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Landscape Estimates of Habitat Types, Plant Biomass, and Invertebrate Densities in a Georgia Salt Marsh

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ABSTRACT. Salt marshes often contain remarkable spatial heterogeneity at multiple scales across the landscape. A combination of advanced remote-sensing approaches (hyperspectral imagery and lidar) and conventional field survey methods was used to produce detailed quantifications and maps of marsh platform geomorphology, vegetation composition and biomass, and invertebrate patterns in a Georgia (USA) salt marsh. Community structure was largely related to hydrology, elevation, and soil properties. Both abiotic drivers and community patterns varied among subwatersheds and across the landscape at larger spatial scales. The authors conclude that measurements of marsh ecosystem structure and processes are spatially contextual and not scalable without detailed geospatial analysis. Efforts to protect and restore coastal marshes must strive to document, understand, and conserve this inherent spatial complexity.

SALT MARSH HETEROGENEITY AND WHY IT MATTERS

Salt marshes are heavily studied habitats (Pennings et al., 2012), but their high level of spatial variability hinders a general understanding of them. Approaching a Georgia salt marsh from the water, one encounters a vista of tall, lush, smooth marsh cordgrass (*Spartina alterniflora*) interspersed with numerous tidal streams and broader rivers. In contrast, approaching from upland forest, one first encounters woody shrubs such as sea oxeye (*Borrchia frutescens*) and marsh elder (*Iva frutescens*) along with dense stands of black needlerush (*Juncus roemerianus*), then comes a high marsh platform covered with a mosaic of salt tolerant “marsh meadow” plants, including perennial glasswort *Salicornia virginica* (or, recently, *Sarcocornia* sp.) and saltwort (*Batis maritima*) interspersed with reflective, unvegetated salt pans. Beyond are large areas of short- to medium-stature marsh cordgrass, and further out, the same bands of tall cordgrass conceal creek beds and adjacent tidal flats with deep, dark muds. Traversing the elevation gradients of entire marshes reveals a diverse landscape of relatively discreet stands of monotypic or low-diversity plant communities; soil substrates with differing colors, textures, and salinities; and varying assemblages of marsh macro-invertebrates—especially crabs, snails, and mussels. Adding to this heterogeneity are areas of wrack transported by tidal flooding (Alexander, 2008) and bare soil patches from marsh “dieback” events (Ogburn and Alber, 2006). Vigorous water flows from two- to three-meter tides shape marsh geomorphology, with

waterway levees creating complex flows and impeded drainage networks, leaving mid- to high marsh platform soils more waterlogged, anaerobic, and sulfide and ammonium enriched (Mendelsohn and Morris, 2000).

Because almost every aspect of salt marsh structure and function varies across the landscape (Wiegert and Freeman, 1990; Klemas, 2013), ecological and monitoring data from individual plots require a landscape context in order to be meaningful. In many cases, we wish to scale up from traditional, plot-based studies of soils, vegetation, and animals to an understanding of what is happening in an entire marsh or watershed. This scaling, however, requires an understanding of how common each “type” of plot is at the landscape scale. To describe the extreme heterogeneity of marshes on multiple spatial scales with plot-based sampling would require large numbers of replicates distributed randomly across the entire landscape. This approach would be very labor intensive, especially where drainages and deep muds impede access, and it is almost never done. Thus, plot-based sampling can result in significant errors in cover estimates of different habitats and individual species.

The marshes of Sapelo Island, Georgia, are among the most extensively studied ecosystems of the world (Pomeroy and Wiegert, 1981). For six decades, scientists working through the University of Georgia Marine Institute have intensively examined plant and animal demographics, biological productivities, food web interactions, soil biogeochemistry and microbiology, detritus sources and fates, surface and groundwater hydrology, and the underlying geology and

archeology. But how can we extrapolate all these studies, typically done in discrete locations at small spatial scales, to the entire watershed, and beyond to the Georgia or South Atlantic Coast? The Georgia Coastal Ecosystems Long Term Ecological Research (GCE LTER) (Alber, 2013) project is addressing this question by coupling advanced geospatial technologies with traditional field survey methods. Working at the scale of the 1,200 ha Duplin River watershed, which forms the western boundary of Sapelo Island (Figure 1), we synthesize field data with high-resolution imaging spectrometer and light detection and ranging (lidar, similar to radar but using pulsed laser light rather than microwaves) aircraft measurements.

Remote-sensing approaches (Adam et al., 2010) offer an attractive methodology for scaling from plots to the landscape. Early remote-sensing studies of salt marshes on the Duplin River (Reimold et al., 1973) used color infrared aerial photography, feature extraction from imagery, and “ground truth” surveys to verify classifications. Modern airborne sensors offer the advantages of higher spectral, spatial, and radiometric

