

## Article (refereed)

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Moffett, Kevan B.; **Robinson, David A.**; Gorelick, Steven M. 2010 Relationship of salt marsh vegetation zonation to spatial patterns in soil moisture, salinity and topography. *Ecosystems*, 13. 1287-1302. [10.1007/s10021-010-9385-7](https://doi.org/10.1007/s10021-010-9385-7)

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Journal:	Ecosystems
Manuscript ID:	draft
Types:	Original Article
Date Submitted by the Author:	
Complete List of Authors:	Moffett, Kevan; Stanford University, Environmental Earth System Science Robinson, David; University of the West Indies, Food Production Gorelick, Steven; Stanford University, Environmental Earth System Science
Key Words:	pattern, salt marsh, vegetation, zonation, edaphic, wetland, geophysics, ECa, Q-DEMI

Relationship of salt marsh vegetation zonation to  
spatial patterns in soil moisture, salinity and topography

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Author Contributions: DAR, SMG, and KBM conceived of and designed the study. DAR and KBM performed field work and processed the data. KBM and SMG developed the analytical methodology. KBM analyzed the data and wrote the article.

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**ABSTRACT.**

An intertidal San Francisco Bay salt marsh was used to study the spatial relationships between biotic and abiotic ecosystem components: specifically, between vegetation patterns and hydrologic and edaphic variables. Multiple abiotic variables were represented by six metrics: elevation, distance to major tidal channels and to the nearest channel of any size, edaphic conditions during dry and wet circumstances, and the magnitude of tidally-induced changes in soil saturation and salinity. A new approach, quantitative differential electromagnetic induction (Q-DEMI), was developed to obtain the last metric. The approach takes the difference in soil induction from dry to wet conditions and converts that information to quantitative maps of tidally-induced changes in root zone soil water content and salinity. The result is a spatially exhaustive map of edaphic changes throughout the ecosystem. Spatially-distributed data on the six metrics were used to explore two hypotheses. 1) Multiple abiotic variables relevant to vegetation zonation each exhibit different, uncorrelated, spatial patterns throughout an intertidal salt marsh ecosystem. 2) Vegetation zones and habitats of individual plant species are uniquely characterized by different combinations of key metrics. The first hypothesis was supported by observed, uncorrelated spatial variability in the metrics. The second hypothesis was supported by binary logistic regression models that identified key vegetation zone and species habitat characteristics from among the six metrics. Based on results from 108 models, the Q-DEMI map of saturation and salinity change was the most useful metric for distinguishing different vegetation zones and species habitats in the salt marsh.

**KEYWORDS**

pattern, salt marsh, vegetation, zonation, edaphic, wetland, geophysics, ECa, Q-DEMI

1 INTRODUCTION

2       The segregation of a few dominant plant species into distinctive zones is characteristic of  
3 intertidal salt marshes. Each zone comprises a distinctive macrophyte assemblage and may also  
4 uniquely sustain other species of concern. For example, stands of native *Spartina foliosa* densely  
5 dissected by tidal channels San Francisco Bay support endangered *Rallus longirostris obsoletus*  
6 (California Clapper Rails), but endangered *Reithrodontomys raviventris* (Salt Marsh Harvest  
7 Mice) favor largely monospecific and undissected *Salicornia virginica* flats (USFW 2008). The  
8 nature and causes of this ecologically important vegetation zonation have been studied for  
9 decades with gradient analyses and paired plot, mesocosm, or transplant studies. Such studies  
10 have determined that the causes of salt marsh vegetation zonation are both physical, determined  
11 in part by variability in soil (edaphic) and tidal conditions (Pennings and others 2005), and  
12 biological, the result of interspecific resource competition and biological response to periodic  
13 disturbance (Bertness and others 1992; Emery and others 2001; Pennings and Callaway 1992),  
14 even as the specific patterns and species vary regionally (Peterson and others 2008).

15       At the ecosystem scale, it remains a challenge to explain salt marsh vegetation patterning  
16 despite knowledge of specific zonation mechanisms at the plant scale. Characterization of the  
17 spatial variability of vegetation within salt marsh ecosystems has thus far relied heavily on  
18 metrics of relative landscape position such as elevation and distance to tidal channels; however,  
19 these geographic metrics, alone, have been insufficient predictors of salt-marsh vegetation zones  
20 (Zedler and others 1999, Silvestri and others 2005). Although remote sensing has been used to  
21 map spatial patterns of tidal channels (e.g., Marani and others 2006) and marsh surface  
22 elevations (e.g., Sadro and others 2007) in relation to salt marsh vegetation, such maps are highly  
23 nonspecific, failing to distinguish unique and consistent salt marsh vegetation habitat

Figure 2 consists of two panels. Panel (a) shows a map of a salt marsh with various zones labeled. Panel (b) shows a bar chart of the percentage of the marsh area covered by each zone. The zones are: 1. High marsh, 2. Intermediate marsh, 3. Low marsh, 4. Submerged, 5. Open water, 6. Shrub, 7. Grass, 8. Forage, 9. Sediment, 10. Sand, 11. Mud, 12. Silt, 13. Clay, 14. Shell, 15. Organic, 16. Inorganic, 17. Sand, 18. Mud, 19. Silt, 20. Clay, 21. Shell, 22. Organic, 23. Inorganic, 24. Sand, 25. Mud, 26. Silt, 27. Clay, 28. Shell, 29. Organic, 30. Inorganic, 31. Sand, 32. Mud, 33. Silt, 34. Clay, 35. Shell, 36. Organic, 37. Inorganic, 38. Sand, 39. Mud, 40. Silt, 41. Clay, 42. Shell, 43. Organic, 44. Inorganic, 45. Sand, 46. Mud, 47. Silt, 48. Clay, 49. Shell, 50. Organic, 51. Inorganic, 52. Sand, 53. Mud, 54. Silt, 55. Clay, 56. Shell, 57. Organic, 58. Inorganic, 59. Sand, 60. Mud, 61. Silt, 62. Clay, 63. Shell, 64. Organic, 65. Inorganic, 66. Sand, 67. Mud, 68. Silt, 69. Clay, 70. 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Sand, 1355. Mud, 1356. Silt, 1357. Clay, 1358. Shell, 1359. Organic, 1360. Inorganic, 1361. Sand, 1362. Mud, 1363. Silt, 1364. Clay, 1365. Shell, 1366. Organic, 1367. Inorganic, 1368. Sand, 1369. Mud, 1370. Silt, 1371. Clay, 1372. Shell, 1373. Organic, 1374. Inorganic, 1375. Sand, 1376. Mud, 1377. Silt, 1378. Clay, 1379. Shell, 1380. Organic, 1381. Inorganic, 1382. Sand, 1383. Mud, 1384. Silt, 1385. Clay, 1386. Shell, 1387. Organic, 1388. Inorganic, 1389. Sand, 1390. Mud, 1391. Silt, 1392. Clay, 1393. Shell, 1394. Organic, 1395. Inorganic, 1396. Sand, 1397. Mud, 1398. Silt, 1399. Clay, 1400. Shell, 1401. Organic, 1402. Inorganic, 1403. Sand, 1404. Mud, 1405. Silt, 1406. Clay, 1407. Shell, 1408. Organic, 1409. Inorganic, 1410. Sand, 1411. Mud, 1412. Silt, 1413. Clay, 1414. Shell, 1415. Organic, 1416. Inorganic, 1417. Sand, 1418. Mud, 1419. Silt, 1420. Clay, 1421. Shell, 1422. Organic, 1423. Inorganic, 1424. Sand, 1425. Mud, 1426. Silt, 1427. Clay, 1428. Shell, 1429. Organic, 1430. Inorganic, 1431. Sand, 1432. Mud, 1433. Silt, 1434. Clay, 1435. Shell, 1436. Organic, 1437. Inorganic, 1438. Sand, 1439. Mud, 1440. Silt, 1441. Clay, 1442. Shell, 1443. Organic, 1444. Inorganic, 1445. Sand, 1446. Mud, 1447. Silt, 1448. Clay, 1449. Shell, 1450. Organic, 1451. Inorganic, 1452. Sand, 1453. Mud, 1454. Silt, 1455. Clay, 1456. Shell, 1457. Organic, 1458. Inorganic, 1459. Sand, 1460. Mud, 1461. Silt, 1462. Clay, 1463. Shell, 1464. Organic, 1465. Inorganic, 1466. Sand, 1467. Mud, 1468. Silt, 1469. Clay, 1470. Shell, 1471. Organic, 1472. Inorganic, 1473. Sand, 1474. Mud, 1475. Silt, 1476. Clay, 1477. Shell, 1478. Organic, 1479. Inorganic, 1480. Sand, 1481. Mud, 1482. Silt, 1483. Clay, 1484. Shell, 1485. Organic, 1486. Inorganic, 1487. Sand, 1488. Mud, 1489. Silt, 1490. Clay, 1491. Shell, 1492. Organic, 1493. Inorganic, 1494. Sand, 1495. Mud, 1496. Silt, 1497. Clay, 1498. Shell, 1499. Organic, 1500. Inorganic, 1501. Sand, 1502. Mud, 1503. Silt, 1504. Clay, 1505. Shell, 1506. Organic, 1507. Inorganic, 1508. Sand, 1509. Mud, 1510. Silt, 1511. Clay, 1512. Shell, 1513. Organic, 1514. Inorganic, 1515. Sand, 1516. Mud, 1517. Silt, 1518. Clay, 1519. Shell, 1520. Organic, 1521. Inorganic, 1522. Sand, 1523. Mud, 1524. Silt, 1525. Clay, 1526. Shell, 1527. Organic, 1528. Inorganic, 1529. Sand, 1530. Mud, 1531. Silt, 1532. Clay, 1533. Shell, 1534. Organic, 1535. Inorganic, 1536. Sand, 1537. Mud, 1538. Silt, 1539. Clay, 1540. Shell, 1541. Organic, 1542. Inorganic, 1543. Sand, 1544. Mud, 1545. Silt, 1546. Clay, 1547. Shell, 1548. Organic, 1549. Inorganic, 1550. Sand, 1551. Mud, 1552. Silt, 1553. Clay, 1554. Shell, 1555. Organic, 1556. Inorganic, 1557. Sand, 1558. Mud, 1559. Silt, 1560. Clay, 1561. Shell, 1562. Organic, 1563. Inorganic, 1564. Sand, 1565. Mud, 1566. Silt, 1567. Clay, 1568. Shell, 1569. Organic, 1570. Inorganic, 1571. Sand, 1572. Mud, 1573. Silt, 1574. Clay, 1575. Shell, 1576. Organic, 1577. Inorganic, 1578. Sand, 1579. Mud, 1580. Silt, 1581. Clay, 1582. 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zonation. Elevation is commonly employed to represent the effects of flood/exposure duration and surface water ponding. A location's distance to the nearest tidal channel represents the likely direction of tidal flooding and groundwater drainage and directional tidal energy effects (e.g., sediment deposition). This study uniquely considered both distances to primary tidal channels, typically identified from aerial imagery, and distances to small (~0.1 – 0.5 cm wide, rarely mapped) surface drainage pathways hidden beneath the vegetation that we term microtributaries.

