5-18-2022

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Recommended Citation

Anderson, C. P., Carter, G. A., Waldron, M. C. (2022). Precise Elevation Thresholds Associated with Salt Marsh–Upland Ecotones along the Mississippi Gulf Coast. *Annals of the American Association of Geographers*.
Available at: https://aquila.usm.edu/fac_pubs/19889

Precise Elevation Thresholds Associated with Salt Marsh–Upland Ecotones along the Mississippi Gulf Coast

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Coastal marshes provide essential ecosystem services related to biodiversity, water quality, and protection from erosion. As increasing rates of relative sea-level rise affect many coastal marsh systems, a thorough understanding of marsh responses to sea-level change, particularly the migration of marsh–upland boundaries, becomes essential. The goal of this study was to determine precise elevation thresholds associated with coastal marsh, the marsh–upland ecotone, and upland plant communities along Mississippi's Gulf of Mexico coast (diurnal, microtidal). Elevations (NAVD88) were measured using survey-grade Global Navigation Satellite System solutions integrated with high-precision leveling. Plant species were sampled at approximately 1-m intervals along each of thirty-three transects extending from intermediate marsh through the marsh–upland ecotone. Elevation thresholds associated with plant community change were determined based on relevant quartiles of the data. Probabilities of occurrence of each plant community type were computed for elevations at the centimeter scale. Results indicated transitions from marsh to ecotone and ecotone to upland at elevations of approximately 0.40 m and 0.60 m, respectively. Understanding the precise nature of these centimeter-scale dependencies of marsh vegetation on coastal elevation will facilitate spatial modeling of marsh transgression in response to sea-level rise, subsidence, changes in sediment flux, and land use change. *Key Words: coastal marsh, elevation, sea-level rise, vegetation.*

Affected by human activity and the coastal environment, salt marshes are specialized systems that provide habitat for many species of flora and fauna, while offering commercial and recreational economic value (Hopkinson and Giblin 2008; Kirwan et al. 2016). Further, they serve as natural buffers against wave energy and shoreline loss, sequester carbon, and filter groundwater recharge (Kennish 2001; Shepard, Crain, and Beck 2011; Hladik and Alber 2012). Although the roles of salt marshes are highly specialized, they are also delicate ecosystems that exist in very narrow elevation ranges, often less than 2 m (Hladik, Schalles, and Alber 2013). Coastal marsh extent is a function of elevation and tidal inundation (Eleuterius and Caldwell 1985; Passeri et al. 2015). As a result, salt marshes are highly vulnerable to the combined effects of sea-level rise (SLR), local subsidence, reduced sediment availability, tropical cyclone impacts, and poor land management practices.

Coastal marshes exist in equilibrium with tidal inundation, SLR, and subsidence by maintaining sediment flux via mechanical and biophysical feedbacks (Orson, Panageotou, and Leatherman 1985; Morris et al. 2002; Passeri et al. 2015; Roman 2017; Alizad et al. 2018). For example, tidal inundation can promote higher levels of organic and mineral sediment trapping among marsh vegetation, offsetting even moderate rates of SLR of up to ~12 mm yr^{-1} (Morris et al. 2002; Kirwan et al. 2010; Kirwan and Megonigal 2013; Wu, Biber, and Bethel 2017; Schuerch et al. 2018; Wu et al. 2020). Sedimentation in marshes must keep pace with SLR for marsh areal extent and biomass production to remain stable. As SLR outpaces sediment deposition, marsh drowning and collapse could occur, causing transgression, fragmentation, and reduction in overall marsh area (Orson, Panageotou, and Leatherman 1985; Passeri

Annals of the American Association of Geographers, 0(0) 2022, pp. 1–16
Initial submission, March 2021; revised submissions, August and November 2021; final acceptance, February 2022

et al. 2015; Kirwan et al. 2016). Even in systems with adequate accommodation space, minimal hydrological modification, and low subsidence rates, such as the Pascagoula River estuary in Mississippi, reductions in marsh area have been observed over recent decades (Waldron, Carter, and Biber 2021).

Very subtle changes in elevation on the order of centimeters to decimeters can drastically alter daily hydroperiods, ultimately affecting plant species composition and spatial distribution (Hladik, Schalles, and Alber 2013). Thus, vertical zonation with distinct changes in marsh vegetation typically occurs from the marsh platform to upland habitats along microtopographic gradients (Eleuterius 1972; Orson, Panageotou, and Leatherman 1985). Of particular interest are the narrow salt marsh–upland ecotones, or transition zones (marine–terrestrial), from the homogenous marsh platform to the more diverse upland habitats, which are marked by a sudden increase in biodiversity with unique specialized plant communities (Traut 2005; Wasson and Woolfolk 2011). These ecotones are largely controlled by a range of edaphic factors that affect plant species composition such as soil salinity and compaction (Wasson, Woolfolk, and Fresquez 2013). The spatial positions of ecotones in an unstable estuary migrate as environmental thresholds are reached, such as when elevation falls below a critical value relative to mean high water (MHW) due to changes in sea level. The plant communities characteristic of marsh ecotones, however, tend to be very stable, yielding a resilient yet spatially dynamic habitat (Wasson, Woolfolk, and Fresquez 2013).

Landward migration of ecotones in coastal wetlands is highly correlated with tidal inundation time. Equilibrium following increased sedimentation and prolonged inundation might not be possible, because upland plant species do not accrete sediments through the same processes as the lower marsh vegetation (Wasson, Woolfolk, and Fresquez 2013). As inundation time is increased with upward shifts in MHW due to accelerated rates of SLR, die back and mortality of upland vegetation allows for seeding and colonization by lower marsh vegetation. Thus, salt marsh–upland ecotones might respond to SLR and subsidence on shorter timescales than more seaward marsh vegetation. It has been suggested that ecotones could potentially serve as a proxy for climate change, SLR, and overall estuary stability because their composition is directly affected by daily hydroperiods (Wasson, Woolfolk, and Fresquez 2013).

Researchers have recognized the growing need to quantify the surface elevation of coastal marshes and model their responses to SLR (Alizad et al. 2020). Elevations used in these models, however, typically rely on remote sensing approaches such as light detection and ranging (LiDAR) or stereoscopic photogrammetry, which might not include correction based on field verification. Although this technology can yield accurate elevation data for surfaces exposed to the sky, accuracy is reduced for ground surfaces covered by dense vegetation (Hladik and Alber 2012; Hladik, Schalles, and Alber 2013; Anderson and Funderburk 2016). Several studies have addressed the need for LiDAR error correction in such environments (Hladik and Alber 2012; Hladik, Schalles, and Alber 2013; Rogers et al. 2016; Alizad et al. 2020). Alternatively, ground survey transects have been used to determine surface elevation in coastal marsh communities (Hickey and Bruce 2010; Wasson and Woolfolk 2011; Wasson, Woolfolk, and Fresquez 2013).