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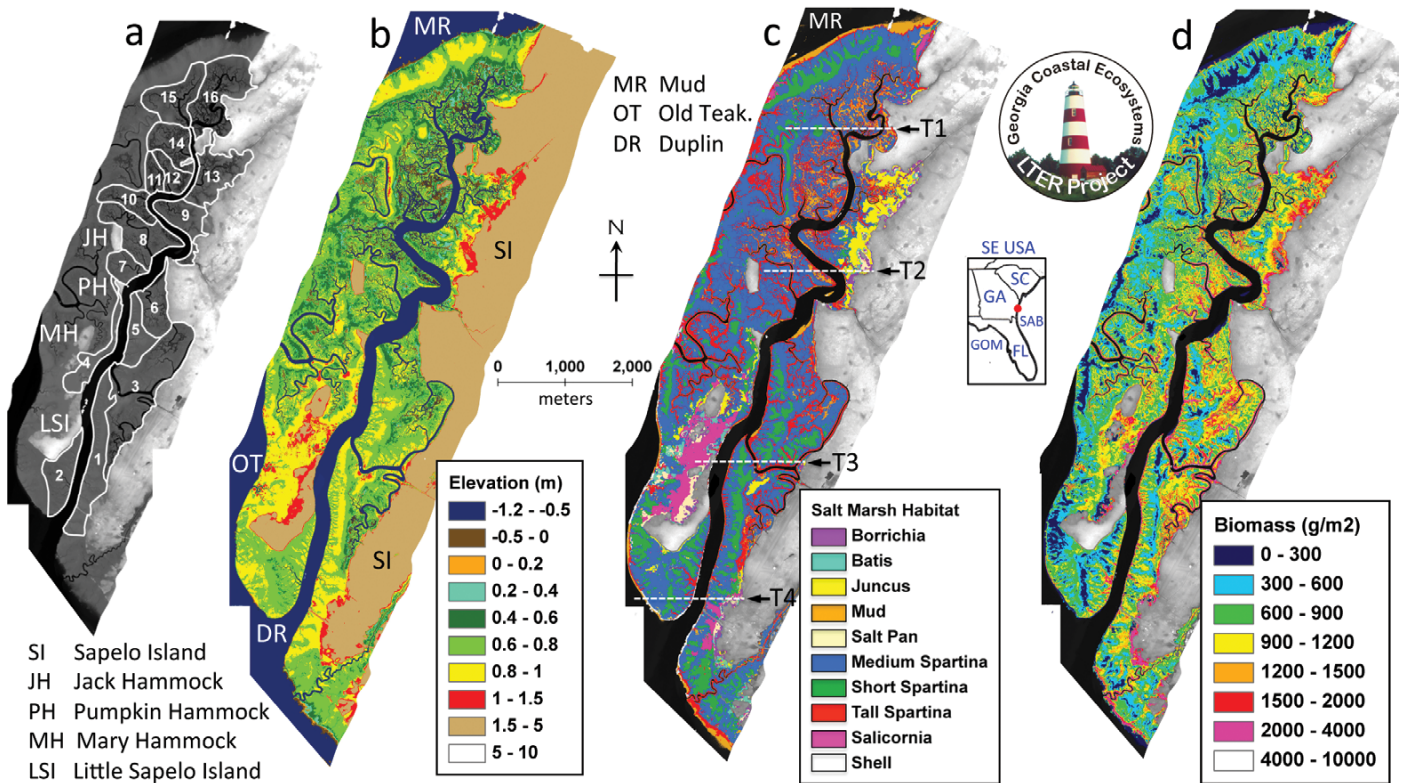


Figure 1. Maps of the Duplin River tidal watershed at Sapelo Island, Georgia (see inset with red dot), showing (a) a gray-scale DEM (digital elevation model) with an overlay of numbered subwatershed units, (b) a DEM with colors assigned to different elevation ranges, (c) a map of vegetation types (with locations of transects 1–4 in Figure 6), and (d) aboveground vegetation biomass estimates, as grams dry weight per square meter. The resolution (cell size) of each map is one square meter. MR = Mud River. OT = Old Teakettle Creek. DR = Duplin River.

resolution. Large areas can be studied, and data from a limited number of areas sampled on the ground can be used to “train” software to classify the entire landscape. This approach eliminates error due to limited or biased sampling, but introduces different sources of error associated with how well the field surveys capture the heterogeneity of classification targets, and how well the software is able to correctly classify the image. Thus, remote sensing offers significant potential advantages, but requires judicious use of training and validation data and iterative procedures to improve classification accuracies. Classification accuracy can be improved by combining remotely sensed vegetation reflectances with lidar data (Morris et al., 2005; Klemas, 2013).

Here, we build on earlier approaches, using advanced imaging spectrometer

and lidar instruments, geometric and atmospheric correction procedures, and detailed ground observations, to determine variation in (1) soil properties, (2) plant community types, (3) aboveground plant biomass, and (4) common invertebrates across the entire Duplin salt marsh watershed. Our results provide a new level of insight into past studies of Georgia salt marshes by evaluating how “typical” the habitats were in which different scientists have worked, and suggest new avenues for future research by employing synoptic perspectives that incorporate geospatial analysis at various spatial resolutions. Our results inform both the research goals of the GCE LTER and the management goals of the co-located Sapelo Island National Estuarine Research Reserve (Sapelo Island National Estuarine Research Reserve, 2008).

DUPLIN WATERSHED MARSH PLATFORM GEOMORPHOLOGY AND SOILS

Sapelo Island is located on the central Georgia coast, and is separated from the mainland by 7.5–12 km of tidal marshes and waterways. At mean low water, tidal wetlands cover 1,002.5 ha of the Duplin watershed, and the Duplin River and tidal tributary creeks cover an additional 197.5 ha (Blanton et al., 2007; Figure 1a). The watershed is bounded on the east by uplands of Sapelo Island, and to the north and west by a broken ridge of Pleistocene sands. The main channel of the Duplin River is ~ 13 km long, with two terminal branches high in the watershed. The Duplin River is ~ 240 m wide at its mouth, and along the lower section the mean depth of the central channel is ~ 6.5 m (McKay and Di Iorio,

2010). The Duplin River can be divided into 16 subwatersheds (Figure 1a) ranging in size from 20.7 to 167.6 ha (Blanton et al., 2007).