The remaining three metrics reflected soil properties under different hydrologic conditions (dry and wet marsh soils) and the magnitude of change between conditions. The soil properties considered, soil saturation, salinity, and texture, are known to contribute to salt marsh zonation (Silvestri and others 2005) but previously could only be measured at points, prohibiting extensive repeat sampling and marsh-wide analysis. Geophysical electromagnetic induction (EMI) imaging of bulk apparent soil electrical conductivity (ECa) captures the combined state of soil saturation, salinity, and texture in one ECa number (Friedman 2005, Rhoades and others 1999) and can be surveyed quickly over a large area. EMI has been used to investigate patterns in soil properties (e.g., Lesch and others 2005, Robinson and others 2009) but its potential to provide new insight into ecosystem patterning is only beginning to be explored (Stroh and others 2001, Robinson and others 2008). Prior to this study the method had not been tested in an environment with as extremely high soil water, salt, and clay contents as in salt marshes. To further the applicability of EMI to salt marsh vegetation analysis, we developed a method to filter out the effects of the soil clay content on the ECa data and leverage the information on changes in soil saturation and salinity from sequential EMI surveys. Our approach was to subtract the data from two EMI surveys (differential or time-lapse EMI; Lesch and others 2005, Robinson and others 2009) and then convert the ECa difference values ( $\Delta$ ECa) to quantitative

607 estimates of soil water content and salinity change using Archie's Law (Quantitative Differential  
EMI, or Q-DEMI). Our Q-DEMI methodology quantified tidally-induced saturation and salinity  
changes in the salt marsh root zone and enabled assessment of their spatial relationship to  
vegetation zonation throughout a marsh in unprecedented detail.

To explore the second hypothesis, that each salt marsh plant species might bear a different  
relationship to a suite of relevant variables, we sought to isolate distinguishing characteristics of  
each of the major vegetation zones and individual species habitats composing the salt marsh  
ecosystem. We used logistic regression modeling to assess the correlation between vegetation  
patterns and the six geographic and edaphic metrics. The geophysical data on salt marsh edaphic  
conditions provided greater insight into the underlying abiotic characteristics of the vegetation  
patterns than was gained from the geographic metrics alone. In particular, spatial variability in  
tidally-induced changes in soil water content and salinity, reflected in the Q-DEMI  
 $\Delta ECa$  metric, were the most effective means of distinguishing vegetation zones and habitats.

Multiple variables combine to support ecosystem structures, functions, habitat  
heterogeneity, integrity, and supply of ecosystem services of salt marshes (Turner and Chapin  
2005, Peterson and others 2008), but these variables are seldom analyzed in a spatially-  
distributed manner. With this study we aimed to better understand how the effects of multiple  
abiotic variables combine into something more than the sum of the parts, a spatially-variable  
abiotic template upon which salt marsh vegetation patterns and biotic interactions are expressed.  
A system-level perspective that integrates both abiotic and biotic variables may help inform the  
maintenance and restoration of coastal wetlands, a matter of increasing interest worldwide amid  
concerns of sea level rise, increased storm activity, and coastal development pressure (Peterson  
and others 2008).



93 MATERIALS AND METHODS

94 Field Site and Hydrology

95       The study site was a 0.9 ha intertidal salt marsh in southern San Francisco Bay, within the  
96 Palo Alto Baylands Nature Preserve (37°27'54" N, 122°6'58" W). The geological and botanical  
97 history of the surrounding Santa Clara Valley were described by Cooper (1926) and the geology  
98 underlying the Palo Alto Baylands by Hamlin (1983). The history and character of the marsh  
99 were similar to that described by Hinde (1954) for the adjacent marsh to the south. The  
100 underlying site stratigraphy consisted of 3-5 meters of fine estuarine mud, predominantly  
101 montmorillonite clay, overlying a saline aquifer system (Hamlin 1983).

102 Vegetation Mapping

103       Plant species at the site were: *Spartina foliosa*, *Salicornia virginica* (*S. depressa*),  
104 *Distichlis spicata*, *Jaumea carnosa*, *Grindelia stricta*, *Frankenia salina*, *Salsola soda*, and  
105 *Atriplex prostrata* (see USDA (2009) for synonymous species names). The habitat occupied by  
106 each species was mapped by: marking the boundaries of assemblages distinguished by the  
107 presence/absence of each of the species, digitizing these polygonal boundaries using streaming  
108 GPS, and identifying the relative abundance of each species within each polygon. This method  
109 was similar to that of Zedler and others (1999) for San Diego Bay marshes, but with greater  
110 emphasis on identifying the locations of assemblage boundaries. Surveys of species' percent  
111 cover within 1-m<sup>2</sup> quadrats verified assemblage composition at 69 locations. The 57/134  
112 assemblage polygons verified by one or more quadrats accounted for 81% of the marsh area.