As SLR and subsidence continue and human populations and activities grow around coastal environments, the need to better understand the relationship of marsh plant communities and ecotones with subtle changes in elevation above sea level is becoming crucial. This study used ground surveys to determine the precise elevations at which three salt marsh plant community types occur within five coastal marshes located on the Mississippi Gulf Coast of the northern Gulf of Mexico (NGOM), with a focus on the ecotone transitioning from salt marsh to upland community types. Coastal marshes under the stewardship of the State of Mississippi and the National Estuarine Research Reserve System (NERR) were sampled to document plant community type and ground elevation along line transects extending from the intermediate marsh platform through ecotones and continuing into upland habitats. The overall goal was to determine the precise range in elevation over which salt marsh to upland ecotones occur across the Mississippi Gulf Coast: specifically, the precise elevations along seaward-to-landward transects at which the ecotone plant community begins and then ceases to be present. From these observations, probabilities of occurrence given centimeter-scale orthometric surface elevation were predicted for marsh, ecotone, and upland community

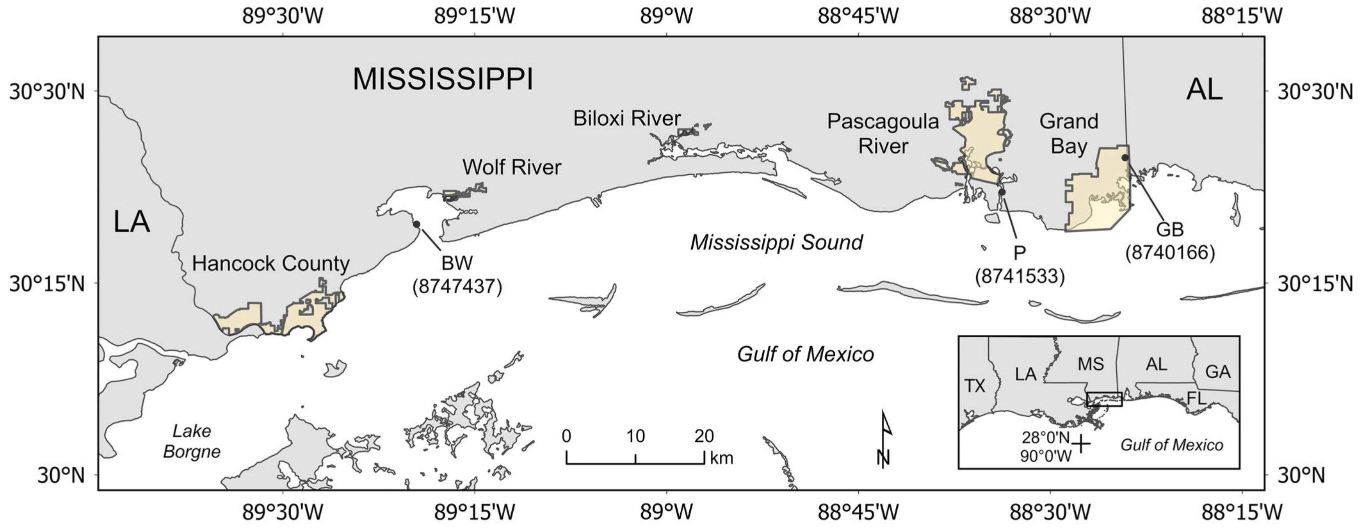

Figure 1. Map of the Mississippi Gulf Coast and surrounding area showing coastal preserves, the Grand Bay NERR (transparent tan polygons) and tide gauges Bay Waveland Yacht Club, Pascagoula National Oceanic and Atmospheric Administration Lab, and Grand Bay NERR included in the study area. NERR = National Estuarine Research Reserve; BW = Bay Waveland Yacht Club; P = Pascagoula National Oceanic and Atmospheric Administration Lab; GB = Grand Bay NERR.

types. The quantification of these relationships demonstrates clearly that the development and spatial positions of marsh, ecotone, and upland plant community types along the NGOM depend on subtle, centimeter-scale changes in sea level.

Materials and Methods

Study Area

Study areas selected to span the Mississippi Gulf Coast included four coastal preserves managed by the Mississippi Department of Marine Resources, plus the Grand Bay National Estuarine Research Reserve (GBNERR). These coastal marshes are located along the coast at ~30°22′ N and span a longitudinal distance of ~106 km. From west to east, these included Hancock County Marsh Preserve (4,313 ha), Wolf River Preserve (345 ha), Biloxi River Marsh Preserve (143 ha), Pascagoula River Marsh Preserve (6,047 ha), and the GBNERR (7,307 ha; Figure 1). The preserves include a mixture of salt, brackish, and freshwater marsh influenced by interactions among the Mississippi Sound, local bays, bayous, and rivers. At the upland boundary, these systems are generally characterized by a transition from aquatic and terrestrial estuarine habitat to upland meadow and forest. The low marsh zone is characterized by fringing *Spartina alterniflora* Loisel (smooth cordgrass), which in many of Mississippi's gently sloping, microtidal coastal marshes quickly transitions to intermediate marsh. The intermediate marsh platform found within the study area is typically dominated by *Juncus roemerianus* Scheele (needlegrass rush) and, to a lesser degree, *Bolboschoenus robustus* (Pursh) Soják (sturdy bulrush) and *Schoenoplectus americanus* (Pers.) Volkart *ex* Shinz and R. Keller (chairmaker's bulrush). In the progression from marsh to upland communities, plant species diversity increases. High marsh species include *Spartina patens* (Aiton) Muhl. (saltmeadow cordgrass), *Panicum virgatum* L. (switchgrass), *Iva frutescens* L. (marsh elder), *Baccharis halimifolia* L. (eastern baccharis), and *Baccharis angustifolia* Michx. (saltwater false willow). Further landward, a transition occurs to various climax woody taxa such as *Pinus* spp. (pine), *Ilex vomitoria* Aiton (Yaupon holly), *Morella cerifera* (L.) Small (wax myrtle), *Quercus* spp. (oak), and *Taxodium* spp. (cypress), as well as many other grasses, sedges, and herbaceous understory plants.

Located in the Köppen climate classification Cfa (humid subtropical) zone along the NGOM, these estuaries experience long growing seasons with extreme summer heat and a lack of severe cold and ground freezing in the winter. Mean air temperatures are ~28°C and ~12°C in the summer and winter months, respectively (Lucas and Carter 2013). Yearly precipitation can be highly variable, especially in years with tropical cyclone impacts, but typically ranges from 1,400 mm to 1,650 mm (Lucas and Carter 2013). The tidal (diurnal) range for the Mississippi

Gulf Coast is classified as low-microtidal. Mean tidal ranges across the study area (west–east) are 0.457 m and 0.413 m at the National Oceanic and Atmospheric Administration's (NOAA) National Water Level Observation Network tide gauge at Bay Waveland Yacht Club, Mississippi (ID: 8747437) and Pascagoula NOAA Lab, Mississippi (ID: 8741533), respectively (NOAA Center for Operational Oceanographic Products and Services 2020b, 2020c).

Ground Survey Site Selection

To examine the relationship of salt marsh–upland ecotone presence with centimeter-scale elevation, survey-grade ground surveys were performed in 2019 at study sites within each preserve. Sites were required to (1) include transitions (ecotones) from intermediate marsh to upland wooded habitats, (2) be accessible by navigable water or road, and (3) lie entirely within preserve or reserve boundaries. The number of sites established per preserve or reserve was determined by linearly scaling the number of study sites to reserve east–west (longitudinal) extent (in kilometers). The site selection criteria limited possible sites in Hancock County to areas mainly in the eastern portion of the preserve. Pascagoula was similarly limited to areas in the southern and western parts of the preserve. A total of twelve study site locations were selected based on the linear scaling method, with five in the Hancock County Marsh Preserve (H1–H5), one in the Wolf River (W1), and two each in the Biloxi River (B1 and B2), Pascagoula Marsh (P1 and P2), and GBNERR (GB1 and GB2; Figure 2).