A digital elevation model (DEM) of the Duplin watershed and vicinity was produced from lidar data obtained by the National Center for Airborne Laser Mapping during a period of minimal vegetation biomass and cover on March 9 and 10, 2009. A Cessna Skymaster carrying an Optech Gemini Airborne Laser Mapper acquired terrain elevation data from an altitude of 800 m during low tide periods. The instrument provided a target point density of 9 laser points per m². A bare-earth DEM was produced using SURFER Version 8 (<http://www.goldensoftware.com>). The lidar data were calibrated with about 1,800 ground control points surveyed with a Trimble R6 Real-Time Kinematic (RTK) GPS receiver with vertical and horizontal accuracies of about 1.0 and 2.0 cm. An iterative analysis using the ground control points in combination with vegetation classifications derived from the AISA-Eagle imagery (see below) was used to correct elevation biases in the lidar data caused by dense vegetation that prevented ground penetration of laser pulses. With these corrections, overall DEM error was reduced from +0.1 m to -0.01 m (Hladik and Alber, 2012).

Salt marsh elevations (referenced to zero for NAVD 88, which corresponds to 0.203 m above mean sea level), ranged from about -0.7 m (lower elevation range of tall *Spartina* habitat along creek banks) to 1.3 m (ecotonal transition to upland, occupied by *Borrichia* and *Juncus*; see Hladik, 2012; Hladik and Alber, 2012). Upland vegetation occurred at elevations above 1.5 m (Figure 1b). RTK measurements indicated that *Spartina* was not regularly

found at elevations above 1.14 m, with mean elevations for tall (> 1.0 m canopy height, Figure 1c), medium (0.5–1.0 m height), and short (< 0.5 m height) form stands of 0.36, 0.77, and 0.87 m, respectively (Hladik and Alber, 2012). RTK-based average elevations of high marsh vegetation stands were 0.95 m for *Salicornia*, 0.99 m for *Batis*, 1.02 m for *Juncus*, and 1.23 m for *Borrichia*. The mean salt pan elevation was 1.01 m.

Between the intertidal creek banks and the halophyte marsh meadows of the upper marsh platform, there is a general increase in soil water salinity and decreases in soil moisture and percent organic matter with increasing elevation (Antlfinger and Dunn, 1979; Lynes, 2008). At elevations above the high marsh hypersaline zone, however, better drainage and proximity to upland ecotones leads to reduced salinities (Pennings and Bertness, 2001). These general trends were supported by soil sampling during our 2006 flyover field survey (described below). Most vegetation types had porewater salinities similar to seawater, but salinities were elevated to ~ 45 in unvegetated mud areas, to 50–60 in *Salicornia* and *Batis* zones, and to > 150 in high-marsh salt pans. In general, soil water content varied inversely with salinity, reflecting the reduced tidal flooding and increased evaporation that produces hypersaline habitats (Lynes, 2008). Variation in soil organic content is likely caused by increased belowground production and reduced decomposition in wetter soils at lower elevations.

MAPPING MARSH VEGETATION COMMUNITY COMPOSITION AND ABUNDANCE

On June 20, 2006, an AISA Eagle imaging spectroradiometer (<http://www.specim.fi>), flown aboard a University

of Nebraska Piper Saratoga, acquired data for the entire Duplin watershed. Four parallel, overlapping flight lines of data (1 m resolution, 63 bands between 401 and 981 nm at bandwidths of 5–10 nm) were captured in a northeast to southwest alignment, 30–90 minutes before low tide. The tidal conditions resulted in extensive mudflat and bank exposures. In our processing, water and upland features were masked. Detailed descriptions of the instrumentation, calibration, and image processing procedures are available in Perk et al. (2009) and Schalles and Hladik (2012).

We collected three types of ground reference data. A set of 373 quadrat plots (1 m²) were sampled in June 2006 along 18 transects (creek bank to upland ecotone) and used to train and verify plant habitat and biomass classifications. At each plot, a photograph was taken, vegetation species were noted, a 0.25 × 0.25 m subplot was harvested for plant biomass, GPS coordinates were measured (submeter accuracy), and a 10 cm soil core was collected for laboratory analysis of percent organic matter, water content, and salinity (Lynes, 2008). Plots were assigned to one of 10 habitat types (see below). Densities of a common bivalve (*Geukensia demissa*) and two gastropods (*Littoraria irrorata* and *Melampus bidentatus*) were determined. To increase coverage, a second set of 483 plots was sampled between June 25 and July 6, 2007. A more limited range of data (photography, dominant vegetation, GPS coordinates) was collected. Finally, between September 2006 and August 2007, multiple vegetation stands were delineated. Relatively homogeneous stands of each vegetation class were selected and boundaries were mapped using differential GPS, taking care to avoid ecotonal margins. This last

technique was an efficient approach to greatly increase the total number of pixels available for classification procedures.

The vegetation data were randomly divided into training and validation data sets, with 75% reserved for supervised classifier training and 25% for validation of the classification results. Imagery was classified in ENVI (Exelis Visual Information Solutions) with an overall accuracy of 90% (Figure 1c; Hladik, 2012) using the maximum likelihood classification algorithm.