113       Vegetation zones were classified by the species of greatest (dominant) cover fraction in  
114 each assemblage polygon. The quadrat surveys confirmed that this was a sufficient means of  
115 identifying vegetation zones since assemblage composition within each zone defined in this

Figure 2 was consistent. In addition to the spatial distribution of major vegetation zones, in this study we were interested in the full range of conditions among which each plant species grew. We refer to a plant species' habitat as all the areas the species occupied regardless of cover density. In our vegetation discrimination analysis we assessed the salient characteristics of zones and species habitats separately and compared the results.

#### Mapping Edaphic Conditions

A logical precursor to understanding salt marsh vegetation distribution is a three-dimensional description of root zone edaphic conditions throughout the ecosystem, but obtaining spatially-extensive data on relevant physical and chemical soil properties has been intractable with point-sampling methods. The combination of heterogeneous soil water content, salinity, and clay fraction was captured in this study by maps of bulk soil electrical conductivity (ECa). The ECa data were obtained on two separate days by repeatedly traversing the field site carrying a streaming EMI instrument (DUALEM-1S, Dualem, Inc., Milton, ON, Canada) and GPS, logged concurrently. Sequential traverses were separated to account for the ~4 m<sup>2</sup> EMI measurement support area. We estimated the vertical soil interval represented by the ECa data was 0-0.40 m depth (see online supplement), approximately the depth of the salt marsh root zone. We post-processed ~5000 ECa measurements per survey (Robinson and others 2008) and corrected for effects of soil temperature (Reedy and Scanlon 2003) to produce kriged ECa maps at 2-m resolution. Successive measurements of ECa at test locations agreed to within 0.01 dS/m, which we take to be the ECa uncertainty, though the EMI instrument accuracy was 0.001 dS/m.

The two EMI surveys were timed to capture different hydrologic conditions. The first survey occurred just prior to the neap-spring tidal transition, when the marsh had not been flooded in eight days (Nov. 19, 2007); we refer to these as data from "dry" marsh conditions.

The second survey was partially into the next spring tide cycle, immediately following a flood tide (Dec. 7); we refer to these as data from “wet” marsh conditions. We use the terms “dry” and “wet” as qualitatively convenient reminders of antecedent tidal conditions although both circumstances represent very moist soils (>80% saturation). Both survey times were near mid-day and no rain occurred while the marsh surface was exposed during the study period.

The field site experiences mixed semi-diurnal tides and a semi-arid Mediterranean climate with winter precipitation (~39 cm/yr). The marsh plain is above mean high water and is flooded by the higher high tide on  $\frac{2}{3}$  -  $\frac{3}{4}$  of days during each spring-neap cycle. To verify ambient hydrologic conditions, we monitored groundwater and tidal conditions at the site by logging pressure and temperature every 10 minutes at the bed of the two primary tidal channels and in 43 wells and piezometers installed 0.5 to 1.0 m into the marsh substrate. We monitored hydraulic heads in the root zone with 23 tensiometer pairs spanning 10-15 and 20-25 cm depths. Tensiometer data were collected manually during the geophysical surveys.

Empirical relationships have shown ECa to increase with increasing soil clay content, water content ( $\theta$ ), or solution electrical conductivity (ECw) (e.g., Rhoades and others, 1999), though not for as high values as occur in salt marshes. We conducted laboratory analyses to establish the specific relationships between ECa and salt marsh soil properties. Twenty-three soil sampling locations were strategically chosen using the ECa data from the first survey and response-surface directed sampling (Corwin and Lesch 2005, Lesch 2005). After collecting ECa data at each location, soil cores (2.5 cm diameter) were collected manually from 0-30cm and 30-60cm depth. The 0-30 cm depth interval was chosen to correspond roughly to the EMI signal depth, enabling correlation with ECa survey data. The 30-60 cm deep samples were used in parameterizing the Q-DEMI methodology, discussed below. The cores were immediately sealed

1627 in plastic bags and promptly weighed in the laboratory. Samples were air-dried for 11-28 days,  
 163 homogenized subsamples weighed, oven-dried at 105°C for at least 12 hours and re-weighed,  
 164 and core water fractions and bulk densities calculated. Duplicate homogenized subsamples were  
 165 analyzed for soil paste extract electrical conductivity (ECe) and soil texture (University of Idaho  
 166 Pedology Laboratory standard procedures). Pore water samples extracted adjacent to the coring  
 167 locations from 30 cm depth using a suction lysimeter (“sipper”,  $\sim \leq 5$  kPa suction) were analyzed  
 168 in the laboratory for pore water electrical conductivity (ECw).

#### 169 Quantitative Differential EMI Methodology

170 Each geophysical survey provided a snapshot of the combination of water, salt, and clay  
 171 conditions throughout the salt marsh at one point in time. We developed a method to transform  
 172 the difference in ECa between dry and wet tidal conditions into spatially-distributed, quantitative  
 173 estimates of changes in root zone soil water content and salinity. The premise of the Q-DEMI  
 174 method was that a change in the ECa value of a location was due to changing soil water content  
 175 and salinity while clay content remained constant. In our Q-DEMI analysis, we subtracted the  
 176 later “wet” ECa data from the earlier “dry” ECa data, simulating a case of increasing soil  
 177 moisture ( $\Delta ECa = ECa_{dry} - ECa_{wet}$ ). We then determined the nature of the edaphic change,  
 178 whether caused by changing soil water content or by changing soil salinity, from the sign of  
 179  $\Delta ECa$ . An observed increase in ECa between dry and wet conditions ( $-\Delta ECa$ ) indicated an  
 180 increase in soil water content: an increase in salt content could not explain the change in these  
 181 areas because tidal waters were known a priori to be less saline (33.4 dS/m) than the marsh pore  
 182 waters ( $ECw \approx 57.2$  dS/m) to which they were added in order to wet-up the marsh. In contrast,  
 183 an observed decrease in ECa ( $+\Delta ECa$ ) indicated a decrease in pore water salinity: under  
 184 conditions of increasing tidal water availability, water content would remain constant or increase

and so could not explain the ECa change in these areas. Because saturation and salinity changes could occur simultaneously with opposing effects, the Q-DEMI calculations represent the conservative case in which all ECa change is ascribed to the dominant process, identified by the sign of  $\Delta ECa$ .

Quantifying saturation and salinity changes was accomplished using Archie's Law in our Q-DEMI methodology. Archie's Law is a well-studied geophysical relationship between ECa and: pore water conductivity ( $EC_w$ ), a formation factor ( $f$ ) related to porosity, the soil saturation ( $S$ ), and the soil mineral surface conductivity due to adsorbed ionic charge ( $\sigma_s$ ) (Kirsch 2006).

$$ECa = EC_w \cdot f \cdot S^2 + \sigma_s \quad (\text{Eqn. 1})$$

The mineral surface conductivity ( $\sigma_s$ ) is important in soils with large clay fractions, such as in our salt marsh, but has not been tabulated for salt marsh clay soils. We estimated  $f$  and  $\sigma_s$  using a simple linear regression between ECa and pore water conductivity ( $EC_w$ ) for saturated samples ( $S = 1$ ). The samples used for this regression were from 30-60 cm depth since these samples were known to be from the saturated zone below the water table. The resulting  $f$  and  $\sigma_s$  parameter estimates compared favorably with estimates from more complicated methods (see online supplement). These parameters permitted Q-DEMI calculation of changes in saturation, due to aerated pore space being filled by tidal waters, and changes in salinity, due to flushing of salt marsh soils, using variations on Archie's Law.