Individual line segments were digitized and then dissolved to represent 10 percent of the total longitudinal extent of each preserve based on the presence of suitable ecotone boundaries (marsh–upland) determined visually from 2016 aerial imagery (National Agriculture Imagery Program, 0.6 m spatial resolution; ArcGIS Pro v2.3, ESRI, Redlands, CA, USA). Points (n = number of study sites determined for each preserve) were placed randomly on the dissolved lines to assign study site locations within each preserve.

Topographic and Vegetation Ground Surveys

Topographic field surveys were performed along transects at each survey site using an integrated method of Global Navigation Satellite System (GNSS) solutions and traditional surveying (total station leveling). The equipment consisted of a survey precision-grade Trimble R10 GNSS receiver along with a Trimble SX10 robotic total station and an R10 360 Prism (Trimble, Inc.) for high-accuracy electronic distance measurement. All GNSS solutions were corrected through real-time field processing providing ±2 cm horizontal and vertical resolutions. This was made possible by using corrections from the Gulf Coast Geospatial Center Real Time Network of continuously operating reference stations that have been established throughout the state of Mississippi (University of Southern Mississippi Gulf Coast Geospatial Center 2022).

Elevation and vegetation surveys at each site were conducted along each of three parallel line transects that were long enough in length to capture the full extent of the marsh–upland transition zone. Transects varied in length from 21 m to 90 m. These were initiated in the intermediate marsh and extended landward through the marsh–upland transition zone. The two outer transects were spaced 25 m from the center transect (Figure 3). Each transect was positioned using an SX10 total station setup and GNSS-derived resection. Transects were then surveyed for elevation via electronic distance measurement starting from the initial station setup resections using the SX10 and R10 360 Prism. This was done to minimize errors that can affect GNSS solutions, such as ionospheric and tropospheric interference. Thus, GNSS error was introduced only once for each transect during the station setup. A flat topographic wide base shoe was used at the bottom of a 2-m-tall survey GNSS/Prism pole to prevent penetration into the soft, muddy soil. Elevation and associated vegetation attributes were recorded at a ground sampling interval of approximately 1 m along each of the transects. Positions were referenced to the North American Datum of 1983 (NAD83) (2011) datum and ellipsoid. Orthometric heights were computed using the local GEOID12B and are reported relative to the North American Vertical Datum of 1988 (NAVD88). At each sample location, plant species composition was recorded by visually identifying the primary dominant species (>50 percent coverage), any secondary species (between 25 percent and 50 percent coverage), and any other species present (occurrence) within a 0.5-m radius of the GNSS/Prism pole.

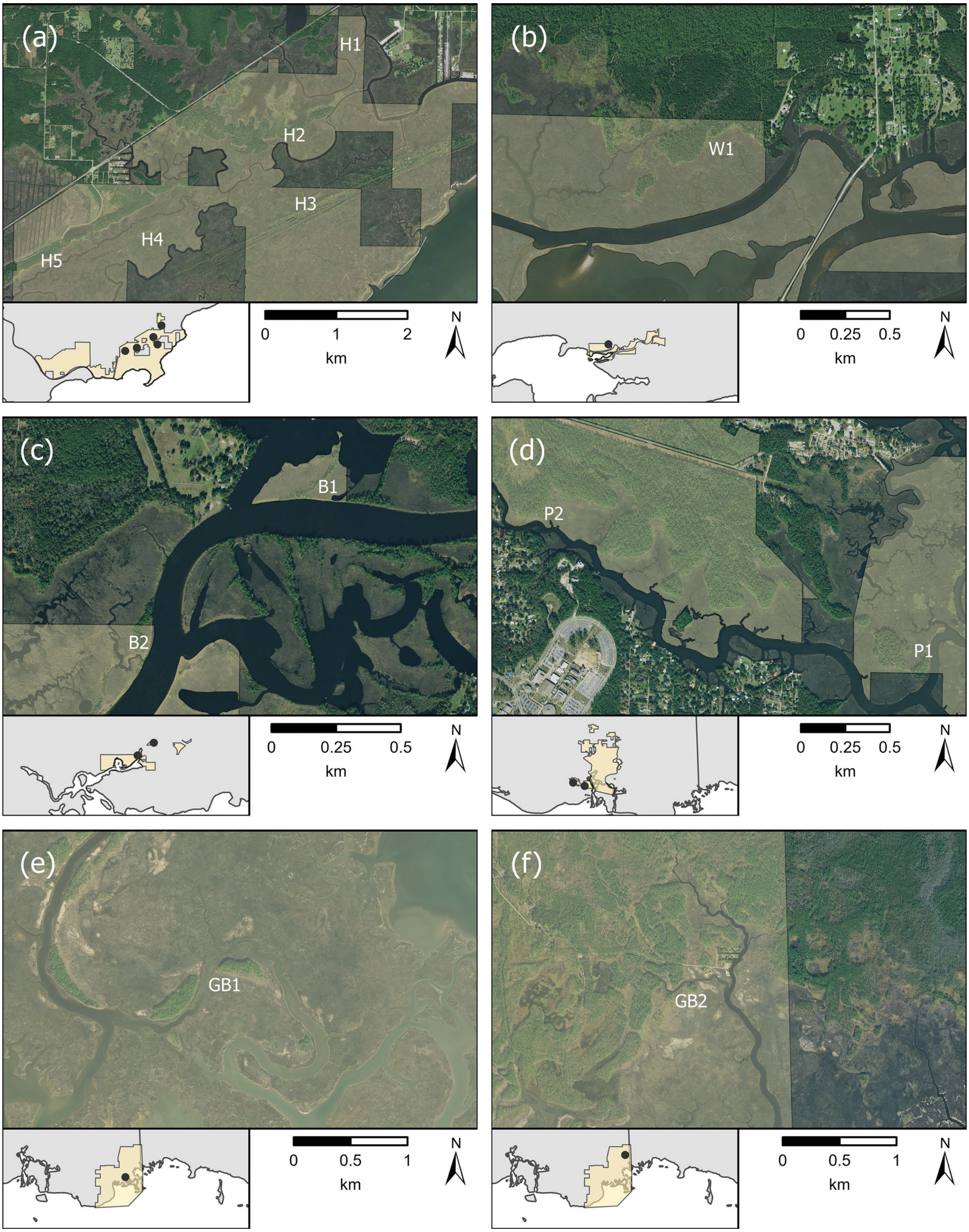

Figure 2. Site maps showing the location of each sample site (shown as white labels) and its respective coastal preserve or NERR (Grand Bay). Locations include (A) Hancock County Marsh Preserve with sample sites H1, H2, H3, H4, and H5; (B) Wolf River Marsh Preserve with sample site W1; (C) Biloxi River Marsh Preserve with sample sites B1 and B2; (D) Pascagoula River Marsh Preserve with sample sites P1 and P2; (E) southern end of the Grand Bay NERR with sample site GB1; and (F) northern end of the Grand Bay NERR with sample site GB2. NERR = National Estuarine Research Reserve.