Vegetation followed a typical zonation pattern from low to high marsh (Wiegert and Freeman, 1990), with tall *Spartina* found along the regularly flooded creek banks in the low marsh and medium *Spartina* dominating mid-marsh areas (Figure 1c). The high marsh was composed of short *Spartina*, *Batis*, and *Salicornia*. At the highest elevations bordering upland areas, *Juncus* and *Borrchia* became the dominant species. Hladik and Alber (2012) were

able to separate some of the salt marsh plant types based on ground elevation, with tall *Spartina*, medium *Spartina*, and *Borrchia* having discrete elevational ranges, while the high marsh plant types overlapped broadly in elevation.

In terms of areal extent, the overall dominant habitat class was medium *Spartina*, representing 60% of the marsh area (Figures 1c, 2, and 3). The three height classes of *Spartina* together comprised 80% of the Duplin watershed, making *Spartina* (all height forms combined) the dominant salt marsh vegetation type (Reimold et al., 1973). Although *Spartina* was dominant overall, *Spartina* coverage was variable across the Duplin watershed. For example, tall *Spartina* was quite abundant in subwatersheds 3, 6, and 8 (percent cover ranging from 18% to 25%; Figure 2) where there are dense creek networks, but cover of tall *Spartina* was less than 5% in higher-elevation subwatersheds 4, 7, and 15, where creek networks are

less extensive. Thus, elevation and creek morphology, and their associated soil characteristics, strongly affect *Spartina* distributions across the domain.

Some subwatersheds contained large proportions of *Juncus* and other high marsh plants. In subwatersheds 9 and 13, *Juncus* comprised 23% and 38% of the area, respectively (Figures 1c and 3). High marsh areas dominated by *Salicornia*, *Batis*, and salt pans occurred in close proximity to Sapelo Island and to marsh hammocks just outside the Duplin watershed. The hyperspectral classification showed large-scale vegetation patterns associated with elevation divides that constrain the watershed and subwatersheds. The divides are observable along the southwestern edge of subwatershed 2, the border between subwatersheds 1 and 3, and the northernmost watershed boundary of subwatersheds 15 and 16 (Figure 1b,c). In these areas, the vegetation classification clearly parallels topographic features in the DEM, due to plants responding to the effects of elevation on soil characteristics. There are large-scale differences in plant communities between the upper Duplin and the lower Duplin watersheds (Figure 2), reflecting differences in elevation patterns, creek density, and hydrology (Figure 1). The upper Duplin (Tidal Prism 3; see Ragotzkie and Bryson, 1955) was generally at a lower elevation, had dense creek networks and extensive intertidal mudflats, and as a result was dominated by tall and medium *Spartina* and intertidal mud. The lower Duplin (Prism 1) was generally at higher elevations, had low creek densities, and as a result had a higher proportion of short *Spartina* and other high marsh species.

In the 2006 plot sampling, above-ground plant biomass averaged $1,510 \pm 1,164$ (SD) g dry wt \cdot m⁻²,

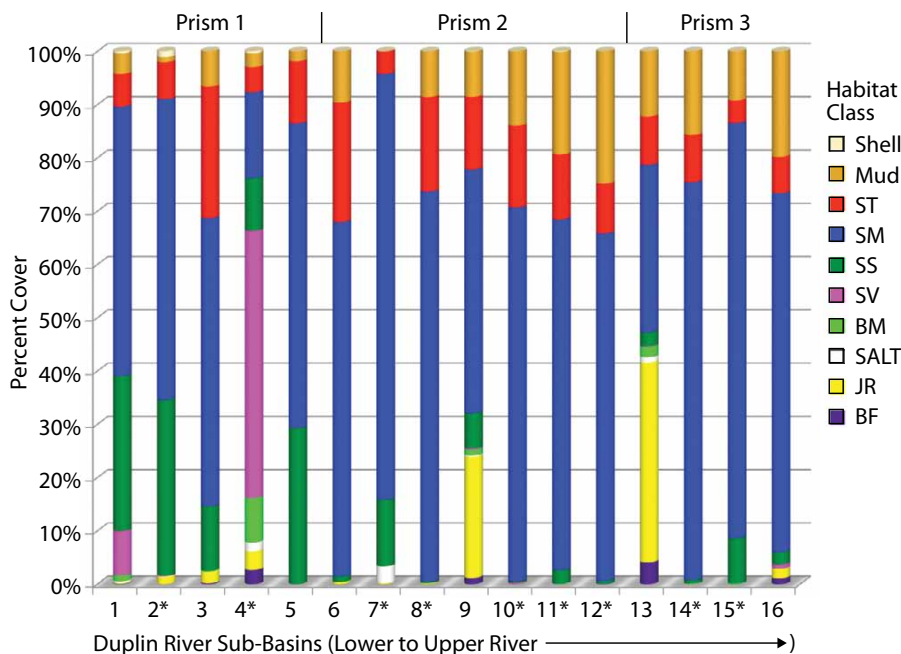


Figure 2. Estimates of the percent cover of the 10 habitat classes (Figure 1c) for each of the 16 sub-watershed units of the Duplin River watershed (Figure 1a). Subwatersheds on the west side of the Duplin River are indicated using asterisks. Hydrographic tidal prism regions from Ragotzkie and Bryson (1955)