In the saturation-change dominated ( $-\Delta ECa$ ) areas of the marsh we solved Archie's Law (Eqn. 1) for the net soil water content change required to account for the observed increase in ECa between dry and wet marsh conditions. To reduce one excess degree of freedom in the calculation we assumed that initially aerated pore space in the soil was completely filled by the flood tide, leading to a minimum estimate of soil saturation change since the effect of any

Figure 2a would have reduced the magnitude of  $\Delta ECa$ . The formula we derived to calculate saturation change ( $\Delta S$ ) is shown below (Eqn. 2). The parameters are the: formation factor ( $f$ ), mineral surface conductivity ( $\sigma_s$ ), tidal flood water electrical conductivity ( $EC_{\text{tide}}$ ), and  $ECa$  during wet ( $ECa_{\text{wet}}$ ) and dry ( $ECa_{\text{dry}}$ ) conditions.

$$\Delta S = \frac{-\left(\sigma_s - ECa_{\text{wet}} - f \cdot EC_{\text{tide}}\right) - \sqrt{\left(\sigma_s - ECa_{\text{wet}} - f \cdot EC_{\text{tide}}\right)^2 - 4 \cdot \left(f \cdot EC_{\text{tide}}\right) \cdot \left(ECa_{\text{wet}} - ECa_{\text{dry}}\right)}}{2 \cdot \left(f \cdot EC_{\text{tide}}\right)} \quad (\text{Eqn. 2})$$

The real solution to Eqn. 2 using a positive discriminant root yielded unrealistic  $\Delta S$  values greater-than one, so was discarded.

In the salinity-change dominated ( $+\Delta ECa$ ) areas of the marsh we solved Archie's Law (Eqn. 1) for the pore water electrical conductivity ( $ECw$ ) under dry and wet marsh conditions. We then used the seawater equation of state to convert each  $ECw$  value to a salinity value. Subtracting the salinity values yielded the change in salinity required to account for the observed decrease in  $ECa$  between dry and wet marsh conditions. To reduce one excess degree of freedom in the calculation we assumed that these areas of the marsh remained water-saturated, leading to a minimum estimate of salinity change since the effect of any concurrent increase in soil water content would have reduced the magnitude of  $\Delta ECa$ . (Field observations suggested that these areas of the marsh did remain saturated throughout dry and wet marsh conditions.)

In addition to the two maps of  $ECa$ , from dry and wet marsh conditions, the map of saturation and salinity changes produced by the Q-DEMI methodology provided a third spatially-distributed metric of salt marsh root zone characteristics against which to compare salt marsh vegetation zonation.

### Mapping Marsh Geometry

Geometric measures of spatial context within the ecosystem have traditionally been employed as indicators of salt marsh ecosystem structure and spatially-variable intertidal

hydrologic effects. The most common such geographic, or “landscape position” (Zedler and others 1999), metrics are elevation and distance-to-channel. We mapped these metrics at the same high resolution as our edaphic data sets. We represented marsh plain topography by a 2-m horizontal resolution kriged map of 742 marsh plain surface elevations surveyed using a total station, verified against LIDAR data. Major tidal channels are typically identified from aerial imagery, but we could find no precedent for mapping the small, connected surficial drainage pathways hidden under the vegetation canopy (“microtributaries”). We identified the banks of major tidal channels and microtributaries by traversing them with a streaming GPS (20-cm post-processed horizontal accuracy). Two distance-to-channel metrics were calculated as the shortest straight-line distances from the center of each elevation grid cell to: 1) the nearest of the two primary tidal channels (bounding and bisecting the study area, Figure 1); 2) the nearest channel of any size.

Statistical Vegetation Differentiation

To contrast the utility of the six metrics described above in differentiating vegetation zones and plant species habitats, we employed binary logistic regression (BLR) models (SPSS 2009). A logistic regression is analogous to a linear regression but with a categorical, instead of continuous, dependent variable. By comparing the vegetation at each location in the marsh to the collocated values of the six metrics and repeating this for all marsh locations, the BLR method built models of those combinations of the six metrics that best distinguished the selected vegetation zone or habitat type. BLR models were assessed at the 95% confidence level.

We tested 108 BLR models, including univariate and multivariate analyses for each vegetation zone and species habitat. In the univariate cases we assessed whether any of the six metrics, alone, could correctly differentiate the marsh areas inside and outside each of the six



Major vegetation zones (6 metrics x 6 zones = 36 zone models). We also tested whether any of the six metrics, alone, could correctly differentiate the marsh areas occupied or not occupied by each species, regardless of its cover density (6 metrics x 6 species = 36 habitat models). These models served to test the univariate predictive capacity of each of the six metrics in relation to vegetation patterning at our site. For these models, the two-fold null hypothesis in each case was either 100% or 0% cover by the selected zone or species.

In the multivariate analyses, we built forward-conditional BLR models for each vegetation zone and species habitat. This approach tested whether a combination of multiple metrics could better identify the distinguishing characteristics of each zone and habitat than a single metric. We tested three metric combinations: 1) the three geographic metrics, 2) the three edaphic metrics, 3) all six metrics, for total of 36 multivariate models (3 combinations x (6 zones + 6 habitats) = 36 models). The forward-conditional BLR method selected only those metrics that significantly contributed to the zone or habitat prediction at the 95% confidence level. For these models, the two-fold null hypothesis in each case was either 100% or 0% cover by the selected zone or species. The results of the BLR models revealed the key characteristics distinguishing each habitat envelope and zone at our site.

## RESULTS

### Vegetation Patterns and Marsh Geometry

The spatial distribution of vegetation zones at the site is shown in Figure 1a, with zones labeled by the genus of the dominant species. Quadrat surveys verified that species identified as zone dominants occupied a majority ( $59\% \pm 16\%$ ) of the zone's cover. Zones dominated by the succulent *Salicornia* (28% of total marsh area) and the grasses *Spartina* (19%) and *Distichlis* (47%) were most prominent at the site, with smaller areas dominated by *Jaumea* (4%),



*Salt marsh spatial patterns and zonation*

Frankenia (1%), and Grindelia (2%). Salsola and Atriplex individuals were present in only a few locations. The thick black outlines in Figure 1a highlight the three major vegetation zones, dominated by Spartina, Distichlis, and Salicornia. Zone assemblage compositions are illustrated by maps of relative cover density for each species (see appendix Figure A1), which were used to assess the total habitat occupied by each species.

The elevation ranges ( $\mu \pm 1\sigma$  m above mean sea level) spanned by the species were not distinct: Distichlis,  $1.04 \pm 0.04$ ; Salicornia,  $1.03 \pm 0.05$ ; Spartina,  $1.00 \pm 0.06$ ; Jaumea,  $1.03 \pm 0.05$ ; Frankenia,  $1.03 \pm 0.03$ ; Grindelia,  $1.04 \pm 0.03$ . Overlap between the elevation ranges of key species is common in salt marshes despite their characteristically distinct vegetation zonation (Silvestri and others 2005, Sadro and others 2007). The average marsh plain elevation from the kriged topographic data was  $1.02 \pm 0.06$  m above mean sea level (m aMSL) and ranged from 0.61 to 1.32 m. The seeming visual correlation between areas of slightly lower elevation and the southern, Spartina-dominated zone (Figure 1b) was not statistically supported because those same elevations elsewhere in the marsh were dominated by different species. Employed in univariate BLR models, elevation failed to justify rejecting the null hypothesis for any of the vegetation zones or species habitats at our site.

Qualitative assessment of marsh locations' distance to primary tidal channels showed the major zones dominated by Spartina, Distichlis, and Salicornia to each occur at any distance from the major tidal channels that bound and bisect the marsh (Figure 2a). The Spartina-dominated zone appeared to coincide with a region of dense microtributaries (Figure 2b), yet neither distance-to-channel metric warranted rejecting the univariate BLR models' null hypothesis for any of the vegetation zones or species habitats.