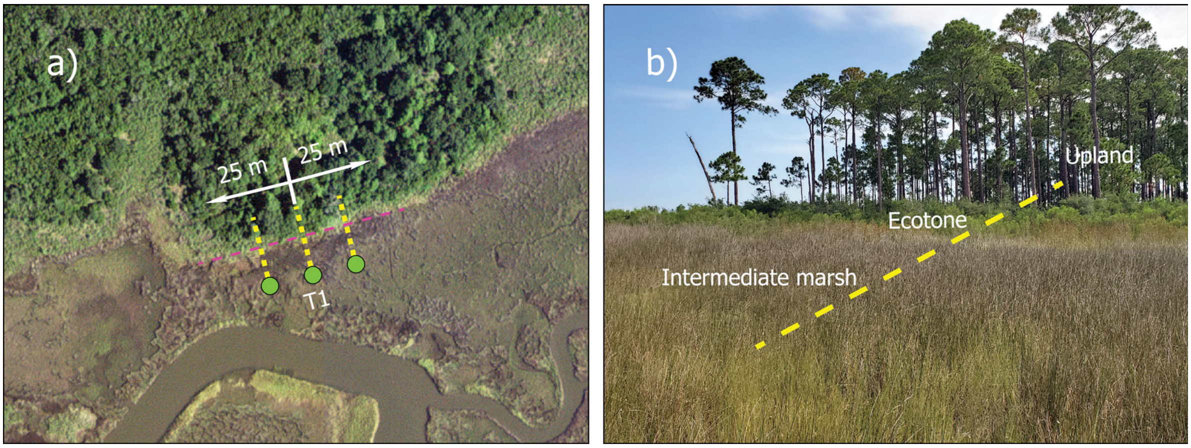

Figure 3. Field sampling layout: (A) Example of study site sampling layout design showing sampling transects (yellow dashed parallel lines) perpendicular to the ecotone boundary (pink dashed line) with the starting transect (T1) and two outer transects, each 25 m from the center transect. (B) Site depiction at ground level.

All ground surveys were conducted during the growing season of 2019. During this period, there were no major physical disturbances of the study area. A Category 1 hurricane (Barry) passed within 280 km of the study area, making landfall in southwestern Louisiana near Vermillion Bay on 13 July 2019. Flooding and other impacts were minimal and short-lived. At the Bay Waveland Yacht Club, Mississippi, National Water Level Observation Network station (ID: 8747437), sustained winds peaked at 53 km h^{-1} and peak storm tides were 0.9 m, with water levels falling back below MHW within fourteen hours of landfall (Cangialosi, Hagen, and Berg 2019; National Oceanic and Atmospheric Administration Center for Operational Oceanographic Products and Services 2020c).

Plant Community Classification

Plant species were identified in the field and subsequently classified as belonging to marsh, ecotone, or upland community type based on species composition and the presence of indicator species (Eleuterius and McDaniel 1978; Duncan and Duncan 1987; Tiner 1993b; Mississippi Department of Marine Resources 2004; Cho, Biber, and Caldwell 2011; Weakley 2015). This procedure employed a combination of established plant community classification schemes, literature regarding the local study area, and wetland indicator status ratings for the Atlantic and Gulf Coastal Plain from the National Wetland Plant List (NWPL; Eleuterius 1972; Eleuterius and McDaniel 1978; Mississippi Natural Heritage Program 2006; U.S. Army Corps of Engineers 2018). The NWPL identifies five wetland rating indicator categories: obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL). These categories are based on the probability of a species occurring in a wetland versus a nonwetland environment (Reed 1988; Tiner 1993b). Although the list serves as a basis for the classification of wetland species, varying local hydrologic regimes and edaphic factors can limit its effectiveness (Tiner 1993b).

Marsh Plant Community

The marsh plant community consists of homogenous stands of salt-tolerant graminoids that extend landward from the shoreline to the marsh–upland ecotone (transition zone). The marsh community was defined by including species from the NWPL Atlantic and Gulf Coastal Plain with the wetland designation primarily of OBL. In addition, several ecological communities from the Mississippi Natural Heritage Program (2006) such as "irregularly and frequently flooded saline marsh," "intermediate marsh," and "brackish marsh" were also used to classify species into the marsh plant community. Some examples of indicator species for this community type included *S. alterniflora*, *J. roemerianus*, *S. americanus*, and *B. robustus*.

Ecotone Plant Community

Typically, the marsh-upland ecotone can be identified by a greater plant species diversity than in the neighboring marsh, notably by the presence of thick grass stands mixed with smaller woody shrubs. Species associated with this plant community have a variety of NWPL-listed wetland rating categories, so these alone are insufficient for classification. For example, *B. angustifolia* and *B. halimifolia*, both indicative of the ecotone plant community, have wetland rating categories of FACW and FAC, respectively, according the NWPL ACGP (U.S. Army Corps of Engineers 2018). Thus, this study used the combination of "Estuarine shrublands" and "Saltmeadow cordgrass herbaceous coastlands" ecological community designations from the Mississippi Natural Heritage Program (2006) and the FACW category for classification of the ecotone plant community. The ecotone plant community type includes indicator species such as *B. halimifolia*, *B. angustifolia*, *Ipomoea sagittata*, and *I. frutescens*.

Upland Plant Community

The upland plant community consists of species less tolerant of tidal flooding in comparison with the ecotone and marsh communities. The community is indicated by the presence of a developed understory and accompanying climax woody vegetation. To classify vegetation into the upland plant community type, the wetland categories of FAC, FACU, and UPL were used in conjunction with the relevant upland and forest ecological communities defined by the Mississippi Natural Heritage Program (2006). The upland plant community includes indicator taxa such as *Pinus* spp., *Quercus* spp., *I. vomitoria*, *Smilax* spp., and *Serenoa repens* (W. Bartram) Small.

Plant Community Elevation Analysis

Statistics indicating central tendency and variability were used to describe ground elevations. The marsh, ecotone, and upland plant communities exhibited distinctive changes in plant species composition but with some overlap at their boundaries. Thus, elevation thresholds for each community type were determined using lower and upper quartiles of elevation data. Four elevation thresholds were defined based on the relevant quartiles of elevation values associated with each plant community: the upper elevation boundary for the marsh community (Q_3), the lower and upper elevation boundaries for the ecotone community (Q_1 and Q_3), and the lower elevation boundary for the upland plant community (Q_1). Also, data were combined among all study areas to determine probability of occurrence that a given plant community type would be found at a given orthometric elevation. Observations for all preserve sites were combined and binned by elevation to the nearest centimeter. Relative frequency of each plant community was then determined for each elevation bin by $P_C = F_C/F_E$, where P_C is the probability of occurrence for a plant community type, F_C is the frequency of plant community type, and F_E is the frequency of elevation. All statistics, probabilities, and graphical results were generated using SPSS Statistics v27.0 (IBM) and SigmaPlot v13.0 (SYSTAT).

Converting NAVD88 orthometric elevations measured in estuaries to local tidal data such as MHW is problematic and presents many challenges due to site-specific hydrological characteristics. This is especially true given that validated tide gauges with a full present tidal epoch (1983–2011) are sparse along the east–west length of the Mississippi Gulf Coast. Additionally, conversion tools such as NOAA's VDatum can introduce unwanted vertical error by as much as 20 to 50 cm along the Mississippi Gulf Coast due to various model inputs such as data updates and local subsidence (NOAA National Ocean Service 2020). Thus, elevations for plant communities were analyzed and reported relative to NAVD88 to retain maximum precision. For the purposes of comparison, plant community elevation threshold heights above MHW were derived from three tide gauges (values relative to NAVD88) located within the study area (Table 1). MHW for all sites combined (0.266 m) was determined by the average of data obtained from the three tide gauges.