with a range of 0 (mud and salt Pan) to 5,840 (tall *Spartina*). Using our clip-plot data and AISA hyperspectral imagery, we compared three algorithms: (1) the Normalized Difference Vegetation Index (NDVI; Tucker et al., 1981; Hardisky et al., 1986), (2) the Visible Atmospherically Resistant Index (VARI), and (3) the Green Normalized Difference Index (Green NDVI; Gitelson et al., 2002, 2003) for estimating aboveground biomass. A standard NDVI index, using NIR band 50 (857 nm) and red band 31 (675 nm) reflectance values, provided the best estimates of biomass, with an r^2 value of 0.601, versus values of 0.500 and 0.416 for the Green NDVI and VARI estimates:

$$\text{Biomass g dry wt} \cdot \text{m}^{-2} = (153.8 \cdot X) + (5,525 \cdot X^2) - (4,077 \cdot X^3) + (7,624 \cdot X^4) \quad (1)$$

where $X = (\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red})$.

NDVI estimates of biomass for vegetation types known to have high biomass (tall *Spartina*, *Juncus*, and the woody ecotonal species *Borrichia* and *Batis*) generally were greater than 900 g dry wt \cdot m⁻² (Figure 1c,d). The high marsh communities with low stature and lower canopy cover plants (short and medium *Spartina*, *Salicornia*) are well matched with the low to intermediate biomass classes of our synoptic map. A notable expanse of low biomass co-occurs with short *Spartina* in the sandy, low ridge separating the Mud River and extreme upper watershed of the Duplin (Figure 1c,d). This low biomass condition consistently occurs on watershed and subwatershed divides throughout the study domain, where subtle differences in elevation affect frequency of tidal inundations and soil salinization and anoxia (Mendelssohn and Morris, 2000).

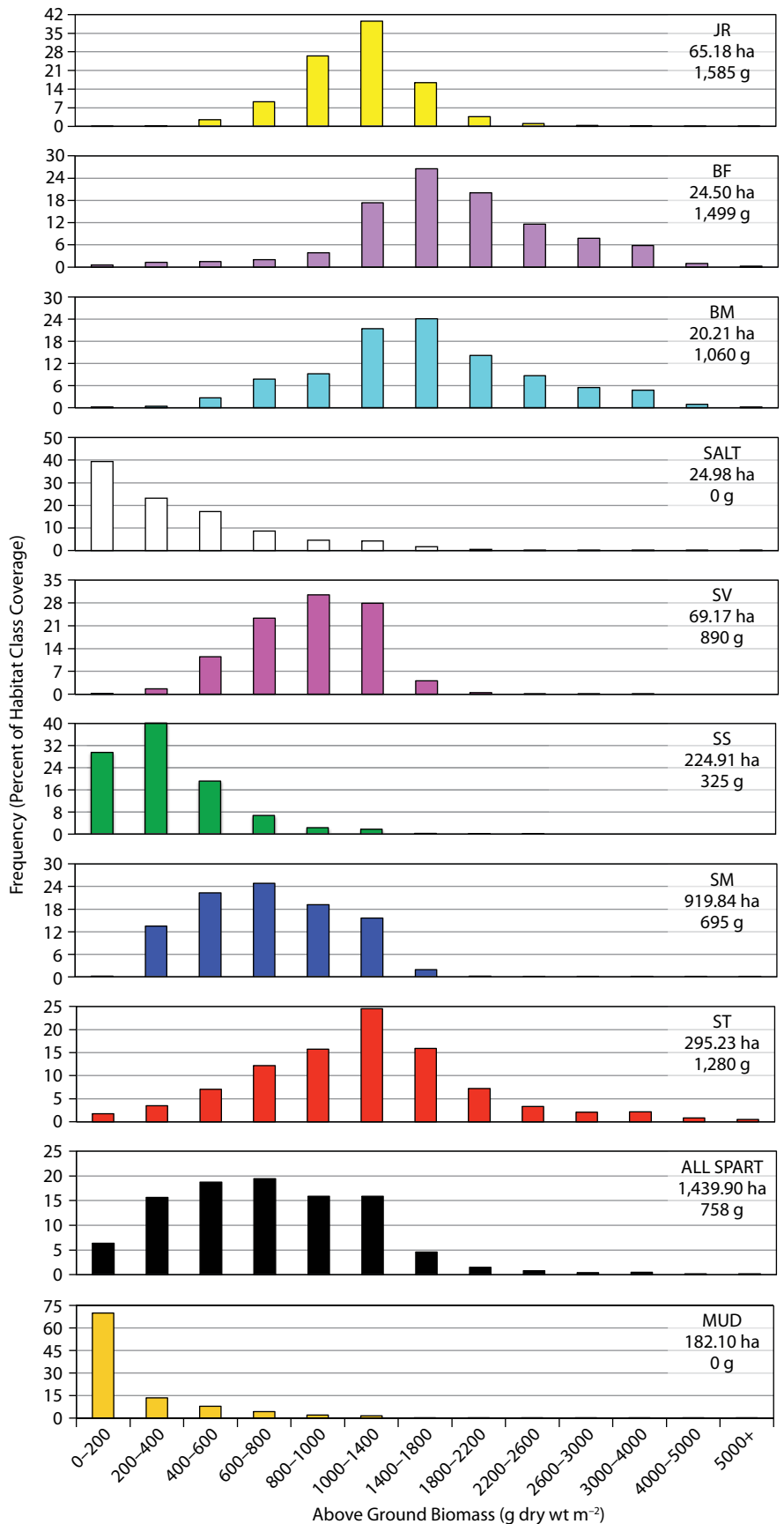


Figure 3. Histograms of the estimated biomass frequencies (as percent of all aerial coverage) for each of the 10 habitat classes (Figure 1c). Respective areas of habitat coverage and median biomass values are shown with each habitat class.