Edaphic Conditions and Vegetation

The spatial structure of edaphic conditions throughout the marsh, and the magnitude of ECa values reflecting these conditions, remained consistent between the dry (Figure 3a) and wet (Figure 3b) surveys. Mean ECa values for the two surveys were 13.37 and 13.71 dS/m, respectively (2.05 dS/m standard deviations; correlation coefficient  $r = 0.83$ ). Tensiometer data confirmed that the root zone was drier during the first, “dry” geophysical survey than during the second, “wet” survey. Tides rapidly and uniformly covered the marsh to a depth of 0.5 m during spring tide flooding events between the surveys. The specific relationships between ECa values and edaphic conditions (soil solution and paste extract conductivities and water and clay contents) determined for this salt marsh are presented in the appendix.

The configuration of vegetation zones (Figure 1a) did not resemble the spatial pattern of edaphic conditions (Figure 3). Instead, interior marsh areas that exhibited persistent high soil water content and/or salinity (high ECa) appeared coincident with major zone boundaries. A phenomenon of stressful edaphic conditions and major zone boundaries occurring in the same location was described for *Spartina* and *Salicornia* in northern San Francisco Bay salt marshes by Mahall and Park (1976a) but had not been illustrated in two dimensions; our result is consistent with this explanation of ecotone locations. Though not consistently correlated with any vegetation zone or elevation, the edaphic variability in the marsh was significantly related to the hydrologic processes represented by the distance-to-channel metrics ( $r = 0.36$  to  $0.54$ ). Low soil saturation and/or salinity (low ECa) occurred close to tidal channels and more stressful edaphic conditions (high ECa) occurred further from the channels. Neither ECa data set provided information sufficient to reject the null hypothesis of the univariate BLR models.

The spatial pattern of tidally-induced changes in edaphic conditions revealed by subtracting the wet and dry ECa surveys ( $\Delta$ ECa, Figure 4a) was more heterogeneous than the

spatial variability in static edaphic conditions (Figure 3). The pattern of change was not altered by the Q-DEMI calculations, which converted  $\Delta\text{ECa}$  values to soil saturation and salinity change quantities (Figure 4b). The conversion was made using values of  $f = 0.223$  and  $\sigma_s = 2.479$  dS/m. The average estimated saturation change in the fluid-exchange dominated areas of the marsh (blue in Figure 4b) was  $6.2 \pm 5.5$  % ( $\mu \pm 1\sigma$ ). The average estimated salt loss from the salt-exchange dominated areas of the marsh (red in Figure 4b) was  $0.77 \pm 0.64$  kg/m<sup>2</sup>. The large standard deviations of these average results were due to highly heterogeneous soil aeration and flushing throughout the marsh. Despite the Q-DEMI methodology producing conservative estimates of the magnitude of edaphic change, we emphasize that the methodology permits mapping the magnitude of salt and water exchange in a spatially-distributed way throughout an ecosystem for the first time.

Spatial patterns of saturation and salinity change did not qualitatively resemble vegetation zonation (Figures 1a, 4b), yet BLR models based on  $\Delta\text{ECa}$  were able to partially describe the zones dominated by every species except *Distichlis*. For the *Salicornia*-, *Spartina*-, *Jaumea*-, *Frankenia*-, and *Grindelia*-dominated zones, the BLR models correctly distinguished 22-44 % of the area inside each zone and 63-67% of the area outside each zone. Though short of the ideal prediction (100% correct both inside and outside each zone), these results using the  $\Delta\text{ECa}$  metric were a substantial improvement over the null hypothesis returned by the models based on the other five metrics.

$\Delta\text{ECa}$  BLR models were more successful at distinguishing between marsh areas occupied and not occupied by each of the six plant species, regardless of cover density (appendix Figure A1).  $\Delta\text{ECa}$  BLR habitat models correctly identified 64% of the observed *Distichlis* and *Salicornia* occurrences and 37% and 44% of observed absences, respectively.  $\Delta\text{ECa}$  BLR

Models for *Spartina* and *Jaumea* habitat correctly predicted 70% and 73% of the observed occurrences and 41% and 46% of observed absences, respectively.  $\Delta$ ECa BLR models for *Frankenia* and *Grindelia* were less successful at correctly predicting occurrences of these species (28% and 23%, respectively) but more successful at correctly predicting absences (63% and 60%, respectively). For all six species, the  $\Delta$ ECa BLR habitat models justified rejecting the null hypotheses (95% confidence).

The patterns in edaphic conditions and geographic metrics of salt marsh structure support our two hypotheses regarding the spatial nature of zonation-relevant variables and their relationship to salt marsh vegetation distribution. 1) Multiple metrics relevant to salt marsh vegetation zonation each exhibit different patterns. These patterns are characterized by different spatial scales and degrees of spatial heterogeneity. 2) Alone, only the  $\Delta$ ECa metric provided information useful in identifying vegetation zones and species habitats. The relation of the  $\Delta$ ECa metric to vegetation differed depending on the species considered and whether the species was considered alone or as a zone-dominant.

#### Multivariate Vegetation Zone and Habitat Discrimination

We hypothesized that a combination of multiple metrics might better discriminate salt marsh vegetation zones and individual species habitats than univariate models. The metric combinations we tested using forward-conditional BLR models were: 1) the three geographic metrics, 2) the three edaphic metrics, and 3) all six metrics. Salient results are presented here; complete BLR model results are provided in the online supplement.

Except in the case of the *Distichlis*-dominated zone, none of the multivariate models identified vegetation zones or habitats significantly better than the univariate  $\Delta$ ECa BLR models. For the *Distichlis*-dominated zone, a BLR model including all three geographic metrics correctly

predicted 45% of the marsh area within the zone and 72% of the area outside the zone, compared to the null hypothesis returned by the univariate  $\Delta ECa$  BLR model. This result suggests that *Distichlis* may be reliant on the hydrologic marsh processes implicit in the elevation and distance-to-channel metrics to maintain a dominant cover fraction. In contrast, the dominance of the other five major species at the site may be related to the magnitude of temporal variation in root zone soil water content and soil salinity, represented by the  $\Delta ECa$  metric. For example,  $\Delta ECa$  was the only significant predictor of the marsh areas that *Jaumea* occupied, whether it was the dominant cover fraction or not, even when the other five metrics were made available to the forward-conditional model. However, a BLR model based on  $\Delta ECa$  correctly predicted 73% of *Jaumea* occurrences in the salt marsh but only 32% of *Jaumea*-dominated zones. The difference between the zone and habitat models suggest that the tidally-induced changes in root zone water and salt content represented by the  $\Delta ECa$  metric may affect the growth and interspecific interactions of a species within a vegetation assemblage differently than the growth and survival of individual plants of that species throughout the marsh.

DISCUSSION

Vegetation Zonation

Our use of geophysical EMI technology was motivated by the inherent spatial limitations of transect- and plot-based methods of investigating in situ salt marsh vegetation patterning. Logistic regression models based on extensive two-dimensional data identified major characteristics that distinguished the vegetation zones and species habitats at our site. The detail of our regression models, based on over 2000 data points, makes it striking that some zones and species habitats were uniquely identified by a combination of multiple variables (e.g., *Distichlis*) but others were best identified by a single variable (e.g., *Jaumea*). It is also significant that there

Figure 2b. Figure 2b shows a large difference in the ability of the models to describe the key characteristics of the total habitat envelope of a species versus the zone for which it provided the dominant cover class. Existing theory suggests that the survival of individual salt marsh plants may be strongly affected by environmental conditions but that the growth rate and relative cover of a species may be more strongly affected by interspecific interactions with its neighbors (e.g., Emery and others, 2001). This hypothesis seems to be supported by the greater success with which our regression models, based on metrics of abiotic ecosystem variability, were able to identify characteristic individual species habitats compared to vegetation zones.

#### Tide-induced Edaphic Change

The most striking result of the vegetation discrimination analysis was the utility of the  $\Delta ECa$  metric, alone, in identifying vegetation zones and species habitats. The Q-DEMI method and soil core analyses showed that  $\Delta ECa$  represented the amount of water and salt exchanged from the root zone (Figure 4b) between two points in time. The data from this study could not definitively separate, however, whether observed changes in edaphic conditions were due entirely to intervening tidal flooding, or due to a combination of physical and biological effects. The lack of correlation between  $\Delta ECa$  and either elevation or distance-to-channel argues against the hydrologic processes implied by the elevation and distance-to-channel metrics as the dominant determinants of spatial patterns in edaphic change.