Results

Ground Surveys

An average of one site was sampled for approximately every 3.3 km of east–west preserve extent, yielding a total of 1,245 observations (Figure 2, Table 2). Due to site access and cellular network connection limitations at three of the twelve sites (H1, W1, and P2), only two rather than three transects could be sampled, reducing the overall number of transects from a planned thirty-six to thirty-three. A total of 118 plant taxa were documented and used to classify sample points into plant community types.

Table 1. Tidal data (epoch 1983–2011) elevations relative to NAVD88 obtained from three tide gauges located within the study area: Bay Waveland Yacht Club, Pascagoula NOAA Lab, and Grand Bay NERR (Figure 1)

		Tidal elevation (m) relative to NAVD88				
Station	Station ID	MHW	MTL	MSL	MLW	MN
Bay Waveland Yacht Club	8747437	0.286	0.058	0.059	–0.171	0.457
Pascagoula NOAA Lab	8741533	0.239	0.033	0.031	–0.174	0.413
Grand Bay NERR	8740166	0.273	0.065	0.053	–0.144	0.417

Note: All values were determined using NOAA's Tides and Currents (National Oceanic and Atmospheric Administration Center for Operational Oceanographic Products and Services 2020a, 2020b, 2020c). MHW = mean high water; MTL = mean tide level; MSL = mean sea level; MLW = mean low water; MN = mean range of tide; NOAA = National Oceanic and Atmospheric Administration; NERR = National Estuarine Research Reserve.

Table 2. Sampling at all sites in the study area

Preserve	Longitudinal extent (km)	No. of sites	No. of transects	No. of observations
Hancock	17	5	14	638
Wolf	3	1	2	61
Biloxi	5	2	6	194
Pascagoula	8	2	5	126
Grand Bay	8	2	6	226
Total	41	12	33	1,245

The greatest number of taxa were sampled at Hancock (seventy-five), followed by Pascagoula (forty-four), Biloxi (forty-three), Grand Bay (thirty-five), and Wolf (twenty-one), with eleven species common to all five preserves.

Marsh Plant Community Type

The mean orthometric elevation for the marsh plant community sampled at Hancock was found to be 0.30 m, with a standard deviation of 0.06 m. The interquartile range (IQR) was less than a decimeter (0.08 m), with a lower quartile (Q_1) and upper quartile (Q_3) of 0.25 m and 0.33 m, respectively (Table 3). Marsh elevations to the east in the Wolf River were lower than those in Hancock, with a mean of 0.26 m and standard deviation of 0.05 m. Quartiles 1 and 3 were also lower, at 0.22 m and 0.28 m. Additionally, the smallest IQR (0.06 m) among all of the preserves sampled for the marsh plant community type was found in the Wolf River marsh. Sites located at the Biloxi River Preserve had a greater mean (0.33 m) elevation than those of Wolf to its west and Pascagoula to its east. The two sites sampled (B1 and B2) combined to have the highest IQR (0.13 m) among all preserves for the marsh community type. The lowest elevations for marsh ($M = 0.20$ m) were observed at sites in the Pascagoula River marsh. Quartiles 1 and 3 for marsh (0.17 m and 0.23 m) were also the lowest in the Pascagoula marsh. The highest mean elevation ($\mu = 0.42$ m) and quartiles ($Q_1 = 0.39$ m and $Q_3 = 0.46$ m) among all of the preserves was observed at Grand Bay, the eastern extent of the study area (Table 3). The differences between the highest (Grand Bay) and lowest (Pascagoula) first and third quartiles for marsh were less than 25 cm (Table 4).

The marsh plant community for all sites combined across the entirety of the study area had a mean elevation of 0.31 m, with a standard deviation of 0.09 m. The IQR was slightly greater than 1 dm at 0.13 m ($Q_1 = 0.25$ m and $Q_3 = 0.38$ m). The upper elevation threshold for marsh (Q_3) was 0.38 m, translating to 0.11 m above MHW (Table 5). Based on plant community type versus elevation probabilities, marsh elevations ≤ 0.27 m resulted in a marsh $P_C = 1$. Increasing in elevation, the reduction in probability of occurrence for marsh was sharp with $P_C < 0.50$ and $p = 0$ at orthometric elevations greater than 0.43 m and 0.54 m, respectively.

Ecotone Plant Community

The ecotone plant community type occurred in the smallest elevation ranges among the individual preserves and across all sites combined (Figure 4).

Table 3. Plant community elevations sampled at each preserve and all sites combined across the study area

		Elevation (m) relative to NAVD88 (±0.02 m)							
	Preserve	M	*SD*	Minimum	Maximum	Q_1	Q_3	IQR	ET
Marsh									
	Hancock	0.30	0.06	0.16	0.46	0.25	0.33	0.08	0.33
	Wolf	0.26	0.05	0.16	0.38	0.22	0.28	0.06	0.28
	Biloxi	0.33	0.07	0.19	0.46	0.27	0.39	0.13	0.39
	Pascagoula	0.20	0.05	0.10	0.30	0.17	0.23	0.07	0.23
	Grand Bay	0.42	0.05	0.30	0.53	0.39	0.46	0.07	0.46
	Combined	0.31	0.09	0.10	0.53	0.25	0.38	0.13	0.38
Ecotone									
	Hancock	0.47	0.06	0.32	0.68	0.43	0.51	0.08	0.43– 0.51
	Wolf	0.46	0.05	0.38	0.53	0.42	0.50	0.08	0.42– 0.50
	Biloxi	0.42	0.07	0.29	0.53	0.37	0.50	0.13	0.37–0.49
	Pascagoula	0.36	0.05	0.29	0.50	0.34	0.37	0.03	0.34–0.37
	Grand Bay	0.54	0.07	0.42	0.69	0.49	0.59	0.10	0.49–0.59
	Combined	0.48	0.08	0.29	0.69	0.43	0.53	0.10	0.43–0.53
Upland									
	Hancock	0.82	0.23	0.51	1.93	0.65	0.97	0.32	0.65
	Wolf	0.63	0.10	0.48	0.87	0.58	0.69	0.11	0.58
	Biloxi	0.60	0.10	0.42	0.78	0.53	0.70	0.17	0.54
	Pascagoula	0.69	0.23	0.41	1.29	0.55	0.78	0.23	0.55
	Grand Bay	0.70	0.08	0.48	0.85	0.64	0.74	0.11	0.64
	Combined	0.74	0.20	0.41	1.93	0.60	0.81	0.21	0.60

Note: ET is expressed as the upper quartile (Q_3) for marsh, lower (Q_1) and upper (Q_3) quartiles for ecotone, and lower (Q_1) quartile for upland. IQR = interquartile range (Q_3–Q_1); ET = elevation threshold.

Table 4. Maximum differences among preserves in quartile elevations (Q_1 and Q_3) for each plant community type.

		Preserve		Elevation (m) relative to NAVD88
Quartile	Community	Highest	Lowest	Δ (Highest – Lowest ± 0.02 m)
Q_1				
	Marsh	Grand Bay	Pascagoula	0.22
	Ecotone	Grand Bay	Pascagoula	0.15
	Upland	Hancock	Biloxi	0.12
Q_3				
	Marsh	Grand Bay	Pascagoula	0.23
	Ecotone	Grand Bay	Pascagoula	0.23
	Upland	Hancock	Wolf	0.28

Note: Δ = difference; Q_1 = Quartile 1; Q_3 = Quartile 3.