The high spatial resolution of our vegetation and biomass delineations allowed us to examine, on a per-pixel basis, the frequency distributions of biomass levels for each respective marsh habitat class (Figure 3). For this analysis, we used the entire coverage area, including adjacent areas of the Mud River and Old Teakettle and New Teakettle Creek watersheds (Figure 1a,c,d) covering a total area of 1,970 hectares of salt marsh and exposed mudflats (i.e., 19.7 million classified pixels). Plant biomass increased across the *Spartina* classes (median values of 325, 695, and 1,280 g • m⁻² for short, medium, and tall classes, respectively; Figure 3). Biomass values for *Juncus*, *Borrichia*, and *Batis* rivaled those of tall *Spartina*. *Salicornia* distribution had a prominent negative skew, perhaps an indication of being outcompeted by other plant species at wetter, less-saline habitats.

SALT MARSH INVERTEBRATE SPATIAL PATTERNS

Quadrat sampling revealed that the density of macro-invertebrates differed strongly among vegetation classes (Table 1). *Littoraria* was most abundant

in short *Spartina*, *Melampus* in *Borrichia*, and *Geukensia* in tall *Spartina*. Similar correlations between marsh crabs and vegetation classes were previously documented, with *Uca pugnator* restricted to mud and *Salicornia* habitats, and *Uca pugnax* rare and *Sesarma reticulatum* most abundant in tall *Spartina* (Teal, 1958; Wolf et al., 1975). These vegetation associations led to markedly different spatial distributions for marsh macro-invertebrates (Figure 4). *Littoraria* was most common in the interior of the marsh, and in parts of the Duplin watershed with large expanses of short *Spartina* (the northern tip and the southeastern portions of the study area). *Melampus* was most common adjacent to upland habitats, and its distribution was also patchy across the Duplin watershed. *Geukensia* was most common adjacent to creeks, and in areas, such as the upper Duplin watershed, that had large expanses of tall *Spartina*. Across the entire Duplin River watershed, we estimate that there were 765.5 million *Littoraria*, 7.7 million *Melampus*, and 46.5 million *Geukensia*. In comparison, Wolf et al. (1975) previously estimated that there were 2.2 billion *Uca pugnax* in

the same watershed.

Causes for the strong associations between different macro-invertebrates and different vegetation types include predation by marine nekton that is most severe in the tall *Spartina* zone (Kneib, 1987; Silliman and Bertness, 2002), desiccation, limited feeding time, predation by birds and mammals in the high marsh habitats (Nomann and Pennings, 1988; Lin, 1989), and competitive interactions among macro-invertebrates (Lee and Silliman, 2006).

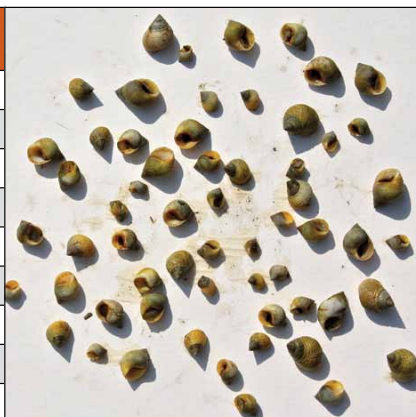
The fact that macro-invertebrate densities vary so widely across the landscape means that certain ecological interactions are likely to be focused in particular parts of the marsh landscape. For example, *Littoraria* in Georgia have modest effects on *Spartina* production at densities of 100–250 per m², have stronger effects at 250–500 per m², and kill vegetation at densities of over 500 per m² (Brian Silliman, University of Florida, *pers. comm.*, 2013), conditions that we estimate occurred over ~ 22, 4.5, and 0.4% of the landscape, respectively, and especially in the short *Spartina* vegetation type. Conversely, building of the marsh substrate by *Geukensia* (Smith and Frey, 1985), and herbivory by *Sesarma* (Hughes et al., 2009; Altieri et al., 2012) will be most important in the tall *Spartina* zone.

COMMUNITY TRANSECTS ACROSS THE DUPLIN WATERSHED

To illustrate the kind of fine-scale spatial heterogeneity that might be encountered in different portions of the watershed, we digitally created four 1,600 m horizontal transects (Figure 1c) of elevation, plant biomass, and habitat classifications at locations perpendicular to the longitudinal axis of the Duplin River (Figure 5).

Table 1. Summary of Duplin watershed invertebrate densities within the nine habitat classifications. Data are expressed as number of animals per square meter. (Photo) Sample of 60 *Littoraria irrorata* collected in a 0.25 m² quadrat at Plot #1 of Transect 9 during the 2006 Duplin survey (short *Spartina* habitat; aboveground plant biomass = 461 g dry wt • m⁻²).