The phenomenon of large, broadly distributed decreases in soil salinity, identified in this study by decreases in  $ECa$  between dry and wet marsh conditions, has not previously been reported and the precise cause is unknown. Potential mechanisms for what was apparently rapid flood tide-induced salt removal from the salt marsh root zone include: diffusion, leaching, or dissolution of salt from the surface; plant salt uptake; or dilution by convective mixing in soil

macropores. On average, the  $0.77 \text{ kg/m}^2$  of salt loss from the salt-exchange dominated areas of the marsh constituted approximately 15% of the salt contained in the root zone pore water fluids. Were dilution the only mechanism in operation, a salinity decrease of this magnitude would have required approximately 70% of the root zone pore water to be replaced by the less salty tidal waters, on average across the marsh. Salt uptake by vegetation would reduce the amount of pore water turn-over required to match the geophysical observations.

Plant – Soil Interactions

Qualitative comparison of tide-induced edaphic change and vegetation zonation (Figures 1a, 4b) suggests that the greatest density of areas experiencing large saturation increases due to tidal flooding occurred in the *Spartina*-dominated zone, the greatest density of areas experiencing salt loss occurred in the *Salicornia*-dominated zone, and changes of intermediate magnitude prevailed in the *Distichlis*-dominated zone. We hypothesize that these spatial coincidences may be related to three different ecosystem engineering effects enabled by the different physiologies and morphologies of these three species.

First, enhanced sediment deposition within, and enhanced erosion around, *Spartina* clusters has been reported at low marsh elevations (Temmerman and others 2007, van Hulzen and others 2007). This mechanism may also explain the great density of microtributaries in the *Spartina*-dominated zone (Figure 2) at our high-elevation marsh site. Because *Spartina* is more productive in low-salinity conditions than *Salicornia* and *Distichlis* (Bertness and others 1992, Mahall and Park 1976b), it may remain dominant precisely where surrounding microtributaries enhance pore water drainage and flushing. This hypothesis is supported by experimental manipulations of marsh hydrology (Balling and Resh 1983, Wiegert and others 1983).



Figure 2. Second, *Salicornia* is one of the most salt-tolerant halophytes, producing more biomass than *Spartina* and *Distichlis* at high salinities and water contents, but less at low salinities (Pearcy and Ustin 1984). We hypothesize that efficient root salt exclusion and water use by *Salicornia* (Mahall and Park 1976b) may locally maintain a saturated and salty root zone, enhancing *Salicornia* competitiveness.

Third, the matted morphology of *Distichlis* may decrease surface water velocities and so inhibit erosion of microtributaries (and so *Spartina*-dominance) in areas of low salinity favorable for both grasses (Bertness and others 1992). *Distichlis*, like *Salicornia*, is quite effective at excluding ions at the root membrane (Marcum and others 2007), and so may persist in areas of intermediate salinity, where it is often found nearly co-dominant with *Salicornia* at our site. A lack of known disturbance at our study site in at least 30 years argues against disturbance as an explanation for the distribution of *Distichlis* at the site; furthermore, both *Distichlis* and *Salicornia* are very effective at recovering from disturbance in northern California salt marshes, neither necessarily competitively displacing the other (Allison, 1995).

## CONCLUSION

This study explored the spatial relationships between salt marsh vegetation patterns and six zonation-related metrics. The metrics were based on geographic and edaphic data: elevation, distance to major tidal channels and to the nearest channel of any size, the soil saturation/salinity state during dry and wet marsh conditions, and the difference in this edaphic state between conditions. The metrics, mapped at high resolution throughout a salt marsh ecosystem, exhibited very different spatial patterns. Among the six metrics, information on tide-induced edaphic change was most useful in discriminating salt marsh vegetation zones and individual species habitats. Unexpectedly poor spatial correlation between edaphic conditions and proxies for



hydrologic forcing suggest, instead, the potential importance of plant-soil relations in spatial patterns of tide-induced edaphic change.

The results of this study supported two hypotheses relating the spatial patterns of salt marsh vegetation and abiotic variables. The hypotheses extend classic concepts of niche breadth and overlap (Colwell and Futuyma 1971) into three spatial dimensions. First, the influence of each resource used by, and stressor endured by, salt marsh vegetation may be spatially variable. These spatial patterns are combined implicitly in nature by superposition and may exhibit emergent patterns and properties that are more than the sum of the contributing variables. Second, multiple contributing variables may affect the distribution of interacting species assemblages differently than the distribution of individuals. Multivariate relationships between abiotic and biotic ecosystem patterns are difficult to assess without high-resolution spatially-distributed data at the ecosystem-scale. Geophysical methods such as EMI and Q-DEMI provide means to obtain high-resolution, spatially-distributed data on root zone soil properties that have previously been prohibitively difficult to obtain. In this study, such edaphic data was more useful in characterizing salt marsh vegetation zones and habitats than traditional geographic metrics such as elevation and distance-to-channel.

The challenge of predicting the vegetation distribution of intertidal salt marsh ecosystems persists. Despite functional similarity between different salt marsh species around the world, regional and latitudinal differences so far prohibit development of a universally-applicable, mechanistic, zonation model (Farina and others, 2009; Pennings and others 2003). Even if such a model were possible, its accuracy would necessarily vary from site to site. Some of the most pressing questions regarding salt marsh vegetation zonation, such as the expected response of a marsh to restoration efforts or to an invasive species, must be answered on a site-by-site basis

Figure 2 requires probabilistic, not deterministic, answers. Three-dimensional mapping, EMI geophysics, and the Q-DEMI methodology can provide a cost-effective, rapid, and repeatable means to statistically characterize a salt marsh site. The resulting spatial and temporal patterns can then be used as a foundation upon which to interpret or predict vegetation distributions and biotic interactions based on existing region- and species-specific knowledge. Linking plot-scale studies of plant-soil relations and interspecific interactions to marsh-scale studies of spatial variability such as this one may provide the most promising means to fill the gap between the general principles and site-specific needs of salt marsh vegetation zonation science.

#### ACKNOWLEDGMENTS

This work was supported by National Science Foundation grant EAR-0634709 to Stanford University. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. We thank the City of Palo Alto Baylands Nature Preserve and K. Brauman, M. Cardiff, S. Giddings, E. Hult, K. Knee, I. Lebron, and K. Tufano for field assistance.

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## APPENDIX

## Vegetation Habitat Distribution Maps

(Figure A1 and caption.)

## Relating ECa to Salt Marsh Soil Properties

Despite the extreme environment, correlations between our ECa and soil core data showed that salt marsh ECa measurements can be interpreted in terms of three key edaphic

properties: water content, salt content, and clay content. Variability in ECa values was significantly related to variability in each of these edaphic properties ( $p < 0.005$ , Table A1). At our site the EMI signal was dominated by the total salt content of the soil (as measured by the soil paste extract conductivity, ECe) but the soil water ( $\theta$ ) and clay contents also contributed. The clay content throughout the marsh was remarkably uniform and so did not figure significantly in our analysis. See the online supplement for comparison of our salt marsh relationships with prior published relationships at lower water, salt, or clay contents. In brief, we conclude that the salt marsh ECa – ECe and ECa –  $\theta$  relationships scale as in other environments but that the soil pore solution conductivity (ECw) and soil clay content of intertidal salt marshes have unique effects on EMI signals.

## FIGURE 1 AND TABLE CAPTIONS

Figure 1. a) Major vegetation zones, classified by the species of greatest cover fraction. b) Site topography, units: meters above mean sea level.

Figure 2. a) Shortest distance to one of the main tidal channels, shown in light blue bounding and bisecting the marsh site. b) Shortest distance to the nearest channel of any size, including microtributaries shown in dark blue.