At Hancock sites, the mean elevation for ecotone was 0.47 m, with a standard deviation of 0.06 m. An IQR of 0.08 m was observed for the first and third quartiles (Q_1 = 0.43 m and Q_3 = 0.51 m). In comparison to Hancock, ecotone elevations for the Wolf River Preserve were slightly lower (*M* = 0.46 m, *SD* = 0.050 m, Q_1 = 0.42 m and Q_3 = 0.50 m). To the east of the Wolf River, the highest IQR (0.12 m) for the ecotone plant community among the preserves was observed at Biloxi. Although this

Table 5. Elevation threshold heights above MHW relative to NAVD88

Community	Elevation threshold height (± 0.02 m) above MHW (m) relative to NAVD88 Hancock (BW)	Wolf (BW)	Biloxi (P)	Pascagoula (P)	Grand Bay (GB)	Combined
Marsh	0.04	–0.01	0.15	–0.01	0.19	0.11
Ecotone	0.14–0.21	0.13–0.21	0.13–0.25	0.10–0.12	0.22–0.32	0.16–0.26
Upland	0.36	0.29	0.30	0.31	0.37	0.33

Note: Results were derived from the nearest tide gauge (abbreviated under preserve) to each preserve and the mean of all three gauges across the study area for all sites combined. Elevation threshold height above MHW is expressed as the difference between the elevation threshold and MHW from the nearest tide gauge and is rounded to the nearest 0.01 m. Ecotone elevation thresholds above MHW are reported as the height above MHW for the lower elevation threshold (Q_1) and the upper elevation threshold (Q_3; see Table 3). MHW for all sites combined (0.266 m) was determined by the average of all tide gauges across the study area. MHW = mean high water; BW = Bay Waveland Yacht Club, Mississippi: 8747437; P = Pascagoula National Oceanic and Atmospheric Administration Lab, Mississippi: 8741533; GB = Grand Bay National Estuarine Research Reserve (NERR), Mississippi: 8740166.

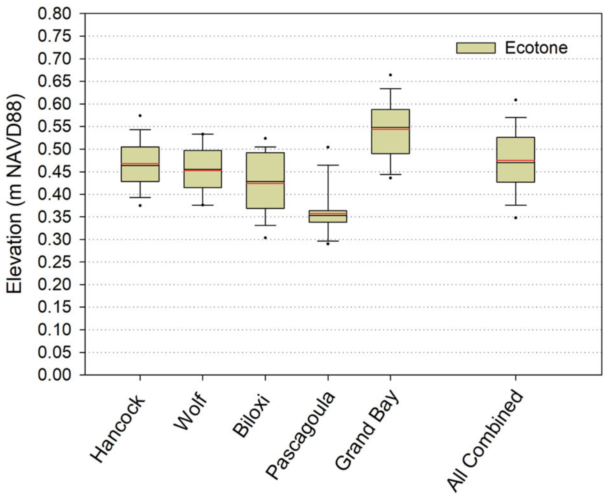

Figure 4. Box plots showing the narrow elevation ranges (± 0.02 m) for the ecotone plant community. Boxes represent the central 50 percent of data values. The black and red lines within the box represent the median and mean, respectively. The error bars and dots represent the 10th and 90th and 5th and 95th percentiles, respectively, of the data.

was the highest IQR recorded for ecotone, the third quartile in Biloxi (0.49 m) was similar to those found at sites located in the Hancock and Wolf preserves. The lowest ecotone elevations among all preserves were observed in Pascagoula ($M = 0.36$ m, $SD = 0.052$ m, $Q_1 = 0.34$ m and $Q_3 = 0.36$ m). The interquartile range, however, was the smallest in comparison with the other preserves. As with the marsh community type, Grand Bay had the highest elevations ($Q_1 = 0.49$ m and $Q_3 = 0.59$ m) recorded for ecotones among the individual preserves (Table 3). The differences between highest (Grand Bay) and lowest (Pascagoula) first and third quartiles for ecotone were less than 25 cm (0.18 m; Table 4).

The mean elevation for all sites combined was 0.48 m, with a standard deviation of 0.08 m. Additionally, the IQR across all sites was 1 dm. Using the lower and upper quartiles, the elevation thresholds for all sites combined were 0.43 m (lower threshold) and 0.53 m (upper threshold), respectively. The lower elevation threshold above MHW was 0.16 m for all sites combined (Table 5). The lowest probabilities ($P_C = 0$) for ecotone with respect to elevation across the study area were found to be at orthometric elevations less than 0.30 m and greater than 0.70 m, a range of 0.40 m (Figure 5). A $P_C > 0.50$ for ecotone was found to be at elevations between approximately 0.44 m and 0.57 m, respectively.

Upland Plant Community

As expected, the upland plant community had the highest orthometric elevations observed across the study area. Additionally, the range of elevation overall was much wider than that of the marsh and ecotone plant communities. Upland in Hancock had the highest elevations recorded ($M = 0.82$ m, $SD = 0.23$ m) compared to all other preserves sampled. It also had the highest IQR ($Q_1 = 0.65$ m and $Q_3 = 0.97$ m). As with marsh and ecotone, upland at Wolf River was lower than that of Hancock ($M = 0.63$ m, $SD = 0.10$ m). Elevations were not as variable at Wolf River, however, with an IQR of around 1 dm. In comparison to the other preserves, the lowest upland communities observed were in sites located in Biloxi ($Q_1 = 0.53$ m and $Q_3 = 0.70$ m). The mean elevation differed from Wolf to its west by only 3 cm, however. Sites in Pascagoula ($M = 0.69$ m) and neighboring Grand Bay ($M = 0.70$ m) had similar mean elevations with a difference of approximately 1 cm. Even though the means were comparable, Grand Bay had a smaller