Habitat	<i>Littoraria irrorata</i>	<i>Melampus bidentata</i>	<i>Geukensia demissa</i>
<i>Borrichia</i>	7.4	3.07	0.00
<i>Batis</i>	36.1	1.69	1.56
<i>Juncus</i>	73.9	0.29	0.74
Mud	0.5	0.00	1.57
Salt Pan	0.4	0.00	0.00
<i>Spartina</i> short	237.1	0.38	6.36
<i>Spartina</i> medium	76.8	1.16	3.87
<i>Spartina</i> tall	14.7	0.00	12.30
<i>Salicornia</i>	80.6	0.29	0.04



In transect 1, the only vegetation is *Spartina*, with growth forms and biomass largely determined by elevation and proximity to the numerous small creek drainages and exposed intertidal muds. Large variations in *Spartina* biomass are closely coupled to elevation differences in the highly dissected relief in the east half of the transect. Tall *Spartina* distributions precisely match the creek bank morphology and provide a very different community structure than that found in the west half of the transect.

Transect 2 is dominated by *Spartina* and small drainages to the west of the Duplin, with an elevated, uniform platform of *Juncus* grading to upslope *Borrichia* east of the Duplin. A major tributary occurs at about 400 m, with high biomass ($> 4,000 \text{ g} \cdot \text{m}^{-2}$) *Spartina* on adjacent levees (Figure 5).

Transect 3 crosses through heterogeneous habitat, including the northern edge of the Little Sapelo Island hammock (Figure 1a) and several small channels. West of the hammock is a large stand of low biomass *Salicornia* and an upslope gradation toward the hammock with *Batis* and *Borrichia* exhibiting two to three times greater biomass. East of Barn Creek, extreme variations in biomass correspond to tall *Spartina* at creek and drainage margins versus more isolated, waterlogged soils with short and medium *Spartina* (Figure 5).

Transect 4 crosses a peninsula of low biomass marsh. During the 2007 surveys, we noted widespread marsh dieback in the poorly drained short *Spartina* zones of the peninsula. The platform east of the Duplin has a gentle rise, with *Spartina* grading to patchy *Salicornia* and *Batis* and a small “knob” between 1,400 and 1,470 m that consists of a stand of *Borrichia* encircled by a salt pan.

These transects illustrate the close

associations between elevation, biomass, and vegetation type, and reveal how variable a Georgia salt marsh can be, both at a single site (transect) and also at the landscape scale (comparing transects). Adam et al. (2010) and Klemas (2013) reviewed studies demonstrating that a combination of lidar, plant classification, and vegetation index data can improve species-level classifications and estimation of biophysical variables such as biomass and leaf area. Our detailed portrait of the Duplin watershed was possible only with the high-resolution imagery and advanced geospatial techniques employed in this study.

SUMMARY AND CONCLUSIONS

This study emphasizes the variability of Georgia salt marshes on multiple spatial scales. At any one site, geomorphology and soils, plant biomass, and the densities of important macro-invertebrates vary asynchronously across the intertidal

landscape. At the scale of the Duplin River, the subwatersheds differ in the relative abundance of vegetation types, abundance of creek drainages and intertidal muds, and associated macro-invertebrates. Moreover, the variation in vegetation type and biomass only increases if the scale is expanded to consider all types of tidal marshes on the Georgia coast (Higinbotham et al., 2004; Craft et al., 2009; Więski et al., 2010). As a result, ecosystem and ecological processes will vary depending on where they are measured. There is no “typical” marsh habitat, and there is no “typical” marsh site. Studies in short *Spartina* will examine a different food web than studies in medium *Spartina*, and studies in the upper Duplin will reach different conclusions than studies in the lower Duplin. We encourage marsh scientists and coastal resource managers and planners to abandon the idea that any site can be representative, and instead to embrace

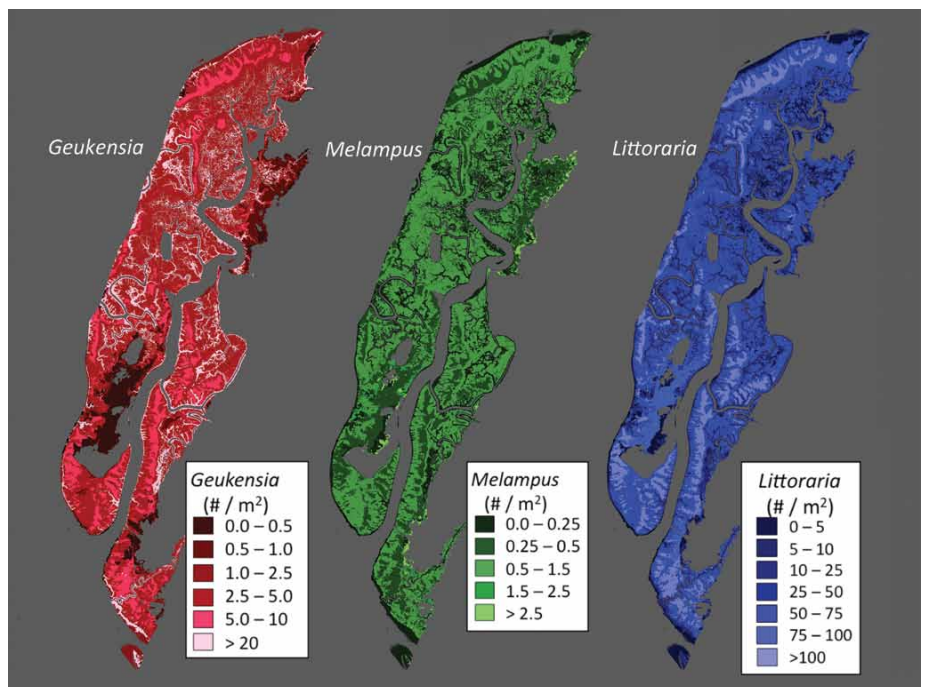



Figure 4. Density estimates (number of individuals per square meter) of three representative macro-invertebrates (*Geukensia demissa*, *Melampus bidentatus*, and *Littoraria irrorata*) within the entire 2006 mapping area.

