aridity and reduced freshwater supply. These changes may shift the estuary toward predominately low-elevation marshes in the future, but those marshes may continue to represent both simple and complex vegetation/channel pattern instances. These site-scale dynamics fit within a broader context of habitat differentiation into multiple stable states at the coastal scale (above) and vegetation zone differentiation into multiple stable states at the sub-site scale (below).

environmental conditions, such as global sea level rise. Like many estuaries of the world, the San Francisco Bay estuary will be subject to future sea level rise, reduced sediment input and reconfiguration of sediment depocenters in the estuary by extensive marsh restoration efforts (Figure 6). The estuary may also increase in salinity in the future, from increased aridity and reduced freshwater supply (Callaway *et al.*, 2007). Old, high-elevation marshes may be lost by drowning, subsidence, or sediment starvation, while new, young, low-elevation marshes may accrete in new depocenters over the next few centuries (Shellenbarger *et al.*, 2013). Given high sediment inputs, mid-elevation marsh areas may expand partly at the expense of high and low-elevation areas; given low sediment inputs, low-elevation marsh areas may expand (and also mid-elevation marshes if sea level rise is slow; Stralberg *et al.*, 2011). Stralberg *et al.* (2011) therefore predict a substantial state shift at the scale of the entire estuary, from the present preponderance of high marshes to an overall preponderance of low-mid marshes. This has likely negative impacts on endangered endemic species such as the California clapper rail (Zhang and Gorelick, 2014).

However, because channel and vegetation complexity were found to be independent of site elevation, there is the potential for sites with complex vegetation and channels and sites with simple vegetation and channels to both

continue to persist as stable states even through these future changes. The conversion of old/high marsh sites to lower elevations and the development of young/low marsh sites in the future would be a considerable change from the present positive relationship between marsh age and elevation in the estuary. Still, the abundant representation of both complex and simple vegetation and channel patterns among today's young marshes suggest that future low-elevation marshes in the estuary will continue to represent both simple and complex biogeomorphic stable states. Because the association between vegetation pattern and channel complexity was stronger for young marshes than for old marshes, it is possible that a reconfiguration of marsh sediments toward more extensive low, young sites might actually strengthen the representation of the two alternative states in the region. Again, although results derived from a particular case study, these trends in climate change, human control of sediment budgets, subsidence and so on are globally distributed influences on coastal wetlands, so these conclusions have global import.

This conceptual model of alternative stable states of biogeomorphic organization at the site scale also has substantial implications for understanding possible restoration trajectories. In the San Francisco Bay estuary, extensive tidal habitat restorations are ongoing (SBSRP, 2015), but identifying reference habitat characteristics to help frame wetland restoration goals is a perpetual

challenge (Kusler and Kentula 1989). The potential for an estuarine marsh site to occupy two alternative stable states may help to explain the difficulty in identifying the trajectory via which a restored or developing marsh site might achieve a comparable state as a reference marsh (Simenstad and Thom, 1996; Callaway, 2005). However, it also suggests that a shift in perspective on the desired 'reference' outcome might help mitigate the problem. Because a marsh occupying one of multiple alternative stable states should tend to remain in its present state, barring massive disturbance or gradually accumulated stress (Rietkerk *et al.*, 2004), this constancy might more quickly allow for mature habitat development if either of the two stable outcomes could be deemed acceptable.

The possibility of alternative stable states seems to suggest that a system that is restoring only slowly, and toward simple vegetation pattern and channel structures, is not necessarily a cause for concern. Such a system is not necessarily fated to have to go through progressively more complex stages of development before becoming mature and stable. This conceptual framework may, however, require re-thinking the presumed correspondence between eco-hydro-geomorphic structure and function in wetlands [e.g., (Cole, 2006)], particularly with regard to functional tidal wetland restoration and compensatory mitigation activities. Restorations undertaken to mitigate negative impacts to wetlands, such as required by the U.S. Clean Water Act, are required to focus on the goal of protecting or restoring wetland 'function' (EPA, 2008, 2010). In practice, however, it is only the structure of a site that can be designed and engineered. Therefore, if damage to a complex marsh site requires compensatory action, it would generally be presumed that an equal area of other complex marsh should be created or restored. Given two equally viable and ecologically equivalent patterns of stable marsh habitat, however, it requires further consideration whether complex marshes must always be replaced by complex marsh area, or not. For example, compensatory restoration of a marsh with simple structure might well achieve most of the habitat value of a formerly complex marsh at a different site, but perhaps be more biogeomorphologically stable in its particular location, and therefore more rapidly achieve the mature marsh function that is the true restoration goal.

CONCLUSION

The results of this study indicate that a shared physiographic setting need not impart relative uniformity in vegetation configuration, channel geometry complexity, or overall marsh organization among spatially proximal tidal marsh sites. Rather, sites sharing a common physiography and general history can exhibit wide variation in vegetation

patterns and channel network complexity. This bears consideration in designing new field studies, and in evaluating prior studies, perhaps warranting increased scrutiny as to which subset of local or global marshes a particular site study can best represent. This also highlights the work yet to be done in modeling states and trajectories of whole tidal ecosystems. The very insightful, zero-dimensional 'point models' of tidal ecosystem states taking on subtidal, tidal flat, or tidal marsh natures (e.g., see Da Lio *et al.*, 2013 and references therein) so far implicitly project the idea that 'a marsh is a marsh'. It seems there is a currently under-studied frontier of investigation at the scale of whole tidal marshes, analysing marsh configurations in two and three dimensions and comparing marsh-to-marsh ecosystem variations. Additional study at this scale may lead to improved understanding of the factors that generate site-to-site structural and functional diversity in tidal marsh environments. This insight would be useful to also better understand the range of healthy ecosystem diversity and plasticity and also of the range of habitat conditions useful to (perhaps endangered) marsh flora and fauna. This largely missing scale of whole-marsh investigation should fit between the maturing practices of modeling unitary coastal-scale ecosystem states (subtidal, tidal flat, tidal marsh) and modeling patch-level vegetation zonation in individual elevation-spanning transects in single marshes (see Da Lio *et al.*, 2013 and references therein).

The results of this study also partly refute the prevalent assumption that younger, lower-elevation marshes have simple vegetation patterns and channel geometries and typically develop toward more complex, older, and higher-elevation marshes. Although the diversity of marsh vegetation *composition* may indeed increase with marsh age and elevation, the evidence from this study suggests that the same is not necessarily true for marsh *configuration*. Marsh biogeomorphic organization is not necessarily dependent on marsh species diversity. Instead, it seems there are multiple common development trajectories among old and young, high and low-elevation marsh sites. Notably, strong associations between complex channel and vegetation patterns and between simple channel and vegetation patterns (but not mixed simple/complex patterns), and abundant representation of these two natures among both old and young marsh sites, suggest a tendency toward two alternative classes of tidal marsh configuration (complex channel and vegetation configuration *or* simple channel and vegetation configuration) that might remain stable over annual to millennial time scales. Although presented here as an hypothesis, the idea of marsh-scale biogeomorphic organization taking on alternative stable states of two-dimensional marsh configuration would neatly explain the occurrence of complex (or simple) vegetation pattern and channel configurations among both young and old sites and lack of a clear

tendency for young/simple sites to necessarily become old/complex sites.

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