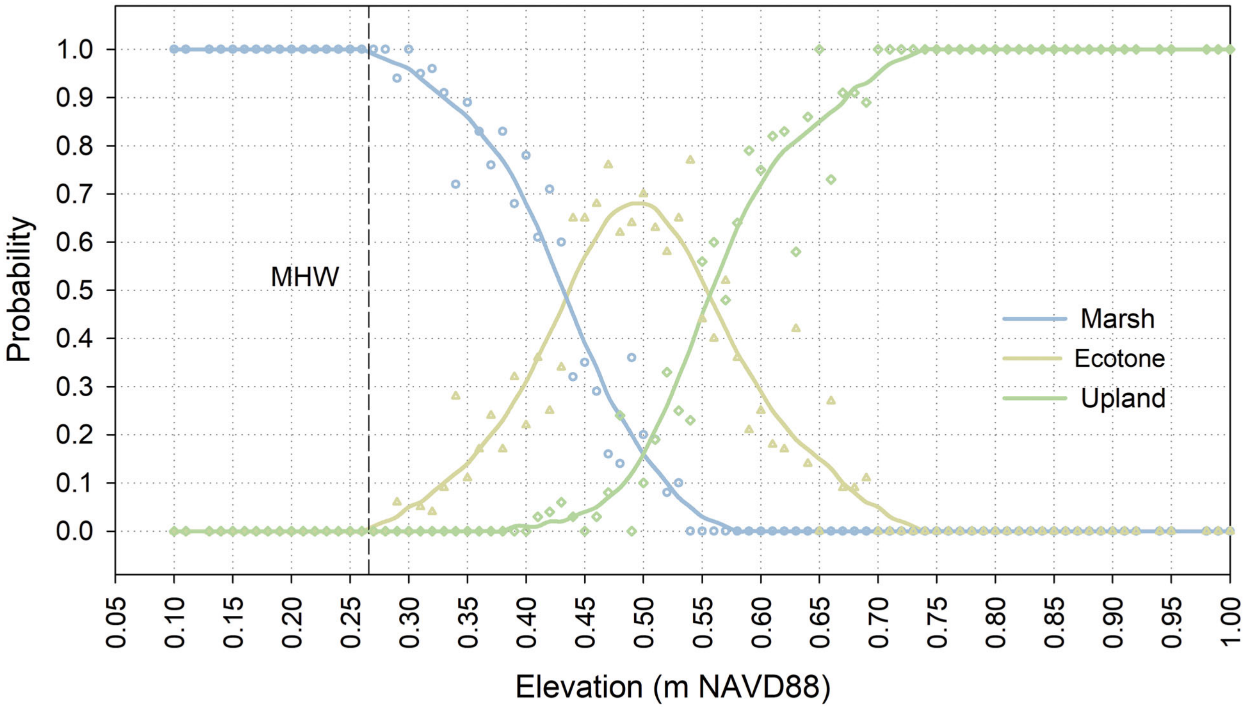

Figure 5. Plant community probability curves (lines) and computed probability data values (symbols) for all preserves combined. The dashed line is the average (0.266 m) MHW from three tide gauges (Bay Waveland Yacht Club 8747437, Pascagoula National Oceanic and Atmospheric Administration Lab 8741533, and Grand Bay National Estuarine Research Reserve 8740166). MHW = mean high water.

IQR with higher Quartiles 1 and 3 (Table 3). The difference between the highest (Hancock) and lowest (Biloxi) elevation for the first quartile was 11 cm. For the third quartile, the difference between the highest (Hancock) and lowest (Wolf) elevation was 28 cm (Table 4).

The upland plant community across all sites combined had a mean elevation of 0.74 m with a standard deviation of 0.20 m. The IQR was just above 2 dm for Quartiles 1 (0.60 m) and 3 (0.81 m). The threshold elevation for upland (Q_1) was 0.60 m with an above MHW elevation of 0.33 m for all sites combined. Orthometric elevations $\leq$0.40 m resulted in the probability of upland occurrence of $P_C = 0$. Occurrence probabilities increased sharply with elevation thereafter with $P_C > 0.50$ and $P_C = 1$ at orthometric elevations >0.55 m and 0.74 m, respectively.

Discussion

On the Edge of Environmental Tolerance

In estuaries, tidal regime is a major determinant in governing the spatial location of plant communities. Tidal inundation frequency and period are largely controlled by topographic elevation (Cahoon and Reed 1995; Hickey and Bruce 2010; Wasson, Woolfolk, and Fresquez 2013). Thus, a tightly coupled relationship exists among vegetation and its associated surface elevation, within marshes and in the transitions to upland. Although ground surveys have examined relationships of marsh vegetation with elevation, they have also addressed differing vegetation compositions under various tidal regimes (Hickey and Bruce 2010; Wasson, Woolfolk, and Fresquez 2013). This study used high-resolution (1-m sampling distance) ground transects to examine centimeter-scale elevations at which salt marsh–upland ecotones and their neighboring plant communities occur in estuaries on the Mississippi Gulf Coast (diurnal, microtidal). Additionally, the probability of occurrence for a given plant community at centimeter-scale elevations was determined. Marsh, ecotone, and upland plant communities were associated with very narrow and precise elevation ranges and thresholds. Further, probabilities of occurrence clearly indicate that transitions among these communities are controlled by centimeter-scale changes in ground elevation.

Although there were differences among preserves in species composition of marsh, ecotone, and upland plant communities, the elevations controlling the spatial distribution of species were similar. Marsh and ecotone plant communities occurred within very narrow elevation ranges. The IQR was a good measure of elevation dispersion because it ignores extreme values, which in our field sampling appeared to be largely attributable to hyperlocal site conditions that were not representative of the larger sampled area. The IQR of marsh for all preserves combined was approximately 13 cm. For ecotone, the IQR was even narrower at 10 cm. Even considering elevations at the 5th and 95th percentiles, elevation range only increased to 28 cm for marsh and 26 cm for ecotone for all preserves combined. Although geographically near each other, Grand Bay and Pascagoula exhibited the highest and lowest elevations among preserves for both marsh and ecotone. The difference between their lower elevation quartiles was 22 cm for marsh and 15 cm for ecotone. MHW at the Pascagoula tide gauge is lower than that at Grand Bay but only by 3.4 cm (NOAA CO-OPS 2020a, 2020b). This suggests that, in addition to differences in tidal frame, sedimentation rate (Wu et al. 2020) or soil salinity (Tiner 1993a) might affect elevation thresholds at each study site. Soil water salinity can be strongly affected by local topography of the intertidal zone. In higher elevation intertidal areas subject to less frequent tidal flushing, salts might accumulate in the soil, especially on the soil surface (Tiner 1993a). Increased soil salinity is pronounced during the summer months and when tidal inundation occurs during daylight hours, allowing increased evaporation (Eleuterius 1984; Eleuterius and Caldwell 1985). In documenting soil characteristics of *J. roemerianus*–dominated intermediate marsh across the Mississippi Gulf Coast, Eleuterius and Caldwell (1985) found in many cases that soil salinities in the marsh exceeded the salinity of the adjacent bayou, bay, river, or sound. High salinity conditions were evident based on species present and vegetative growth forms at Grand Bay, where freshwater flushing is limited due to a lack of fluvial influence. In contrast to Grand Bay, which exhibited the highest elevation thresholds for both marsh and ecotone, sites proximal to freshwater sources that might be assumed to have generally lower soil salinities exhibited the lowest elevation thresholds. This indicates a greater ability of upland and ecotone vegetation to compete with marsh vegetation at lower elevations in lower salinity conditions. This observation warrants further study, because future changes in salinity might lead to changes in lower elevation thresholds for the ecotone and upland plant communities.

When describing threshold elevation for plant communities and particularly for ecotones, it is important to note that these communities exist within a range of elevations rather than at a particular elevation. Describing thresholds in terms of a mean value with standard deviation serves to indicate variability, but these metrics are influenced by extreme outliers. For example, at several locations in lower marsh plant communities, plants indicative of the ecotone had become established on dead and down trees. This resulted in outlier data because higher elevated (~20 cm) ecotone vegetation occurred with lower elevated marsh vegetation within the same 0.5 m sampling radius. Thus, lower (Q_1) and upper (Q_3) elevation quartiles were superior descriptors of threshold elevations governing wetland plant communities because they excluded extreme outlier data values. For all preserves combined, the threshold elevation for marsh was less than or equal to 0.38 m (upper quartile). For the marsh–upland ecotone, elevation thresholds were determined to be from 0.43 m to 0.53 m (lower and upper quartiles). The upland plant community began at elevations greater than 0.60 m (lower quartile). Elevation thresholds for the upland plant community were similar to the lowest elevations noted for *Pinus elliottii* (slash pine) on Cat Island, Mississippi (Funderburk, Carter, and Anderson 2016), and woody species such as *M. cerifera* on Hog Island, Virginia (Bissett, Zinnert, and Young 2014), using field observations and LiDAR analysis.