this variation by explicitly examining how marsh functioning varies at multiple scales across the landscape. Moreover, we advocate for a remote-sensing approach for assessing ecological heterogeneity

and landscape patterns to provide the landscape context for localized studies and for coastal planning, conservation, and restoration efforts. Clearly, wetland mitigation banking and other wetland

protection projects should demonstrate that a restored or created wetland habitat provides a comparable, heterogeneous landscape with spatially appropriate ecosystem functions and services.

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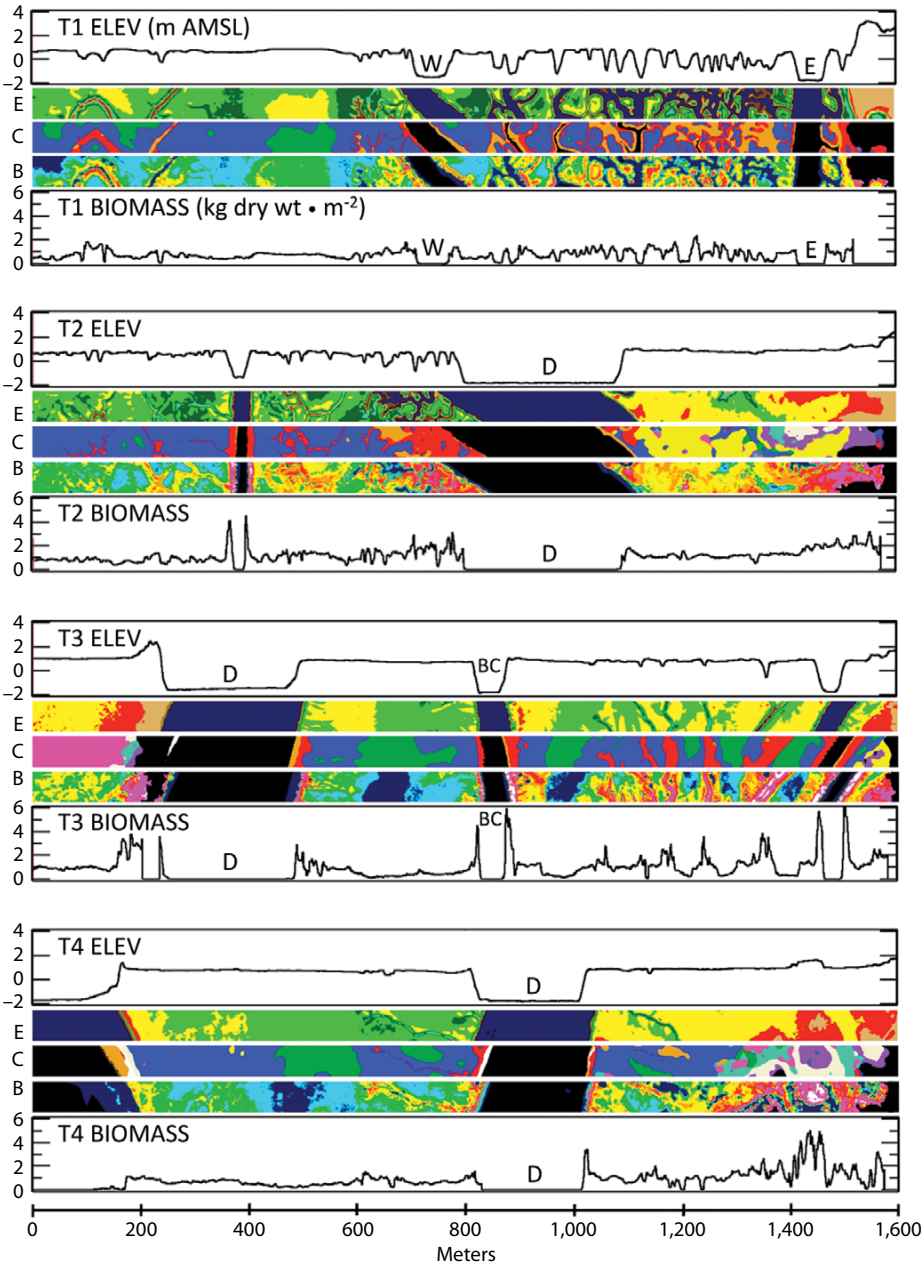


Figure 5. Four horizontal transects (see Figure 1c for location of transects) along the north to south longitudinal gradient of the Duplin River watershed. In each of the four transects, a 1,600 m x 60 m area is represented in three panels: E = elevation (see Figure 1b), C = habitat cover classes (see Figure 1c), and B = aboveground biomass (see Figure 1d). Graphs of elevation (m – MSL [mean sea level]) and aboveground biomass (grams dry weight per square meter) were prepared from line profiles using ENVI software. The graph profiles are values for a single row of 1,600 pixels across each respective transect panel, and they are located halfway (30 m) between the north (upper) and south (lower) borders of respective map panels. D = Duplin River. E and W = the east and west forks of the upper Duplin River. BC = Barn Creek.

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