Figure 3. Root zone bulk soil electrical conductivity (ECa) from (a) dry and (b) wet marsh conditions. Dark blue lines are channel and microtributary banks, black lines depict major vegetation zone boundaries.

Figure 4. a) Edaphic change between dry and wet marsh conditions, represented by the change in bulk soil electrical conductivity ( $\Delta\text{ECa}$ , dS/m). b) Result of Q-DEMI conversion of  $\Delta\text{ECa}$  to changes in root zone saturation (%) or salinity ( $\text{kg/m}^3$ ) between dry and wet marsh conditions. Blue areas were dominated by net saturation increase between dry and wet conditions, red areas were dominated by net salinity decrease. Dark blue lines are channel and microtributary banks, black lines depict major vegetation zone boundaries.

Figure A1. Relative cover fraction of each major plant species at the site: primary cover, secondary cover, tertiary cover, present as minor cover. Clockwise from lower left: *Distichlis spicata*, *Salicornia virginica* (*S. depressa*), *Spartina foliosa*, *Grindelia stricta*, *Frankenia salina*, *Jaumea carnosa*.

Table A1. Relation of ECa data to soil properties.



FIGURES

Figure 1a, 1b.

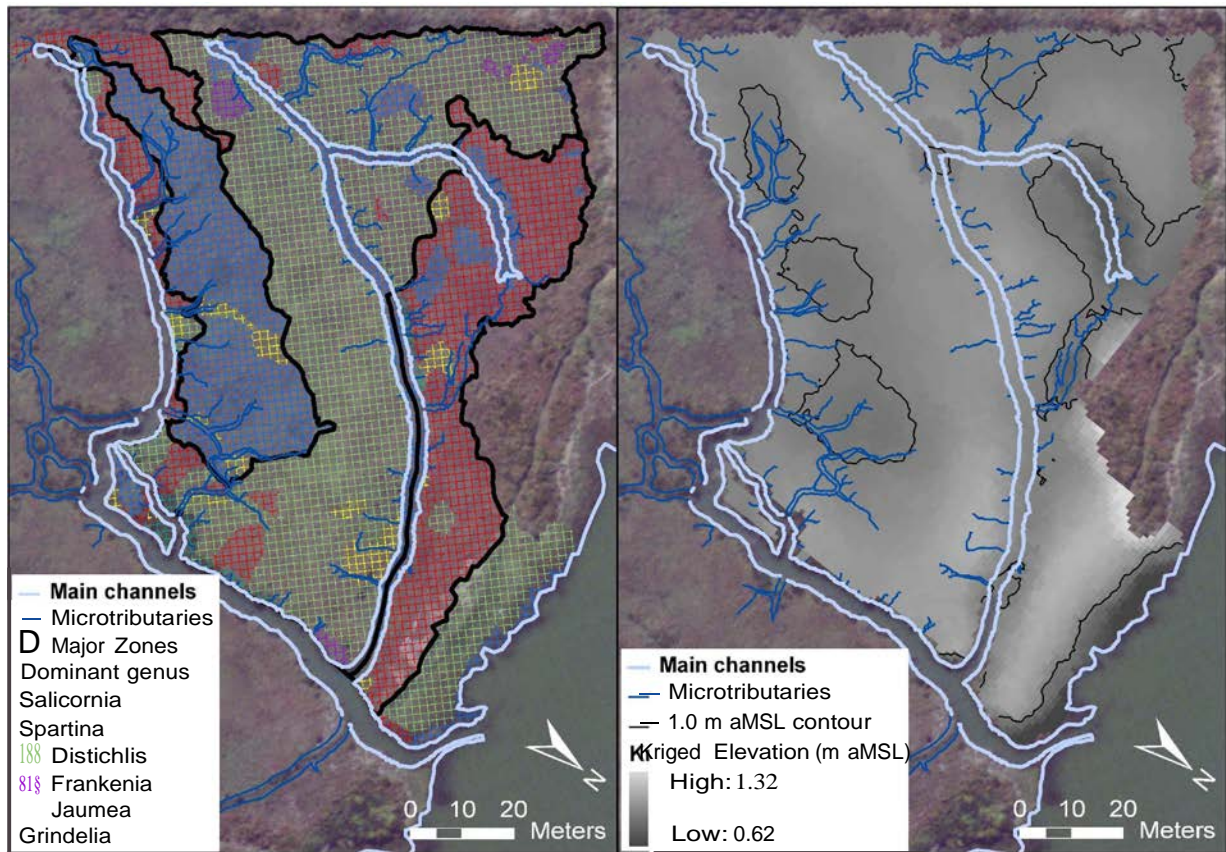
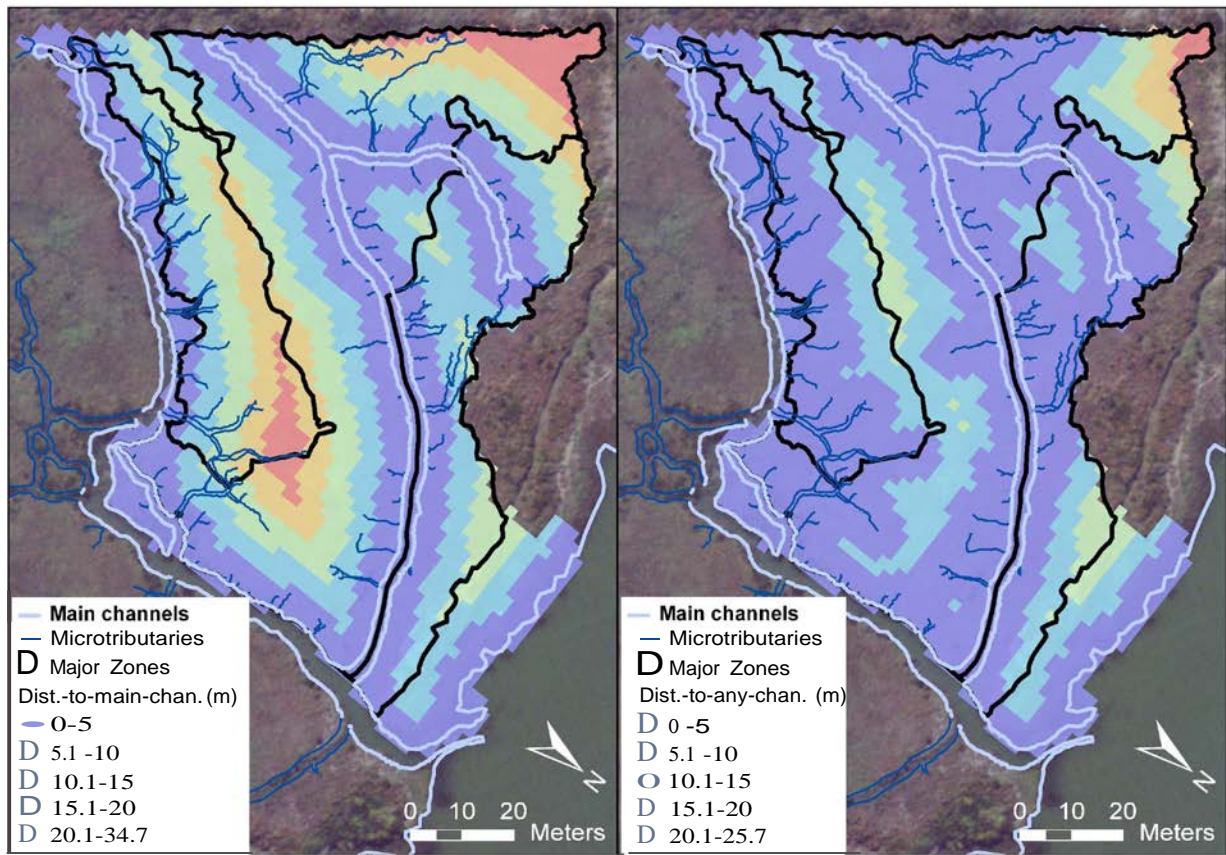


Figure 2a, 2b.