Probability curves (Figure 5) for all preserves combined support the threshold elevation findings as marsh occurrence decreases rapidly for elevations higher than 0.30 m. Ecotone probabilities sharply increase at elevations above 0.30 m, peaking at 0.50 m, and sharply decrease with further increases in elevation. Additionally, probability of occurrence for the upland plant community sharply increases at 0.50 m, with a $P_C = 1$ at elevations greater than 0.70 m. These probabilities further highlight the distinct vertical zonation found in the estuaries. Additionally, they show the very narrow elevation band in which the salt marsh–upland ecotone begins and ends. Although there is some overlap in the elevations of plant communities within these estuaries,

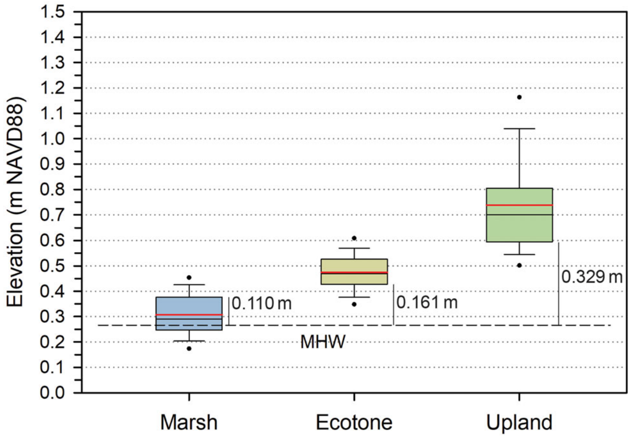

Figure 6. Box plots showing elevation ranges and elevation threshold (±0.02 m) above the average of MHW (0.266 m, NAVD88) from three tide gauges (Bay Waveland Yacht Club 8747437, Pascagoula National Oceanic and Atmospheric Administration Lab 8741533, and Grand Bay National Estuarine Research Reserve System 8740166; black dashed line) for plant communities from all preserves combined. Threshold elevations are represented for marsh by its upper quartile and for ecotone and upland by their lower quartiles. The box represents the central 50 percent of data values. The black and red lines within the box represent the median and mean, respectively. Error bars and dots represent the 10th and 90th and 5th and 95th percentiles of the data, respectively. MHW = mean high water.

this overlap is minimal for the marsh, ecotone, and upland plant communities, which can be characterized by distinct elevation bands. Overall, a 5-cm band of plant community overlap exists between marsh and ecotone, and a 7-cm band of overlap exists between ecotone and upland.

The elevations of plant communities in estuarine environments should be examined with respect to their local tidal frames to consider tidal inundation and period. Thresholds for marsh and ecotone were on the average 11 cm and 16 cm above MHW, respectively, for all preserves combined (Figure 6). Because the threshold elevation for marsh was its upper quartile and for ecotone its lower quartile, departures from MHW values were similar and the differences mimic those of their community overlap as discussed previously. The upland plant community elevation threshold above MHW (33 cm) was only 17 cm higher than that of the lower ecotone elevation threshold of 16 cm above MHW (Table 5). This illustrates the precise elevational tolerance governing the lower boundary of the salt marsh–upland plant community. As sea levels rise, the ecotone plant community will respond via transgression into upland habitats in search of equilibrium with respect to its local tidal frame, as dictated by its threshold elevations. This study does not model SLR or quantify sedimentation. It is evident, however, that salt marsh–upland ecotones exist along very precise elevation contours (0.43 m–0.53 m NAVD88) that make them highly vulnerable to SLR. SLR trends at the Bay Waveland Yacht Club, Mississippi (ID 8747437), were reported to be 4.55 ± .76 mm yr^{-1} (NOAA 2020c). Current understanding of estuaries shows that marsh degradation and transgression can be kept in check when equilibrium exists among SLR, local subsidence, and sedimentation (Morris et al. 2002). Waldron, Carter, and Biber (2021), however, reported significant losses in marsh extent over recent decades within the Pascagoula estuary, where little hydrological modification has disturbed natural sediment flux. This suggests that acceleration in relative SLR might be outpacing sedimentation in the estuary. Assuming the current rate of SLR at the Bay Waveland Yacht Club remains constant or accelerates, with minimal to no positive changes in sediment flux in the Hancock Preserve, ecotone transgression into upland plant communities is likely to occur in the coming decades.

Implications for Future Studies

The results show a surprisingly narrow range of elevation for salt marsh ecotones along the Mississippi Gulf Coast. This highlights the need for future work using ground surveys to better quantify the precise elevation of marsh–upland ecotones and their neighboring plant communities in other coastal estuaries. This is especially pertinent considering the widespread use of elevation data from various sources, such as remote sensing–derived products, as inputs for coastal SLR, marsh vegetation, and suitability models. Studies have shown remotely sensed ground elevations in homogeneous *J. roemerianus* marshes to be overestimated by as much as 20 cm (Hladik and Alber 2012; Anderson and Funderburk 2016). Present results show the range in elevation for the marsh–upland ecotone alone to be less than 20 cm. Further, the boundary between plant communities can be even harder to discern from remotely sensed data due to the vertical precision at which these boundaries occur, which is often much greater than the precision of the remotely sensed data. These errors can be problematic for the creation of digital elevation models and resulting products involving estuaries. Although advances have been made in these technologies, consideration must be given to the fine scale at which changes in elevation affect landscape change. An integrated approach using high-precision, high-accuracy in situ field measurements combined with remote sensing techniques should be considered to balance the need to sample large spatial extents while mitigating elevation overestimation caused by dense vegetation canopies.

Conclusions

Coastal evolution is dependent on feedbacks between the natural and human systems (National Academies of Sciences Engineering and Medicine 2018). As human settlement along the U.S. Gulf Coast becomes increasingly dense, greater pressure is placed on estuarine ecosystems (NOAA 2011). Human encroachment toward naturally retreating shorelines will also make coastal communities more vulnerable to nuisance tidal flooding and tropical cyclone impacts. Thus, as coastal populations grow, coastal vegetation becomes increasingly important in terms of protection of inland areas from coastal flooding, filtering of impurities and excess nutrients from estuarine waters, and supporting the coastal economy. To facilitate an understanding of the spatial distribution and extent of coastal plant communities into the future, defining and modeling the precise tolerances of marsh, marsh ecotone, and salt marsh–upland vegetation to tidal inundation is of utmost importance, particularly in the modern era of accelerating SLR.

Based on the quartile thresholds and probabilities of occurrence derived by this study, marsh along the Mississippi Gulf Coast exists up to around 0.4 m (NAVD88), the marsh ecotone from around 0.4 m to 0.6 m, and upland plant communities at 0.6 m or higher, with dramatic changes in plant community occurring on the decimeter scale. Because of the fine scale of these elevation gradients, traditional-style surveying proved highly effective in determining precise elevation relationships with marsh plant communities that might not have been reliably detected by other means, such as with airborne LiDAR. As tidal inundation period is increased, and if sediment availability is reduced or even remains neutral, estuarine plant communities will adjust vertically to find equilibrium with the tidal frame, as a floating dock rises with a rising tide, and marshes will transgress landward, adjusting their horizontal locations to meet their associated elevation thresholds above MHW. In documenting the precise elevations at which these estuarine plant community changes occur, the results of this study will allow for a more thorough understanding of how and where marsh transgression will proceed as sea level rises.

Acknowledgments

This research was conducted under a permit provided by the U.S Fish and Wildlife Service and the Grand Bay National Wildlife Refuge, and with guidance from the Mississippi Department of Marine Resources (MDMR) Office of Coastal Preserves. The authors would like to thank Ian Stewart and Bill Funderburk for help with data collection, and Chris Brown, Les Graham, and Debra Armstead for facility and technical support.

Funding

This research was supported by the National Oceanic and Atmospheric Association, National Geodetic Survey (Regional Geospatial Modeling Program).

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