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628 Figure 3a, 3b.

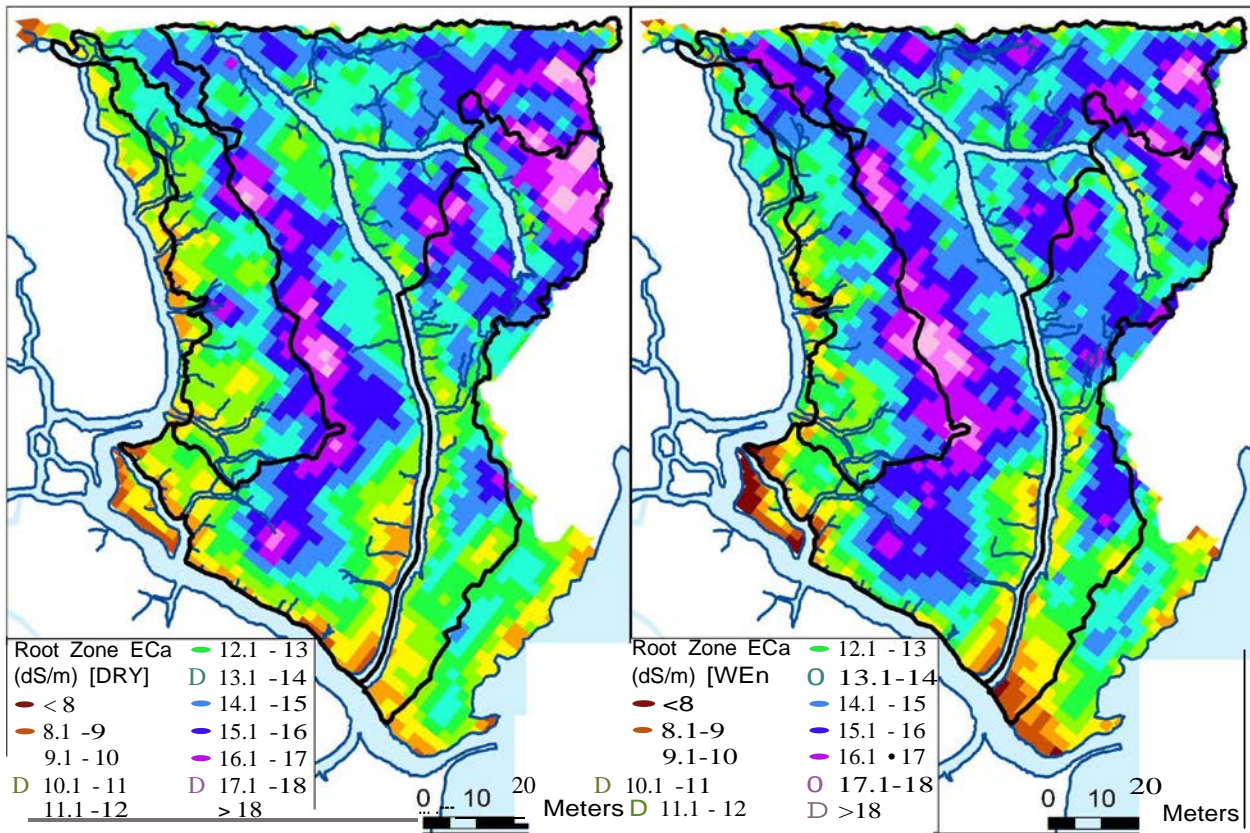
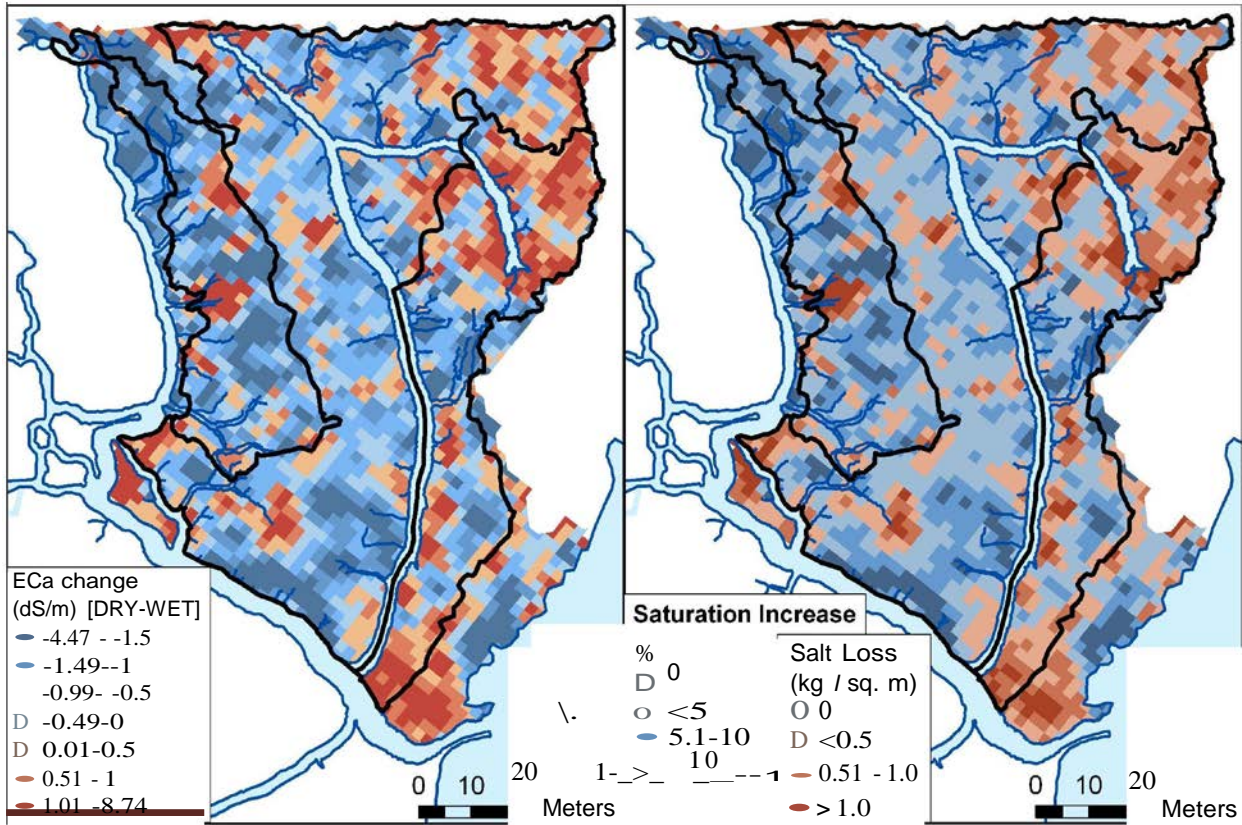


Figure 4a, 4b.







## Salt marsh spatial patterns and zonation

Moffett, Robinson, Gorelick

631

Table A1. Relation of ECa Data to Soil Properties			
Property	Sample Statistics		Correlation with ECa
	Mean	Standard Deviation	
Soil Paste Extract Electrical Conductivity <sup>i</sup> (ECe, dS/m)	68.9	15.0	0.67
Soil Pore Water Electrical Conductivity <sup>ii</sup> (ECw, dS/m)	57.2	7.0	0.53
Soil Volumetric Water Content <sup>i</sup> (%)	0.83	0.15	0.43
Soil Clay Content <sup>i</sup> (%)	61.8	9.4	0.51
Soil Temperature <sup>iii</sup> (dry conditions, °C)	13.98	0.54	--
Soil Temperature <sup>iii</sup> (wet conditions, °C)	11.56	0.41	--
Tide Water Electrical Conductivity (EC <sub>t</sub> , dS/m)	33.4	--	--
<sup>i</sup> N = 23, <sup>ii</sup> N = 17, <sup>iii</sup> N = 14			

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